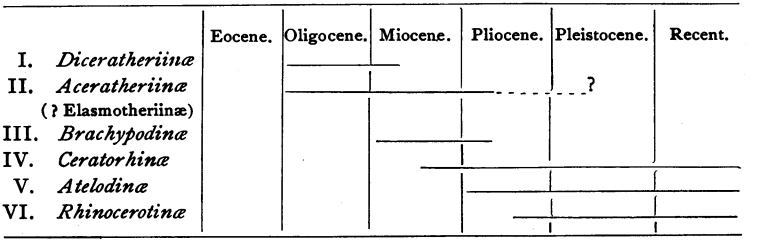
Article XIX.—PHYLOGENY OF THE RHINOCEROSES OF EUROPE.

RHINOCEROS CONTRIBUTIONS, No. 5.[1]

By HENRY FAIRFIELD OSBORN.

By far the most striking generalization of recent mammalian palæontology is the *early separation, absolute distinctness, and great age of numerous phyla leading up to modern types.* If confirmed by more detailed research, the phylogeny here proposed will bring the Rhinoceroses also under this *law of early divergence;* the supposed original or stem forms having been pushed steadily back into the older Cenozoic. It sets aside several homoplastic characters heretofore employed in Rhinoceros evolution and attempts to establish a firmer basis *in the fundamental proportions of the skull, whether dolichocephalic or brachycephalic, in the correlated proportions of the body, and in the location of the horn-cores.* These characters are found to be more distinctive of phyla than the pattern of the molar teeth.[2]

Our present hypothesis is that, as distinguished from the Amynodonts and Hyracodonts, *the true tertiary and modern Rhinocerotidæ belong to at least six*[3] *genetic series or phyla which have no known relation to each other.* By Flower and Lyddeker the Rhinoceroses have been placed in one genus, *Rhinoceros*, and divided into five groups, which correspond approximately to our phyla. A characteristic subfamily name is herein given to each phylum, for the sake of clearness, brevity, and convenience, since several of these series have a prodigious range in time, as shown in the following table.



[1] See Contributions 1–4, in Bibliography.

[2] The grouping proposed by Depéret ('85, p. 268) and by Lydekker ('86) is partly upon homoplastic characters of the teeth.

[3] See Osborn, '98, pp. 77, 121; a division of the Rhinocerotidæ into *four* subfamilies.

If this or some similar phylogenetic hypothesis can be established, it will not elucidate the origin, which remains an enigma, but it will at once simplify the whole problem of the succession, development, migration, and taxonomy of this hitherto baffling group.

Phylogeny and Taxonomy.

A clear conception of phylogeny is an essential preliminary to taxonomy; the nomenclature is still, as my friend Schlosser expresses it, "ein wahres Elend"; in no European or American museum are the Rhinoceroses properly identified or catalogued.

This paper therefore, besides setting forth an hypothesis of descent, is a preliminary statement of very interesting systematic and comparative results obtained by visits in 1898 and 1900 to the collections of London, Paris, Lyons, Munich, Darmstadt, Stuttgart, Augsburg, Vienna, St. Petersburg, and Moscow. Many kind friends aided in this work, especially the following palæontologists: Messrs. Lydekker, Woodward, Andrews, Gaudry, Boule, Thévenin, Depéret, Filhol, Zittel, Schlosser, Roger, Lepsius, Fraas, and Fritsch. The recent writings of Lydekker, Pavlow, and Roger have been of great service.

This extended comparison was undertaken before writing Part II of 'The Extinct Rhinoceroses' memoir, because in studying the American Rhinoceroses I soon learned that their close relations with those of Europe rendered it necessary for me thoroughly to understand the types of both countries.

The stratigraphical or geological basis is of the utmost importance and is set forth in recent correlation papers (Osborn, '00).

As regards nomenclature: first, the discovery that the type Acerathere, the classic *Aceratherium incisivum* Kaup, has *a rudimentary median frontal horn*, does away with the application of the generic term *Aceratherium* to many of the ancestral hornless types; second, valid reasons are found for reviving the discarded generic terms *Atelodus*, *Ceratorhinus*, etc., and, third, the final nomenclature will be an expression of phylogeny. The first steps towards clearly attacking the taxonomic problem are:

(1) To conceive of the early adaptive radiation of the Rhinoceroses from an unknown stem.

(2) To conceive of the possibly independent origin of certain

phyla in North America, Europe, Asia, or Africa, and the subsequent intermingling of these phyla by migration.

(3) To recognize the succession of species in separate phyla or lines of descent, designating them as subfamilies by the terminal *inæ*.

(4) To sharply mark off each subfamily or phyletic series of species from its contemporaries as soon as its earliest members appear.

(5) To anticipate within each phylum the probable development of *collateral* as well as of *direct* lines of species, by the laws of local adaptive radiation.

Among the main divergent characters for the discrimination between subfamilies or series of species are :

1. *Proportions :*
   - *a.* Long-skulled (dolichocephalic), and long-footed (dolichopodal), or long-limbed types, *e. g.*, *Atelodus simus.*
   - *b.* Short-skulled (brachycephalic), short-footed (brachypodal), or short-limbed types, *e. g.*, *Teleoceras fossiger.*
2. *Reduction of digits :*
   - *a.* Precociously tridactyl types, *e. g.*, *Cœnopus tridactylus.*
   - *b.* Persistently tetradactyl types, *Aceratherium tetradactylum.*
3. *Development of horns :*
   - *a.* In lateral pairs on nasals, *e. g.*, *Diceratherium pleuroceros.*
   - *b.* Single on nasals, *a*, on tips, *e. g.*, *Teleoceras*, *b*, on centre, *e. g.*, *Rhinoceros.*
   - *c.* In longitudinal pairs on nasals and frontals, *e. g.*, *Ceratorhinus.*
   - *d.* Single on frontals, *e. g.*, *Aceratherium incisivum*, *Elasmotherium.*
4. *Cutting teeth :*
   - *a.* 'Megalodine types,' in which the cutting teeth persist, *e. g.*, *Rhinoceros indicus.*
   - *b.* 'Atelodine types,' in which they degenerate, *e. g.*, *Atelodus simus.*

Some of these *divergent* characters also become *convergent* or *homoplastic* and are employed to distinguish the generic and

specific stages of several distinct subfamilies or phyla. Thus several 'megalodine' types gradually pass into 'atelodine.' Correlated with the above fundamental divergent characters are numerous minor characters which are of great service; for example, dolichocephalic and brachycephalic Rhinoceroses frequently exhibit also distinctive types of auditory meatus, of occiput, of premolar and molar teeth, and of limbs.

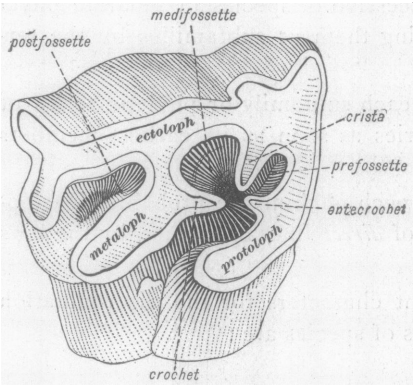


Fig. 1. Typical Rhinoceros molar, showing terminology.

An early division is observed into *heavier* and *lighter* types, correlated with speed; while *collateral brachyodont* (shrub-eating) *and hypsodont* (browsing) *species may arise within the same phylum;* example, *A. simus* and *A. bicornis.*

Family RHINOCEROTIDÆ.

Oligocene phyla.—Two similar lines appear simultaneously in the Oligocene of Europe; the most precocious of these is the subfamily Diceratheriinæ, represented in Europe and America; the less precocious is the Aceratheriinæ, probably represented in both countries also. The characters of both are sharply defined. It is probable but not yet demonstrated that the smaller Rhinoceroses throughout the Oligocene chiefly represent the Diceratheriinæ; nevertheless it is best to leave certain species *incertæ sedis* (*R. velaunum*, *R. gaudryi*), one or both of which may belong to the Amynodontidæ.

Subfamily DICERATHERIINÆ. PHYLUM I.

Smaller Oligocene Rhinoceroses; dolichocephalic, with paired nasal horns, full-sized cutting teeth; cursorial, long-limbed, with relatively slender bodies well raised from the ground.

General characters.—1. Manus precociously tridactyl (as observed in American species), correlated with swift motion. 2. Horns developed in lateral pairs

on the nasals, beginning in the Middle and Upper Oligocene stages. 3. Lower canines sub-triangular in section, flattened on outer and upper sides, slightly convex on lower side (as observed in Middle and Upper Oligocene American and European types). 4. First lower premolar early reduced or wanting, as observed in European and American types (also in *R. gaudryi* and *R. velaunum*). 5. Molars quadrate, frequently exhibiting a conical cingule or cusp at the opening of the median valley. 6. Narrow skull, with narrow elevated occiput, expanding and notched above. Zygomatic arches suddenly expanding posteriorly.

These are some of the characteristic features which are observed in both European and American types and reach their full development in the Upper Oligocene. The nomenclature is

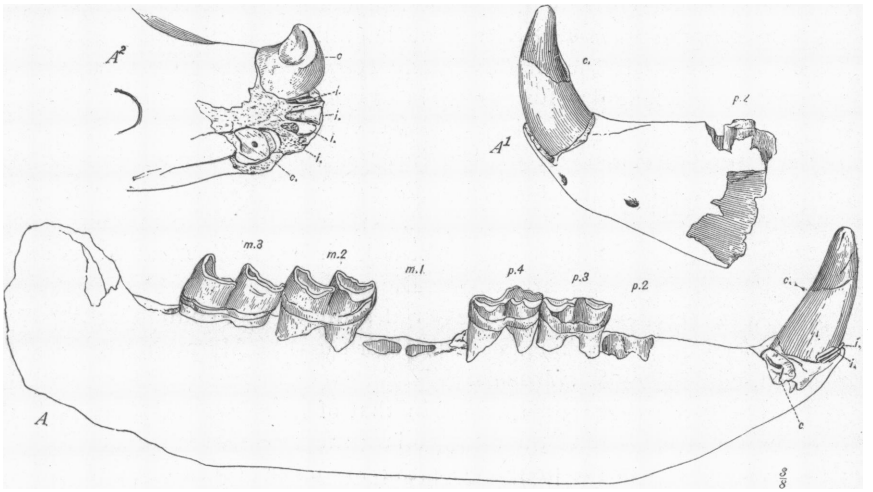


Fig. 2. *Ronzotherium gaudryi.* Type: PARIS. *A*, Internal view of left ramus. A^1, External view. A^2, Superior view. × $\frac{3}{8}$.

still uncertain; to the Lower Oligocene forms, which probably possessed upper canine teeth, the generic name *Ronzotherium* Aymard possibly applies. It is possible that the type species, *R. velaunum*, belongs to the Amynodontidæ, in which case it may anticipate the genus *Amynodon* Marsh. If, however, it belongs to the Diceratheriinæ it may anticipate the genus *Cænopus* Cope (primitive hornless Rhinoceroses with precociously tridactyl feet), or the genus *Leptaceratherium* Osborn, or *Trigonias* Lucas (primitive hornless Rhinoceroses with persistent upper canine teeth). To the Upper Oligocene form, *Diceratherium* Marsh is applicable.

1. Lower Oligocene. Incertæ Sedis.

Ronzon, Argiles du Cantal, Phosphorites, Cadibona.

A most interesting primitive Lower Oligocene type is :

Ronzotherium gaudryi *Rames.* Type : a lower jaw, Paris Museum. Locality, Brons, Cantal. Definition : dentition $\frac{0}{0}\ \frac{0}{1}\ \frac{3}{3}\ \frac{3}{3}$; second pair of lower incisors greatly reduced ; median or first pair typical ; lower canines erect, laterally compressed ; first lower premolars wanting ; premolars 3–4 with internal and external cingulum ; molars 2–3 without internal cingulum ; premolars 2–4 much worn but apparently simple in pattern, *i.e.*, without complete posterior crests.

Systematic Position.—The *erect* lower canines indicate the existence of upper canines, as in the Amynodontidæ or in *Leptaceratherium trigonodum* Osborn ; the laterally compressed shape of the canines resembles that in *Leptaceratherium* and is distinct from the more triangular form seen in *Amynodon*, but, if a member of the Rhinocerotidæ, this animal was very primitive. Since it is certainly not a member of the genus *Aceratherium* it may be provisionally referred to the genus *Ronzotherium* Aymard, the type of which is a lower jaw from Ronzon, similar in some respects. The absence of the first lower premolar in *R. gaudryi* and *R. velaunum* is also distinctive of the Diceratheriinæ.

According to M. Boule the Argiles du Cantal, containing *R. gaudryi*, are, if anything, a shade older than the Marnes de Ronzon, containing *R. velaunum.*

The jaw is slightly smaller than that of *R. velaunum*,[1] there is a wider space behind the third molar ; the dentition is similar in the simplicity of the premolar teeth ; in fact it may subsequently prove that *R. velaunum* and *R. gaudryi* are allied.

Space occupied by lower grinding series, premolar 2 to molar 3 inclusive	*Ronzotherium gaudryi*.....	170 mm.
	(estimated) *Ronzotherium velaunum*...	194 mm.

The lower grinding series of *R. gaudryi* is closely equal in size to that of the Upper Oligocene *D. minutum* series (p2–m3 = 173) in the Paris Museum.

Ronzotherium velaunum *Aymard.*—Type : A lower jaw, Collection Aymard, Puy Museum. The writer has not personally examined the type and must rely upon the descriptions and figures

[1] M. Filhol gives no measurements but figures the jaw of *R. velaunum* as ⅔ natural size (Plate xii, figure 69, pp. 75, 266, Mammifères Fossiles de Ronzon).

(Fig. 3) given by M. Henri Filhol; as above stated the incomplete condition of the jaw leaves it uncertain whether this animal

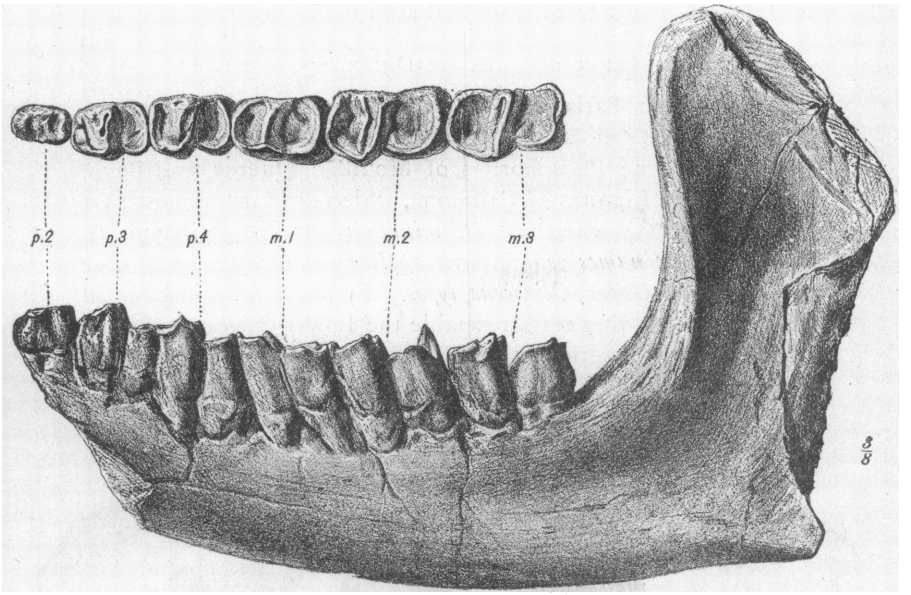


Fig. 3. *Ronzotherium velaunum.* Type: PUY. External view of left ramus. × ⅜, after Filhol.

from the Lower Oligocene of Ronzon is a primitive member of the Diceratheriinæ, Aceratheriinæ, or Amynodontidæ.

Characters.— Premolars 2, 3, 4, with incomplete crests; premolar 1 missing in the type specimen; coronoid and condyle greatly elevated (as in *Amynodon*); tetradactyl, fifth digit of manus believed to be present (as in *Amynodon* and *Aceratherium*).

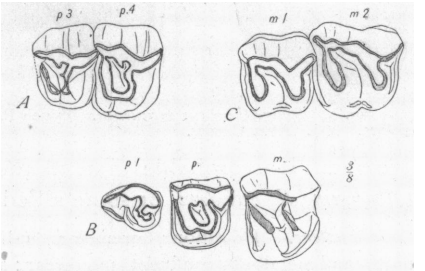


Fig. 4. Superior grinding teeth. *A*, Third and fourth premolars, *Cadibona*, MUNICH. *B*, First and fourth premolars, first molar, *Phosphorites*, MUNICH. *C*, First and second molars, *Phosphorites*, PARIS. All figures × ⅜.

It should be noted that the American Diceratheres of the Lower Oligocene are tridactyl; the American Amynodonts (Cadurcotheriidæ or Amynodontidæ) are tetradactyl, but with a much larger fifth digit than that associated by Filhol with *R. velaunum*.

The most primitive species of American Rhinoceros, *Trigonias osborni*, recently described by Lucas, presents an entirely different type of cutting teeth from that seen in *R. gaudryi*.

Superior Molars of Diceratheriinæ.

In London, in Paris, and in Munich are numbers of small extremely primitive molar and premolar teeth from the Middle and Lower Oligocene Phosphorites of Mouillac, Quercy, and Bach, also from the Lignites of Cadibona, which are for the most part erroneously catalogued as *D. minutum* and its synonym, *D. croizeti*, *specific names which were applied originally to much more highly evolved Upper Oligocene types.* In point of evolution all these upper grinding teeth resemble the Lower Oligocene Diceratheres types of America, especially such species as *Cænopus* (*Aceratherium*) *copei*; but, as in the case of the lower jaws (of *R. gaudryi* and *R. velaunum*) above described, it is not possible to determine their phyletic relations or exact systematic position at

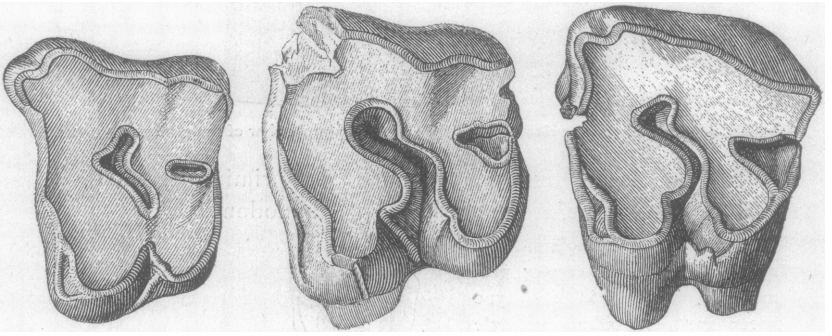


Fig. 5. *Diceratherium minutum.* Type: Paris. Fourth premolar, first and second molars. × ½. After Cuvier.

present. It is probable that all these teeth belong either to *R. velaunum*, *R. gaudryi*, or some allied species. (See Fig. 4.)

Characters.— Dentition: premolars unlike molars; premolars 2–4 with proto- and metalophs confluent upon wear; a crista in premolars 3–4; *milk premolars* dp^2–dp^4 with complete crests resembling the molars; *molars* with rudimentary antecrochet (protoconule fold); more or less marked external cingulum, rudimentary metaconule fold; variable cingulum suggesting a 'cingule' at entrance of median valley (Fig. 4).

London, British Museum Collection: No. M. 1732, superior molars 1 and 2, Loc., Phosphorites, Bach, Lalbenque (Lot), France (see Fig. 17, Lydekker,

Cat. Foss. Mamm. Pt. III, p. 142); also No. M. 4507, superior deciduous premolars 1–4, Loc. Phosphorites, Mouillac, France. In the MUNICH collection from *Cadibona* are two small upper premolar teeth, pm 3–4, which answer this description; others from the Phosphorites, Quercy, are found in the Munich collection (m^1, m^2, pm^1, pm^2). In PARIS[1] from *Quercy* (Coll. Massénat) are also small isolated premolar and molar teeth (p^1–m^2) of the same character, found both in the Jardin des Plantes and the École des Mines collections.

Conclusions.—The *small* European Lower Oligocene species of Rhinoceroses, although *incertæ sedis*, are partly Diceratheriinæ, partly Amynodontidæ; they should be referred to *R. gaudryi* or *R. velaunum* or to new species. The *large* Lower Oligocene species of the Phosphorites should be referred to the Aceratheriinæ.

2. UPPER OLIGOCENE.

St. Gerand-le-Puy, Moissac, Gannat, Eselsberg (Ulm), in part.

Diceratherium minutum *Cuvier.*—Type: Upper premolar 4 and molars 1–2. PARIS, No. 2346, Loc., Moissac, Upper Oligocene (Fig. 5).

Definition: Dentition $\frac{1}{1}\frac{0}{1}\frac{4}{4-3}\frac{3}{3}$; upper incisors small; lower canines sub-triangular; with flat outer and sharp inner edge, procumbent; first lower premolars variable; upper and lower premolars 2–4, with two crests resembling the molars; upper premolars with small antecrochet, with crista and crochet; upper molars with crista (soon disappearing), pointed crochet (disappearing in old age), antecrochet and postfossette; cusp or cingule at entrance of median valley. Measurements: type p^4–m^3 = 100; p_2–m_3 = 173; p^2–m^3 = 173–180.

This represents the Upper Oligocene species of the French and German Museums, which are readily distinguished from the Lower Oligocene species by the complication of the teeth; but exhibit little or no increase in size. In PARIS are Cuvier's types described in the 'Ossemens Fossiles'; also a cotype lower jaw No. 2343; also Duvernoy's *R. pleuroceros* (synonym) type skull from Gannat. The finest series of upper and lower teeth are those in the MUNICH collection from Eselsberg and Eckingen near Ulm, which are catalogued as *A. croizeti* Pomel. In the STUTTGART collection from the same localities we find especially Nos. 4757 and 9861, rightly identified as *D. minutum*.

[1] Unless otherwise stated PARIS refers to the Galerie de Paléontologie, Jardin des Plantes, under the direction of Professor Gaudry.

Additional Characters.—PARIS: *Cuvier's type:* Fourth superior premolar with protoloph and metaloph confluent in old age, small antecrochet; molars with antecrochet, crochet, metaconule fold, postfossette, and median internal cingule. *Duvernoy's type* (*R. pleuroceros*): molars agreeing precisely in size with above; skull and jaws of dolichocephalic type, paired horn-cores on nasals, occiput narrow elevated; zygomatic arch convexity as in *Cænopus tridactylus* Osborn. In the Paris jaw (Gannat) the first lower premolar is wanting, in Munich and Lyons specimens it is vestigial, indicating that, as in the American Diceratheriinæ, this tooth was variable; m 1–m 3 = 100. Tibia (Gannat) = 260. MUNICH and STUTTGART (Eselsberg, Ulm, specimens): first lower premolar very small; pm 2–4 molariform with elevated posterior crests; lower canines sharp, subtriangular with flattened outer surface, flat upper face partly destitute of enamel, slightly convex lower face and sharp inner edge; canines large in males, small in females (this tooth is very similar to the canines of the American species *C. tridactylus* Osborn); unworn *premolars* (catalogued *A. croizeti*, Munich) as in Cuvier's type without antecrochet, but with crista and pectinate crochet (see Nos. 4757, 9861, STUTTGART, Eggingen); *unworn molars* exhibit crista, crochet, and antecrochet, while *worn molars* lose crista and show greater prominence of antecrochet and crochet, and postfossette (especially in p 4–m 2), also an internal cingule or cusp in the median valley as in American Diceratheres. This animal is exactly the size of *Cænopus mite* of the American Lower Oligocene. LYONS: A small jaw (catalogued *A. croizeti*) with vestigial pm 1.

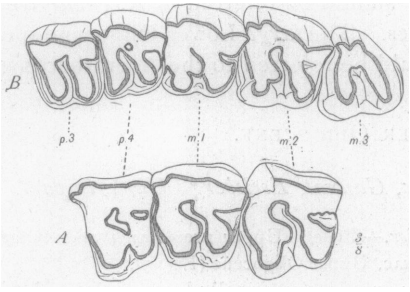


Fig. 5*a*. *Diceratherium minutum*. *A*, Type premolar and molars. × ⅔. PARIS. *B*, Part of left superior grinding series. Ulm, MUNICH.

Affinities.—By this comparison there is little question that all these teeth belong to the Upper Oligocene *Diceratherium* and, so far as we know, to the single species *D. minutum* Cuvier, which presents many features of close resemblance to the American Diceratheres. In Paris the skull of the Upper Oligocene *D.* (*Pleuroceros*) *minutum* is now placed in the case side by side with that of the Middle Oligocene *Cænopus occidentalis* from South Dakota; it exhibits a remarkable similarity in the form of the occiput, the zygoma, and the paroccipital region.

3. Lower Miocene.

Sables de l'Orléanais, Eselsberg (Ulm, in part), Bugti Beds.

The Eckingen, Ulm, formation also contains a Lower Miocene fauna, indicating that the Diceratheres may have persisted into this period.

Other indications as to Miocene persistence are those afforded by a juvenile lower jaw and a maxillary series in the École des Mines collection, Paris, from the Sables de l' Orléanais, typical Lower Miocene; these were kindly shown the writer by the Curator, M. Douvillé; they are of about the size of *A. platyodon* Mermier, but they almost certainly constitute a new species which probably belongs in the Diceratheriinæ. The animal is considerably larger than *D. minutum*.

Incertæ Sedis.

Diceratherium douvillei,[1] sp. nov.

Type: A maxillary series Coll. École d. Mines, Paris. Definition: Type: Upper premolars with crenulated anterior border of metaloph, and reduced antecrochet; upper molars with large crochet and antecrochet, crista not apparent in worn teeth.

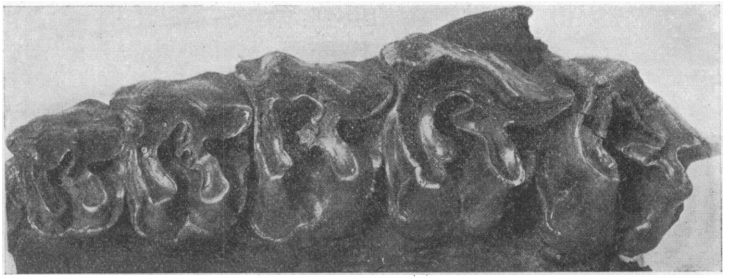


Fig. 6. *Diceratherium douvillei.* Type: Paris. After a photograph by M. Douvillé.

This species is placed *incertæ sedis*, phyletically. The indications that it belongs to the Diceratheriinæ are, first, the crenulated or pectinate anterior border of the metaloph in the upper premolars as in *C. tridactylus;* second, the tubercle in the valley of

[1] Dedicated to M. Henri Douvillé, to whose kindness the author is indebted, both for the permission to describe the type and for the accompanying photograph (Fig. 6).

m^3. It is also possible that it represents an ancestor of *R. sansaniensis*, which is placed in the *Ceratorhinæ* below. It certainly is not *Teleoceras aurelianensis*, and it apparently cannot be referred to *Aceratherium platyodon*; these are the only strictly Lower Miocene (Burdigalien) Rhinoceroses hitherto described in France.

Subfamily, ACERATHERIINÆ. PHYLUM II.

Large Oligocene and Miocene Rhinoceroses of Europe; dolichocephalic with long, narrow nasals; smooth or with rudimentary horns at sides of the tips; frontals finally developing horns; large cutting teeth; relatively persistent tetradactyl manus; long-limbed.

Contemporary with the small Diceratheres is this phylum of large Rhinoceroses which appears to rise in a large but primitive species in the Lower Oligocene, *A. filholi*, and pass through *A. lemanense* and *A. tetradactylum* into *A. incisivum* of the Lower Pliocene, which in turn is possibly the ancestor of *Elasmotherium* and the Elasmotheriinæ. The European Lower Oligocene Acerathere is exactly similar in size to *A. platycephalum* Osborn, which is possibly the American representative of this type; but it differs widely in the mode of transformation of the upper premolar teeth; for this reason it is referred to a new species.

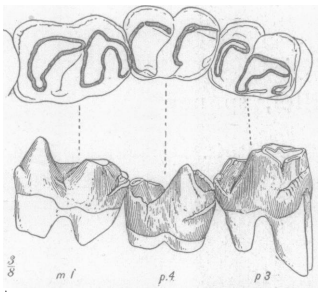


Fig. 7. *Aceratherium filholi*. Cotype: PARIS. Lower third and fourth premolars and first molar.

1. LOWER OLIGOCENE.

Phosphorites, Quercy, Cazark, Escamps.

Aceratherium filholi,[1] sp. nov.

Type: Left maxilla containing second premolar to third molar inclusive; Paris, Coll. Rossignol, Loc. Phosphorites. Cotype: Paris, lower jaw, containing pm^3, pm^4, and m^1 (Figs. 7, 8*A*).

Definition: Large upper premolars, simple, unlike molars, with incompletely formed crests; upper molars with internal cingulum and strong protoconule fold, small antecrochet, no crochet; depression in posterior face of metaloph of third

[1] Dedicated to my friend M. Henri Filhol, who has contributed so extensively to our knowledge of the fauna of the Phosphorites.

molar; third and fourth lower premolars with depressed and incomplete posterior crests. Measurements: pm^2–m^3=224.

This new species is well represented by teeth in the Paris, Munich, and British Museum collections from the Phosphorites of Quercy and Cazark, mistakenly catalogued as the Upper Oligocene *A. lemanense*, from which it differs widely. No true *A. lemanense* remains are found in the Phosphorites, which is believed by the writer not to extend into the Upper Oligocene. None the less *A. filholi* is probably ancestral to *A. lemanense* and represents the first known member of the tetradactyl, dolichocephalic phylum which directly or through collaterals leads up to *Aceratherium incisivum* of the Lower Pliocene.

The distinctness of this species was independently recognized by M. Boule, who in recent lectures has compared it with *A. platycephalum*. M. Filhol and M. Depéret also both concur with the writer that it is distinct from *A. lemanense*, and M. Filhol assures me that it is equally distinct from *R. velaunum*, which is a much smaller animal. The name *Aceratherium* may be retained for all members of this phylum, although technically the names *Badactherium* Croizet or *Aphelops* Cope might be applied to the ancestral truly *hornless* Aceratheres.

The entire absence of a crochet and the non-molariform premolars distinguish this species sharply from *A. lemanense*; the internal cingulum is partly a sexual character; it varies in different specimens, although strongly marked in the type.

Besides the admirably preserved and highly characteristic PARIS types, in MUNICH we find two large molar teeth, m^2 and m^3 from the Phosphorites (Escamps, Lalbenque, Dép. Lot); also a single well worn molar, m^2, and two isolated upper molars, m^1 (Phosphorites, Cazark, Dép. Lot), of exactly the same size as the *A. platycephalum* from our Lower Oligocene; also from Cazark two upper premolars, p^3, p^4, which exhibit imperfectly formed crests and a crista. In LONDON (British Museum) are lower premolars and molars (Phosphorites, Caylux, Nos. M. 1457, 1458, 1459, also upper molars M. 1455, m^1–m^2) all catalogued *R. lemanensis*. There can be no question that all these teeth belong to the same species, *A. filholi*, which is far more primitive than the Upper Oligocene *A. lemanense* to which they have been referred; not only the premolars but the molars are simpler. The premolar

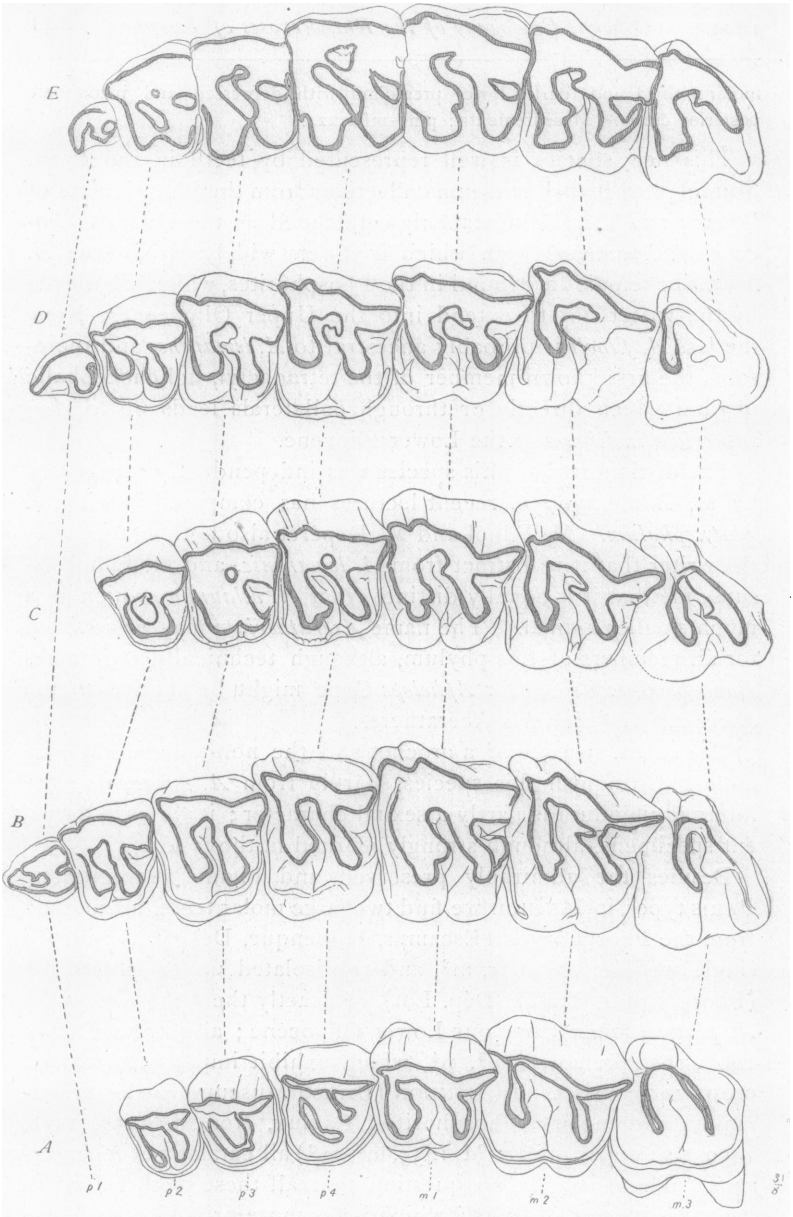


Fig. 8. Evolution of the grinding teeth in the Aceratheriinæ. *A*, *Aceratherium filholi*. Type: PARIS. Lower Oligocene. *B*, *Aceratherium lemanense* (reversed). PARIS. Upper Oligocene. *C*, *Aceratherium lemanense*. Ulm, MUNICH. Upper Oligocene. *D*, *Aceratherium tetradactylum*. PARIS, No. 2379. Middle Miocene. *E*, *Aceratherium incisivum*. Type: DARMSTADT. Lower Pliocene. All contours, × $\frac{2}{3}$.

evolution differs from that of the American *A. platycephalum* as shown in the diagram above (Fig. 8); other resemblances, however, are so strong that one is tempted to consider the *possibility* that these animals belong to the same Aceratherine race which is distinct from, but contemporary with the Diceratherine race. A fossa representing the vestige of the postvallum in m^3 is seen in these specimens, also in *A. platycephalum.*

2. Upper Oligocene Stage.

St. Gerand-le-Puy, Gaillac, Gannat, Randan, Eckingen, (Ulm).

A. lemanense *Pomel.*—This well known species is represented by superb materials in Paris, Lyons, Munich, Stuttgart. These specimens represent different (early or primitive and later) stages of development; some are less progressive and probably of Middle Oligocene age, others are more modernized and probably of Lower Miocene age, but in all the premolars and molars are far more advanced than in *A. filholi.*

Sexual differences are pronounced as in the Diceratheriinæ and Rhinoceroses generally; the females have small canine tusks and long very narrow or slender nasals; the males have large tusks and rudimentary rugosities or horn supports on the sides of the extremities of the nasals. Adaptive radiation is also marked and probably certain *collateral species* are given off from the direct line.

All these animals are readily distinguished from the Diceratheriinæ by much larger size.

General Distinctions of Teeth.—Lower canines lance-shaped, lenticular in section; first lower premolar small, usually present; *superior premolars* with crista, producing a medifossette upon extreme wear; large antecrochet; premolars 2–4 with complete crests, which in the more primitive stages unite in extreme wear; an internal cingulum. *Molars* with strong antecrochet, becoming stronger in wear; with crista becoming weaker in extreme wear; crochet also becoming weaker with extreme wear; metaconule fold becoming stronger with wear; protocone small; postfossettes indicated in both m^1 and m^2, with internal cingulum reduced or confined to median valley. Measurements: pm^1–m^3=265.

Effect of age upon molar pattern.—It is extremely important to observe that, exactly as recorded above in the Diceratheriinæ,

the *newer characters*, namely the crista and crochet, are formed near the summit of the crests and are thus worn away in old teeth; while the *older characters*, such as the antecrochet, are at the base of the crests and thus become bolder in extreme wear. The same law applies to the newer and older characters in the molar teeth of the horse.

General Distinctions of Skeleton.—Skull and jaw of dolichocephalic type (measurements, symphysis to condyles=630); nasals long and narrow, more or less separate, notched at sides, slender in females; tetradactyl, a well developed 5th metapodial, lunar wedge-shaped distally; symphysis of lower jaw varying with sex, short in females, longer in males.

These characters may be verified in the following specimens: PARIS, No. 2372 (*Badactherium*[1] *borbonicum* Croizet, type, loc. Auvergne), an old individual with well worn molars. Duvernoy's fine type skeleton of *A. gannatense* (Gannat, Allier), probably a *female*, with small lower canines and short symphysis of lower jaw, large and powerful skeleton; skull measuring 630 from symphysis to condyles; superior teeth partly worn and finely preserved; pm^1–m^3=265; femur measuring 460. Also *A. randanense*, No. 2302 (Randan, Auvergne), lower jaw containing pm 2–m 1, with a very long symphysis (unlike the *A. gannatense* type); this is possibly a sexual or *male* character. Also a complete jaw (Gaillac, Tarn) with small lower canines, probably *female*, small pm 1 on left side. Portion of left anterior foot, No. 2373 (Gannat, Allier), showing characteristic tetradactylism.[2] LYONS: (1) *A. lemanense* (Gannat), skull, nasals long and thickened at the ends, but separate in median line, notched at the sides; this type represents an *early stage*, because the premolar crests are bridged internally and would unite upon extreme wear. (2) Large lance-shaped lower canines of lenticular section, unworn (Allier). (3) Two maxillæ from Gannat exhibit molar and premolar characters entirely agreeing with those above described. (4) A complete skull and skeleton, probably *female*, lower jaw with small canines, medium-sized upper canines, molars agree with Pomel's type in character, size below that of Pomel's type; nasals extraordinarily long, slender, extend-

[1] This is possibly a MS. name. It is not recorded in Trouessart's 'Catalogus Mammalium.'

[2] See Duvernoy's Memoir, Plate viii.

ing over premaxillaries, with smooth surfaces (this length, slenderness, and smoothness is also a female character in *C. occidentalis* and *C. tridactylus*); a sagittal crest, occiput high and narrow. (5) Another skull (loc. Pyremont between Lyons and Geneva) has the same general characters but the nasals exhibit distinct and quite well marked rugosities at the sides of the tips; this is evidently a *male;* the digits are somewhat shorter than in *A. lemanense*, namely, Mtc. III=140, Mts. III=125; Depéret regards the animal as a distinct species and will describe it as such. MUNICH: (1) The maxilla from Eselsberg, Eckingen, near Ulm, is beautifully preserved; it belongs to an *early stage* because the premolar crests are bridged and unite when worn; the premolars exhibit medifossettes; the molars show the strong crochet, antecrochet, and metaconule folds. (2) An unworn molar from Eckingen shows a crista, antecrochet, and crochet, and the characteristic small protocone of this species. STUTTGART: (1) Molars of a *later stage* (Eggingen, Ulm) show a more prominent crista and crochet which unite to form a medifossette. (2) A fine pair of lower jaws (Ulm) with large lower canines and no traces of pm 1 probably also represent a later stage (*i. e.*, Lower Miocene).

We thus find that *A. lemanense* is the characteristic Upper Oligocene species, presenting various stages of premolar transformation and probably giving rise to some collateral species.

3. LOWER MIOCENE STAGE.

Sables de l' Orléanais, Royans.

A. platyodon *Mermier*, represents this stage.—LYONS: The type skull, probably belonging to a small female, pm^1–m^3=207, exhibits unique, extremely elongate, slender, and slightly separate nasals; the lower canines, as the specific name indicates, are excessively flattened toward the extremities but exhibit a triangular mid-crown section; the premolars (Mermier, '96, Pl. II) have a prominent crista and medifossette; the crests unite early upon wear. The teeth may be readily distinguished from those of the contemporary Brachypodinæ by the small size of the protocone.

A. blanfordi *Lydekker*.—A jaw is ascribed to this species

(Lydekker, '86) from the Lower or Middle Miocene Bugti Beds of Sind. It is *incertæ sedis* here.

4. Middle Miocene Stage.

Sansan, Simorre.

A. tetradactylum *Lartet.*—This is the noble species of Sansan (Nos. 3378 male, 2379 female, 2389 female, etc.) and Simorre, represented finely in the Paris Museum. It shows striking resemblances to *A. lemanense*, together with all the progressive characters which we should expect to find in a descendant, and unquestionably belongs to the same line. The scapula is high and narrow as in dolichopodal types generally. The hind limb

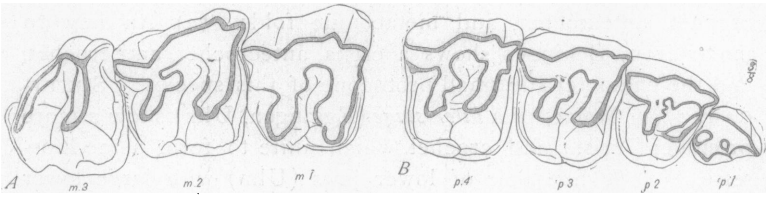


Fig. 9. *Aceratherium* (*incisivum*) *tetradactylum.* Georgensgemünd. Munich.

(femur and tibia) is of approximately the same length as in *A. lemanense*, but the metapodials are longer, and more stilted (Mtc. III=160–180, Mts. III=135–165), indicating that the phylum was developing a progressive running power. The progressive and retrogressive changes in the skull and jaws are most interesting and significant as seen in a magnificent male specimen (No. 3378, Loc. Sansan). As compared with *A. lemanense* note the following

Skeletal Distinctions.

Skull.—A slight loss of size, symphysis to condyles of skull = 559, *A. tetradactylum*; symphysis to condyles of skull = 630, *A. lemanense.* Nasals, *males* (No. 3378) slightly less elongated, similarly notched at sides, roughened or rugose distally, but not thickened (a sexual character); *females* (Nos. 2379, 2389, Coll. Lartet) very narrow and elongate, separate in median line, not expanding distally. Premaxillæ slender. Occiput elevated, spreading superiorly. Sagittal crest lower but still well marked. Premaxillæ slender. Jaw with elongate symphysis, wide diastema, angle deep, projecting backwards. Manus tetradactyl (Coll. Lartet, Nos. 2518, 2537), with reduced metacarpal V; lunar of tridactyl type (foreshadowing the loss of metacarpal V, which is now reduced

in length to 75), PARIS, Coll. Lartet, Nos. 2518, 2537; long, stilted digits; metacarpal III enlarged; metacarpals II, IV relatively smaller. Scapula vertically elongate, with long neck, as in all long-limbed, speedy types.

Dental distinctions.—Inferior canines less lance-shaped, with internal flare and flattened external section. First lower premolar sometimes present (in the slightly older Sansan specimens). *Sup. premolars* and *molars* (No. 2379) with somewhat reduced antecrochet and very strong crochet placed near ectoloph; this unites with the ectoloph when well worn and forms a conspicuous medifossette (No. 2388). Crista conspicuous in unworn premolars and molars. Antecrochet somewhat reduced and becoming conspicuous only in old or worn teeth. Molars with cingulum entering median valley between crests, a crest in the bottom of median valley (No. 2388), or embracing protoloph only; with postfossette in m^1; and traces of external cingulum; posterior cingulum of m^3 (also observed in *A. platycephalum* and *A. lemanense*) persisting. Measurements, female, $pm^2 - m^3 = 230$.

The scapulæ and limb bones of large size in the Paris Museum (which are catalogued *R. sansaniensis*) undoubtedly belong to *A. tetradactylum*. Some of these indicate an Aceratherine race as large as or larger than the *A. lemanense* type.

PARIS: This species is also represented in the slightly higher levels of Simorre, especially by a very large jaw of a *female*, with small lower canines, first lower premolar absent, formula: p_3—m_3; of marked dolichocephalic type. LONDON: The jaw from Sansan (Hastings Collection, No. 27454, catalogued *R. goldfussi*) also represents this species; it is large and dolichocephalic in type; the lower canines are flattened with a marked internal flare.

5. UPPER MIOCENE STAGE.

Georgensgemünd.

MUNICH: Upper teeth with closely similar characters (catalogued *A. incisivum*, Georgensgemünd, Bav.) are seen here in a shade *earlier stage* of evolution, because we observe more of a bridge between the premolar crests and somewhat greater prominence of the antecrochet as well as of the internal cingulum of the molars. Another specimen is a characteristic

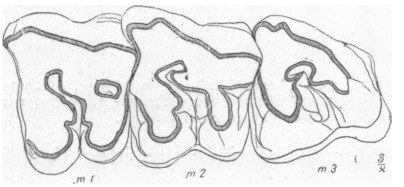


Fig. 9*a*. *Aceratherium tetradactylum*. No. 3378. × ⅜. PARIS.

long and straight lower jaw of this race. (A maxilla, mistakenly catalogued *A. incisivum*, Georgensgemünd, belongs to the Ceratorhine or *C. sansaniensis* race.) VIENNA: A large maxilla, containing pm 1–m 3 (without label) has all the distinctions of the Aceratherine race.

6. LOWER PLIOCENE STAGE.

Eppelsheim, Maragha.

Relations of A. incisivum to Elasmotherium.

Aceratherium incisivum *Kaup.*—DARMSTADT: In cranial characters this classic species is less dolichocephalic. In *dental* characters it follows closely upon its predecessors (Fig. 8 *E*); in fact, most writers, beginning with Kaup, have not hesitated to unite the *A. tetradactylum* with this animal. The cranial characters, however, are much more progressive, the nasals are shorter and more upturned, the frontals are thickened and bore a rudimentary horn in the males at least. The latter character (Osborn, 99, p. 162) is very significant. One can imagine that this phylum, having failed in the development of horns upon the mechanically weak nasals (as indicated in the Lyons specimen), began to evolve frontal horns.

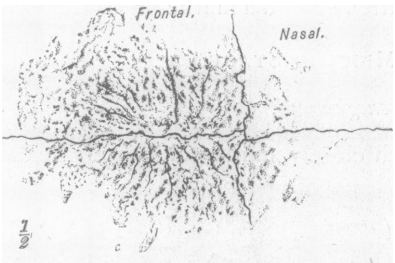


Fig. 10. *Aceratherium incisivum.* Type: DARMSTADT. Rudimentary frontal rugosity, with lines of convergent nutrient arteries.

There is no question that the frontals are not only thickened to support a horn (they are very thin in the contemporary *T. brachypus*), but that they show a well marked rugosity with the characteristic converging depressions of nutrient arteries (Fig. 10). It is this character which led the writer to advance the idea that this animal is an ancestor of *Elasmotherium*, an hypothesis which depends upon the future discovery of intermediate forms. It may be observed here, moreover, that *Elasmotherium* has long, narrow, smooth nasals of a type found only in the Aceratheriinæ and that there is theoretically no

difficulty in deriving the enormous frontal horn of the Pleistocene species from the vigorous rudiment in *A. incisivum;* or the ptychodont Pleistocene molars from the simple Lower Pliocene stage.

There is a fine skull of *A. incisivum* in HALLE as well as the two in Darmstadt.

7. EASTERN TYPES.

Incertæ Sedis.

The Siwalik Aceratheriinæ have not yet been carefully compared by the writer. *A. perimense* is a very large animal from Perim Island with a skull which, as restored by Lydekker ('81, Pl. X), suggests this phylum, although higher and shorter.

Subfamily BRACHYPODINÆ. PHYLUM III.

Brachycephalic Rhinoceroses, short broad skulls. Teleocerine, horns when developed appear on tips of nasals. Megalodine, large cutting teeth. Brachypodal, short spreading feet, short limbs, body and trunk near the ground. Tridactyl, probable early reduction of lateral digits. Known Geological Distribution, Lower Miocene to Lower Pliocene, inclusive, Europe and America.

These Rhinoceroses, short and broad in all their proportions, including their spreading grinding teeth, represent, so far as we know, the sudden occurrence of a new type in the Lower Miocene of Europe; for they have no known prototypes in the Oligocene of either Europe or America. Either the original home of this type is Africa, and if so, they came into Europe with the Mastodons, or they represent an offshoot of the Aceratheriinæ. Typical species are *T. aurelianensis* Nouel; *T. brachypus* Lartet; *T. goldfussi* Kaup; *T. fossiger* Cope. Doubtful species are *A. persiæ* and *A. blanfordi.* The phylum Brachypodinæ takes its name from one of the oldest known forms, *T. brachypus* Lartet, although it first appears geologically in the *T. aurelianensis* Nouel of the Lower Miocene (Sables de l' Orléanais of France), and includes a great variety of European and American types, extending to the Lower Pliocene, *T. goldfussi* Kaup. The feet in *T. brachypus* and *T. fossiger* become extremely short. Associated with the shortening of the skull is a shortening and broadening of the grinding teeth—the *very broad fourth upper premolar* distinguishes the higher members of this series, notably as developed

in the Lower Pliocene *T. goldfussi* Kaup. In the superior molars the protocone is very prominent and rounded, giving a circular form in extreme wear. The lower and upper cutting teeth attain an enormous size, hence the adjective ***megalodine*** is appropriate. The shortening of the skull lowers the middle portion of the cranium and in the typical species causes the nasals to project upwards at the tips; thus the irresistible tendency of every Rhinoceros to develop a horn finds expression in the laterally compressed rugosities of the tip of the nasals (*T. aurelianensis, T. fossiger*), while an abortive horn may appear on the frontals (*T. aurelianensis*). The strong resemblance of *T. fossiger* to this series was noted by Mme. Pavlow.

The generic name *Teleoceras* Hatcher is the first applied to a member of this series and will be of service to distinguish its members throughout. Valid specific differences are found between the Lower, Middle, and Upper Miocene and Lower Pliocene stages; there are certainly three and possibly four species in Europe.

1. Lower Miocene Stage.

Sables de l'Orléanais.

Teleoceras (R.) aurelianensis *Nouel.*—Type: A skull. Loc. Neuville-aux-Bois, Loiret.

Paris: Characters of type. (1) Three lower premolars in jaw associated with skull; also observed in an isolated better preserved jaw, thus: $p\frac{1}{4-3}$, $m\frac{3}{3}$; flattened outer face of inferior molars is

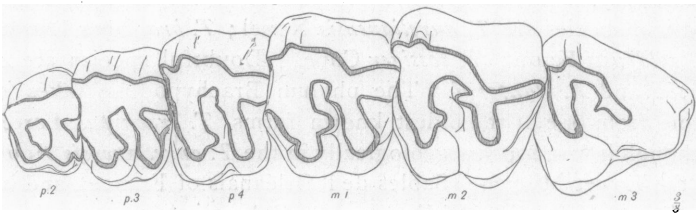


Fig. 11. *Teleoceras aurelianensis.* Type: Superior molars. × ⅓. Paris.

another characteristic; superior premolars 3–4 shorter than the molars and provided with antecrochet, as seen also in maxillary series (Collection Vibraye). The strong simultaneous development of antecrochet and crochet distinguishes the molars, as well

as the stout cylindrical protocone. Occiput broad, in a vertical plane; jaw with a decided angle. Front view of nasals is very characteristic (Fig. 12, *D*), a rugosity appears upon each tip with a cleft between (as in *T. fossiger*); there is also a very slight swelling and faint rugosity upon the *frontals* immediately above the eyes which may indicate the rudiment of a median horn. As compared with the Aceratheriinæ the fore and hind limbs and feet in the Paris Museum are relatively short, but they are longer than those of its Upper Miocene relative *T. fossiger* mounted beside them; this species is also distinguished by narrower premolars. (2) A fine lower jaw (Loiret) exhibits premolars with flattened outer wall, also a very small, single-fanged pm_1. (3) The maxillary series (Coll. Vibraye) above alluded to shows a cement layer on the molars as in some Upper Miocene American types.

Lartet in a letter to Nouel expressed the opinion that this species was identical with the Middle Miocene *T. brachypus*. A close comparison of the teeth of these two species in the Paris Museum reveals the following resemblances and differences:

T. aurelianensis.	*T. brachypus.*
Premolars broad	Premolars broad
Antecrochet strong in p 3, p 4	Antecrochet reduced or wanting
Metaloph of p^4 long	Metaloph of p^4 long
Molars, internal cingulum wanting	Cingulum strong

2. Middle Miocene Stage.

Simorre, Sansan (?).

T. brachypus *Lartet.*—Paris: A fine maxillary series from Simorre, Gers (Coll. Lartet No. 2386); fourth superior premolar (p^4) compressed anteroposteriorly and extending transversely more than in *T. aurelianensis;* superior molars with strong internal cingula; inferior molars with extremely flattened outer faces; enormous upper incisors. This species is generally said not to occur at Sansan, but a single lower canine tooth (catalogued *R. tetradactylum*, Paris Museum) probably represents it on this level.

3. Upper Miocene Stage.

Grive-St.-Alban, Steinheim.

T. brachypus.—The finest examples of this species are found in the Muséum d'Histoire Naturelle of Lyons and have been described and figured by Depéret. Relying upon his determination ('87, p. 178) we observe the following dental characters:

Superior premolar 1 simple ; premolars 3–4 without antecrochet (thus differing from *T. aurelianensis*); premolars 2–3 with small crista and crochet ; premolar 4 with crista and forked crochet ; molar 1 with small crista, strong crochet, antecrochet reduced (as compared with *R. aurelianensis*); molars 1–3 with internal cingulum extending around inner face. *Inferior* premolars with flattened outer faces. Measurements, Mts. III = 110.

Depéret observes that the true *T. brachypus* always has an internal cingulum upon the upper molars. I do not, however, feel convinced that this specific determination is correct.

HALLE : A distinct variety of this type occurs at Steinheim, and was shown to me in this fine collection through the kindness of Professor Fritsch ; it is distinguished by very thick enamel, square posterior fold of ectoloph (due to the antero-posterior compression of the dentition correlated with the brachycephalic skull), crista, crochet, and antecrochet all showing in well worn superior molars ; cingulum only around protoloph of molars (in typical *T. brachypus* it embraces metaloph also). This variety may become known as a distinct species, *T. eurydactylus*, for there certainly are some minor differences between this and the typical *T. brachypus.*

MUNICH : The foot bones of manus and pes, Mtc. III = 145, Mts. III = 110, astragalus = 50 (types of *R. eurydactylus* Haushalter), are almost identical in size and proportions with those of our Upper Miocene species, *T. fossiger* Cope, of America. A lower jaw (Steinheim) exhibits the following characters : symphysis, short ; diastema very short, first lower premolar vestigial, single-fanged, close to canine ; second lower premolar comparatively simple, reduced, single-lobed. There is also a fragmentary skull from the Dinotherium Sands near Günzburg with occiput low and broad as in *T. fossiger.* Also from Steinheim a large collection of isolated upper molars, with the following characters : superior fourth premolar broader than first molar (as in *T. goldfussi*); superior first molar with very thick enamel, a crista, large antecrochet, and broad internal cingulum extending around protoloph only. The Steinheim teeth of Munich therefore agree closely with those in the Halle collection and indicate that the northern (? *T. eurydactylus*) variety differed in a definite particular from the southern typical *T. brachypus* race, namely : *cingulum extends around protoloph only ;* this character (cingulum around

protoloph only) is also observed in a cast of four molar teeth (Mantscha bei Graz) in the Munich collection, but it is not seen in the Augsburg skull.

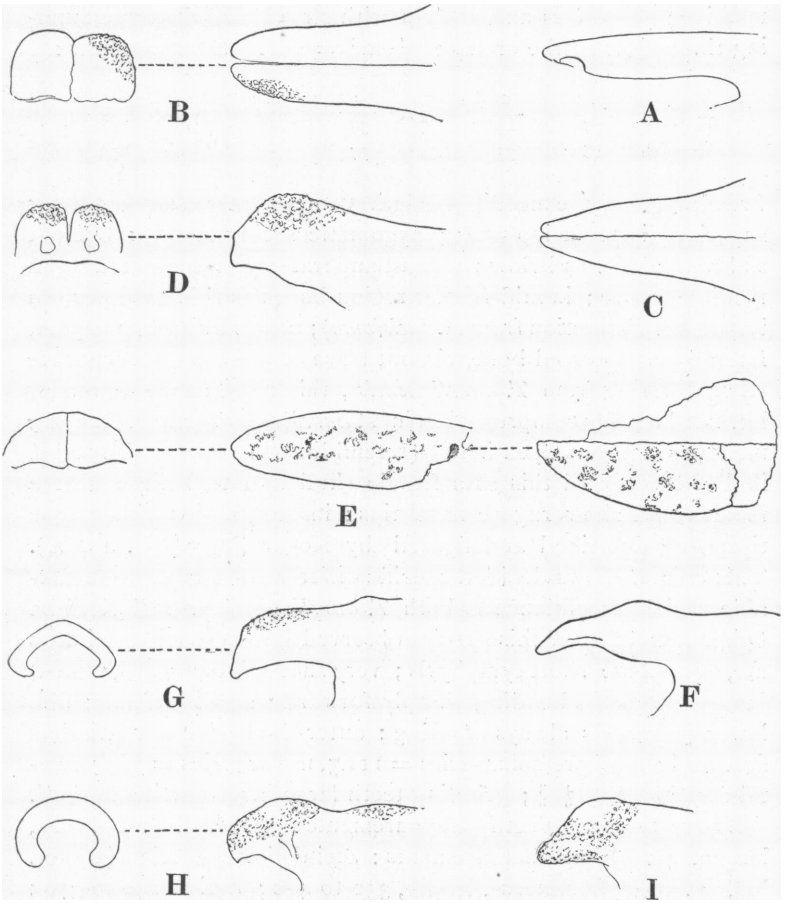


Fig. 12. Characteristic types of nasals and nasal rugosities. A, *Aceratherium tetradactylum*, PARIS. B, *A. lemanense*, LYONS (Pyremont). C, *A. incisivum*, HALLE. D, *Teleoceras aurelianensis*, PARIS. E, *Incertæ Sedis*, AUGSBURG. F, *Rhinoceros sansaniensis* (restored). G, *R. platyrhinus*. H, *Atelodus bicornis*. I, *A. simus*. Mostly after rough sketches by the author.

AUGSBURG: Other characters of this variety are given by the fine specimens in this museum shown to the writer through the kindness of Dr. Otto Roger, also communicated by letter (May 30, 1899), but especially in his very full and valuable paper

(Roger, '00), received just as this paper was going to press. Locality: base of lower Dinotherium Sands, near Augsburg. Very aged skull (Roger, '00), found at base of sands, short and massive; premolars and molars with strong cingulum surrounding three sides of the crown; p^1–m^3 = 260. Measurements:

	p. 1	2	3	4	m. 1	2	3
Length	27	29	35	37	40	49	58
Breadth	18	35	48	57	56	56	53

Breadth greatly exceeding length throughout upper grinders; superior diastema i–p = 85; zygomatic arches strong; occiput as broad above as below; supra-temporal crests separated by a median groove; in mid-frontal region bones as thin as paper (an important distinction from *A. incisivum*); nasals a single, compact, laterally compressed bone without trace of median cleft or suture (thus differing from *T. aurelianensis*), thickened at the extremity but not laterally compressed as in *T. aurelianensis* and *T. fossiger;* meatus auditorius open below (resembling *R. sumatrensis*). I am inclined to regard this as a female skull and to believe that a male would show rugose nasal tips; in fact, nasals with rugose tips were described and figured by Roger ('85) (Fig. 12, *E*). This animal shows decided specific differences, but an unmistakable racial resemblance to both *T. aurelianensis* and *T. fossiger.* Other characters of this species observed in Augsburg specimens are, *lower jaw:* short symphysis; very short diastema (10); small coronoid process bending sharply forward; small incisors; first lower premolars always wanting; outer face of lower grinders flattened; total premolar series = 111.5, molar series = 165; dental formula, $\frac{1}{1}\ \frac{0}{1}\ \frac{4}{3}\ \frac{3}{3}$; grinding teeth large in proportion to skull.

STUTTGART: Teeth measurements: Pm^4, breadth, 60, length, 40. Limb measurements: Steinheim collection (Roger, '00, pp. 16–17), humerus, length, 350 to 420; radius, 290 to 370; femur 390 to 540; tibia, 290 to 340; metatarsals, I = 108, III = 112, IV = 96; these measurements indicate that the limbs are somewhat longer than those of *T. fossiger* (*cf.* Osborn, '98, p. 57). The pointed vestigial first lower premolar is preserved in one jaw; lower incisors small and sharply pointed. A maxillary series (Steinheim, No. 6314) is referred by Roger ('00, p. 14) to this species, mistakenly, I believe, because the

long narrow measurements of the grinding teeth indicate that they belong to a dolichocephalic type, probably *A. tetradactylum.*

A jaw recently excavated by Professor Fraas himself (Steinheim) exhibits small pointed incisors and a vestigial pointed pm_1.

LOWER PLIOCENE STAGE.

Eppelsheim.

T. goldfussi *Kaup.*—The foregoing studies enable us to determine that the tooth which Kaup selected from the sands of Eppelsheim for the *type* of this species is not a molar, as he supposed, but a *fourth superior premolar;* this tooth has a broad internal cingulum ('Ossements Fossiles,' Darmstadt; in 'Akten d. Urwelt,' 1841, he adds as *cotypes*, a lower molar, and upper incisor; in 'Beitr. z. Näher. Kennt.' he figures an upper molar, Taf. II, fig. 20; a lower molar, fig. 15). In the same Eppelsheim sands are found other teeth with characteristic peculiarities of this brachycephalic-megalodine phylum, viz.: greatly enlarged upper incisors, upper molars with crochet and antecrochet projecting into median valley, lower molars with flattened outer wall.

T. goldfussi is very imperfectly known; it cannot now be distinguished specifically from *T. brachypus*, except by its larger size. So far as we know it was the last member of the subfamily Brachypodinæ.

Types. Incertæ Sedis.

The Siwalik Rhinoceroses have not yet been carefully examined by the writer. The *Aceratherium blanfordi* Lydekker, type, resembles the Brachypodinæ in the structure of its superior molars. From the Lower Pliocene or Maragha is another remarkable interesting form, *A. persiæ* Pohlig, which appears to be distinct from *A. blanfordi.*

Aceratherium persiæ *Pohlig.*—This species is richly represented in VIENNA (Collection Polak) by ten more or less complete skulls; there is also a fine skull in the HALLE Museum. Characters: Last superior molar quadrate with an exceptional extension of ectoloph, and a vestige of posterior valley; ectoloph of molars in a nearly straight line; antecrochets and crochets of molars very prominent, giving a complex pattern upon extreme wear;

enamel thin; protocone large, strongly constricted off. These dental characters approach those of *Teleoceras fossiger*.

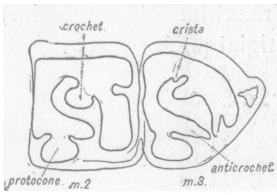


Fig. 12*a*. *Aceratherium persiæ*. Second and third superior molars. HALLE.

In some of its cranial characters it approaches *A. incisivum*, except in the extraordinarily broad chin which is hollowed out in the median line (see also lower jaws referred to *A. blanfordi* in British Museum); thus the lower canines diverge and are set widely apart, with the persistent alveoli of lower incisors between; nasals short, straight and smooth; a sagittal crest; occiput higher than broad; zygomatic arch slender. A strong rugosity upon the molars beneath the eyes for the origin of the masseter muscles, which are inserted in a strong ridge on the outer border of the angle of the jaw. Tibia and fibula closely united (as in Brachypodinæ). Limbs of medium length.

Subfamily CERATORHINÆ. PHYLUM IV.

Middle Miocene to recent Rhinoceroses; dolichocephalic, with frontal horns, and nasal horns upon a distinct mid-nasal convexity, not terminal; nasals more or less pointed and recurved anteriorly; cutting teeth large in early members, gradually reduced in certain branch phyla; cursorial limbs.

The first known of this series, *R. sansaniensis* of the Middle Miocene, appears to represent *a new arrival and a new phylum in Europe;* it certainly has no ancestors among the previously known Diceratheriinæ, Brachypodinæ, or Aceratheriinæ, for the structure of the entire upper portion of the skull is different; it is barely possible that some of the teeth referred to *A. minutum* from the Upper Oligocene may represent its ancestors; but this is not probable. Its successors or collateral descendants, however, are probably determined as the *R. simorrensis* of Simorre, the *R. steinheimensis* of the Upper Miocene of Steinheim and Grive-St.-Alban; these animals apparently gave off: (*A*) a *smaller race*, the last of which appears in the Lower Pliocene, Eppelsheim; in Eppelsheim and Pikermi, however, there also appears (*B*) the *larger race* of *R. schleiermacheri* possessing many of the same characters as *R. sansaniensis*, but with certain notable distinctions.

The generic name *Rhinoceros* may be retained at present for members of this series, but in case a relationship to the Sumatran

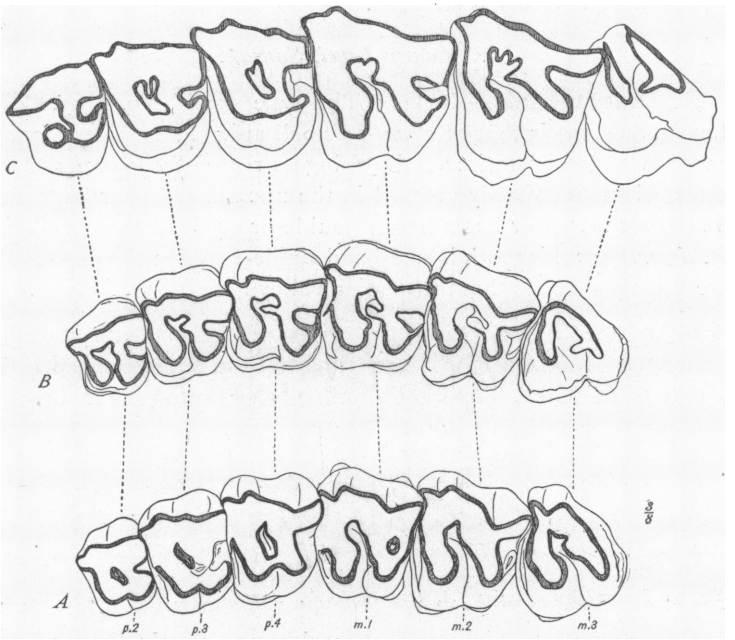


Fig. 13. Superior molar series. *A*, *R. sansaniensis*. Type: PARIS. *B*, *R. simorrensis*, No. 2380. PARIS. *C*, *R. schleiermacheri*. STUTTGART, after Kaup. All × ⅔.

Rhinoceros should subsequently be demonstrated, it would be well to apply Gray's term *Ceratorhinus* throughout.

A. Smaller Race. Middle Miocene to Lower Pliocene.

1. MIDDLE MIOCENE STAGE.

Dental Characters.—Large lower canines (males) in Miocene; first lower premolars relatively persistent (unlike Diceratheriinæ), retained to Middle Miocene, then reduced; upper premolar transformation retarded, crests confluent upon wear in *R. sansaniensis*, free in *R. simorrensis*; upper molars and premolars with internal cingula reduced or absent; molar-premolar series of moderate length ($pm^2 - m^3 = 190$ in *R. sansaniensis*), much shorter than in the contemporary Aceratheriinæ, proportionately longer and narrower than in the Brachypodinæ; molars retaining a feeble antecrochet.

Cranial characters.—Nasals short and broad, triangular when seen from above ; median horn precociously (Middle Miocene) developed upon both nasals and frontals ; occiput both broad and high (very distinct from Aceratherine, Diceratherine, or Brachypodine types).

a. Lower Level, Sansan.

R. sansaniensis.—PARIS : The type skull (No. 2395, Coll. Lartet, Sansan) is that of a *male*, a small animal ; it is very much crushed antero-posteriorly, disguising its real *dolichocephalic* character, which is strongly marked in the uncrushed lower jaw ; the first lower premolar has a broad double or grooved fang, while in *R. simorrensis* this tooth is small and single-fanged ; the premolars are greatly worn so that the median valley has almost disappeared

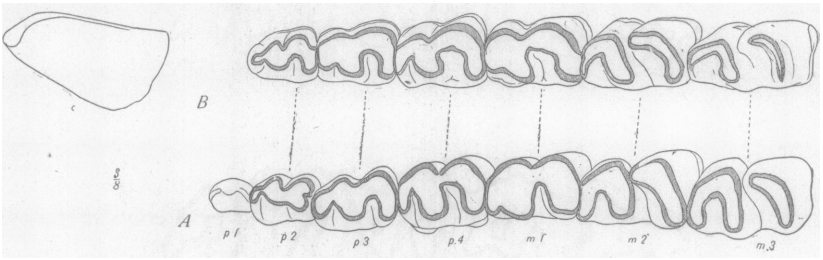


Fig. 14. Lower grinding series. *A*, *R. sansaniensis.* PARIS. *B*, *R. simorrensis.* PARIS.

and the crests are quite confluent : although a male (because of its well developed horns) the inferior canines are smaller than in the *R. simorrensis* jaw ; the simple character of the molar crests in this specimen is deceptive, and is due to extreme wear, the crochet (a superficial fold) having been worn off, the protocone and antecrochet are indistinctly marked (quite unlike the Aceratheriinæ and Brachypodinæ of this geological period) ; the inner face of the molars is without cingulum (unlike Aceratheriinæ and Brachypodinæ) ; there are indications that young teeth would show both crista and crochet ; the nasals and occiput have a very characteristic shape, somewhat similar to that of Gaudry's *R. schleiermacheri* of Pikermi ; the nasals are especially distinctive, being broad and rugose behind, where they carry the horn, but converge to a smooth point anteriorly ; (See PARIS, Nos. 2395, 551); metatarsals (erroneously catalogued *A. tetradactylum*), of moderate length, probably belong to this species.

b. Higher Level, Simorre.

R. simorrensis *Lartet.*—PARIS: (1) In this animal from a higher level (100 metres) we observe distinct specific progression: the size is the same; the lower canine is larger; the first lower premolar is single-fanged, reduced or wanting; the crests of the upper molars (Lartet Collection: No. 2380, catalogued as *A. tetradactylum*) are more distinct; the younger molars have a feebly indicated antecrochet and a very strong crochet; upon extreme wear the antecrochet comes out more strongly. (2) A handsome lower jaw shows the vestigial pm_1 persisting on the left side, wanting on the right (Fig. 14); the lower grinders are small, fine, and delicately built; the diastema is rather short. (3) A maxillary series (Coll. Lartet, No. 2380) is beautifully preserved; the fourth superior premolar is fully molariform, with a prominent antecrochet; the superior molars show a reduced antecrochet and a very prominent crochet. Measurements: $pm^1 - m^3 = 193$ (Coll. Lartet, No. 2380); $pm_2 - m_3 = 195$.

LYONS: Two fine maxillæ of *R. simorrensis* are found in the Muséum d'Histoire Naturelle and present characters exactly similar to the above; strong postfossettes are observed in $pm^2 - m^1$ and strong and prominent crochets on $pm^2 - m^3$; the molars have the internal cingula feeble or wanting. LONDON: Upper jaws and teeth (No. 33525, Villefranche, d'Astarac, Gers, France) a beautifully preserved apparently *female* skull with no trace of median horns on frontals; molar teeth with the same characters, $p^1 - m^3 = 193$. A lower jaw (No. 33526, same locality) exhibits a single-fanged and evidently much reduced first premolar. The *R. austriacum* Peters is represented in Munich by the third superior molar tooth. The type of this species from Eibiswald-Leiding is doubtfully distinct from the foregoing.

2. UPPER MIOCENE STAGE.

Steinheim, Grive-St.-Alban.

The Upper Miocene stage of this small race is the so-called *R. steinheimensis* Jäger, from Steinheim. (1) The finest example of this stage is a maxilla in STUTTGART (Steinheim, No. 6032);

pm^1 is quite simple ; pm^2 shows a crista and small antecrochet ; pm^3 shows a prominent crochet ; pms^{3-4} differ from molars in the absence of antecrochet fold ; the molars show a crista, reduced antecrochet, and very prominent crochet. (2) Another maxilla (No. 4230) shows a larger size, $pm^1 - m^3 = 200$. LYONS: similar teeth are found from Grive-St.-Alban. It is probable that this stage represents a distinct species, in which case it should be termed *R. steinheimensis* Jäger ; at present, however, we know no means of distinguishing it from *R. simorrensis.* MUNICH : A fine example of maxillary series from Georgensgemünd (catalogued *A. incisivum*) exhibits premolars and molars without internal cingulum ; the premolars have complete internal crests.

Conclusions.—There is a gradual advance in size (molars from 190 to 200) and in the evolution of the premolars, as we pass from the Middle to the Upper Miocene Ceratorhinæ.

3. LOWER PLIOCENE STAGE. LAST OF SMALLER RACE.

Eppelsheim.

R. steinheimensis.—Kaup referred the smaller teeth of Eppelsheim to *A. minutum* Cuvier ; this was an error. One of these Eppelsheim teeth, a third superior molar, is in LONDON (British Museum, No. 1257) ; it agrees closely in every particular with those of *R. simorrensis* both in size and character ; it is a much worn tooth and shows a large antecrochet. Casts of the Eppelsheim molars (M. 2739, 2740, 2742) are also identical with those of *R. simorrensis.* DARMSTADT : An examination of Kaup's originals in this Museum confirms the above determination (see Kaup, '62, Taf. II, figs. 6, 10, 11, 13). There is little doubt, therefore, that this smaller race of Ceratorhinæ persisted in the Lower Pliocene ; the specific characters of this stage are undetermined.

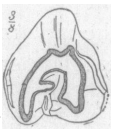


Fig. 15. *R. steinheimensis.* Last superior molar. Steinheim, MUNICH.

B. Larger Race.

4. LOWER PLIOCENE STAGE.

Eppelsheim, Pikermi.

We can imagine that the *smaller race* arrived in Europe (either from Asia or Africa), was arrested in size development and

terminated in the smaller Eppelsheim species; then from the same original stock, by subsequent migration, a collateral *larger race* arrived, which in general had developed along the same lines, but had retained certain primitive characters.

Such a collateral species is Kaup's *R. schleiermacheri* of Eppelsheim (Fig. 13, *C*). It exhibits molar-premolar teeth measuring 260; it is thus nearly one-third larger than *R. steinheimensis*; it resembles the *R. sansaniensis* series in the following points: superior molars: antecrochets reduced; a crista (progressively bifid); a prominent crochet; skeleton: metapodials of medium length; tridactyl manus. It differs as follows: premolars with crests internally confluent upon wear (primitive); first lower premolar persistent (primitive); a sagittal crest (primitive); small cutting teeth (progressive); very large nasal and frontal horns (progressive); no postfossettes in the molars; wide distance between orbit and naso-maxillary notch (this space is somewhat shorter in *R. sansaniensis*, indicating a progressive lengthening of the skull in *R. schleiermacheri*).

Therefore, as placed together in the Paris Museum the Middle Miocene *R. sansaniensis* and the Lower Pliocene (Pikermi) *R. schleiermacheri* exhibit first a striking racial similarity in form; second, a difference in size exactly such as one would expect in the progression from a Middle Miocene to a Lower Pliocene type; third, certain primitive and progressive differences which render the theory of direct descent of one from the other impossible. If one compares the skulls closely one sees the striking racial likeness in the form, and especially in the proportions and positions of the horns upon the nasals; the occiput of *R. schleiermacheri* is relatively lower and is somewhat broader below. In both specimens the infraorbital foramen is very close to the naso-maxillary notch; thus it is evident that these species, although not genetically related, represent collateral branches of a similar race. The growth of the skull between the orbit and anterior nares points to progressive dolichocephaly and to correlated elongation of the limbs and feet.

The successors and relatives of this Ceratorhine phylum are, apparently, *R. leptorhinus* Cuvier, Middle Pliocene, represented by a fine skull (Paris Museum, Montpellier, Hérault); the long-limbed *R. etruscus* from the Upper Pliocene of Italy, France, and

England, with a nasal septum; *R. platyrhinus* of the Pliocene Siwaliks of India (which Lydekker has mistakenly associated with the Atelodinæ); finally, the smaller and somewhat primitive living species, *R. sumatrensis.*

Subfamily ATELODINÆ. PHYLUM V.

Lower Pliocene to recent Rhinoceroses. Dolichocephalic, long low skulls, moderately broad, depressed, backwardly inclined occiput; two large horns developed upon nasals and frontals; nasals square or blunted anteriorly, horns extending to the extremities; Atelodine, cutting teeth vestigial or wanting; mesopodal, moderately long limbs and digits, similar to those of R. indicus.

1. Lower Pliocene Stage.

Pikermi, Maragha.

In the Lower Pliocene of Pikermi there suddenly appears in Europe a fifth type which cannot be derived from any of the preceding; the cutting teeth are precociously vestigial or wanting (hence the term Atelodinæ); the skull is easily distinguished by the form of the temporal fossa and occiput, by the form of the nasals and by the absence of front teeth in the dolichocephalic megalodine *R. schleiermacheri*, which appears in the same beds. The species is not found in the more northern Eppelsheim beds, and in view of the many resemblances which the Pikermi type, *R. pachygnathus*, bears to the existing African species (*R. simus*, *R. bicornis*), we may not consider as unreasonable the hypothesis that this is an African phylum which entered southern Europe with the numerous Antelopes and Giraffes of Pikermi; the later members of this phylum are the Pleistocene *R. hemitœchus* and *R. antiquitatis* (= *tichorhinus*), and the recent *R. simus* and *R. bicornis*. The main characters of this phylum are given above.

R. pachygnathus *Wagner.*—Paris: A fine skull and skeleton of this type have been described and figured by Gaudry. Even in the young skull there is a decided thickening for a frontal horn; the nasals are very broad and thick at the extremities; the lower jaw is without distinct angle, and a single convex sweep from condyle to angle is very characteristic; correlated with this we observe a weak zygomatic arch and early reduced front teeth; the most distinctive feature is the backward sweep of the temporal fossa, the low, backwardly inclined occiput. The molars are *brachyodont.* In the older jaw the formula is: $i\frac{0}{0}c\frac{0}{0}p\frac{2}{2}m\frac{3}{3}$.

Duvernoy actually attributed *R. pachygnathus* to the Pleistocene species *R. antiquitatis*, from resemblances in the limb bones, and Gaudry remarks ('62, p. 177) that this was very natural because the bones are extremely similar. Again, as originally remarked by Gaudry, *R. pachygnathus* resembles *R. bicornis* (the smaller brachyodont shrub-eating species of Africa), and ('62, p. 178) closely also *R. simus* (Burchell's Rhinoceros, the larger hypsodont, grass-eating species of Africa); I have verified these remarks by very careful studies of specimens in Paris and London. *R. simus* has a square upper lip, with broadly truncate upper nasals, the horn rugosities being carried to the very extremity, and its cranial resemblance to *R. pachygnathus* is remarkable. *R. bicornis* has, on the contrary, a pointed prehensile upper lip, and its somewhat more pointed nasals may be correlated with this narrower snout, but the horns are carried to the very extremity (at which there is sometimes a slight cleft, British Museum specimen).

Atelodus neumayri, sp. nov.[1]

Type, a large male skull, Vienna Museum, from Pikermi or Maragha (Persia), (erroneously catalogued as *R. schleiermacheri*). This skull resembles *R. pachygnathus* as follows: large frontal and nasal horn cores; auditory meatus closed; zygomatic arch slender (correlated with reduction of angle and masseteric muscles); lower border of jaw convex; dentition: $\frac{?}{?},\frac{?}{?},\frac{3}{3},\frac{3}{3}$. It differs from *R. pachygnathus* as follows: molars elongate, tending to hypsodontism; cement covering sides of molar crowns; the pattern of the premolar and molar teeth unique and without precedent; there is no true antecrochet on the protoloph, but a fold, which might be considered as an aberrant crista, projects into the median valley from its outer portion, that is, *external* to the crochet (whereas the antecrochet always appears *internal* to the crochet); the prominent crochet is placed internally to this; strong hypostyle fold and postfossette on p^8 to m^1.

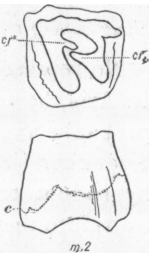


Fig. 16. *Atelodus neumayri*. Type: Second superior molar. VIENNA.

An apparently similar fold is observed in *R. antiquitatis*, and connects the protoloph diagonally with the metaloph; *A. neumayri* therefore resembles *R. antiquitatis* more closely than *R. pachygnathus*, both in the presence of this fold and in the greater hypsodontism of its molar teeth.

[1] Dedicated to the late distinguished Austrian geologist, Melchior Neumayr.

2. PLEISTOCENE AND RECENT STAGES.

An adaptive parallel to these types is presented in the Middle and Upper Pleistocene species: *R. antiquitatis* resembles *R. simus* (and less closely *R. neumayri*) with broadly truncate nasals, slender zygoma, and hypsodont, small, very narrow molar teeth; while *R. hemitœchus*[1] resembles *R. pachygnathus* and *R. bicornis*, with brachyodont molar teeth. In both *R. hemitœchus* and *R. bicornis* the nasals are somewhat narrower and the upper lips more prehensile and pointed. These large Pleistocene animals (which co-existed for a while) thus differed in details of dentition in adaptation to local differences of feeding ranges and habits, but resembled each other in (1) extreme dolichocephaly, (2) backward inclination of the occiput, (3) powerful nasal septum, (4) horns on extremities of nasals.

The existing African species, *R. simus* and *R. bicornis*, like *R. sumatrensis*, in the Ceratorhine series, are, however, both less specialized than the Pleistocene types.

Subfamily RHINOCEROTINÆ. PHYLUM VI.

Brachycephalic or intermediate between extreme dolichocephalic and brachycephalic types; occiput inclined forwards. Single horns upon mid-nasals; nasals pointed and generally smooth at the extremities. Megalodine, large upper and lower cutting teeth.

No representatives of this phylum have been found in Europe. In Asia, however, the Pliocene Siwaliks yield species which are probably ancestral to the typical *Rhinoceros unicornis* of India. Lydekker ('81, Pl. X) shows that *R. palœindicus* leads into the hypsodont or grass-eating *R. unicornis* type, while *R. sivalensis* leads into the brachyodont or shrub-eating *R. sondaicus* type. All these four species exhibit a skull with forwardly inclined occiput, concave and hornless in the frontal region, nasals with a large horn in the middle portion which does not extend to the smooth and pointed extremities; well developed cutting teeth.

The origin and relationships of this phylum are unknown; it will be noted that it is exclusively south Asiatic in distribution and this (Oriental Region) may ultimately prove to be its home and exclusive centre of adaptive radiation.

[1] See Geol. Mag. (2), Vol. I, Pl. XV, as figured by Davis.

FAMILY RHINOCEROTIDÆ. THEORETICAL SUCCESSION OF PHYLA I–VI IN EUROPE.

	Subfamily: I. Diceratheriinæ.	II. Aceratheriinæ.	III. Brachypodinæ.	IV. Ceratorhinæ.	V. Atelodinæ.	VI. Rhinocerotinæ.
	Recent			Ceratorhinus sumatrensis	Atelodus bicornis " simus.	Rhinoceros indicus. " sondaicus.
Pleistoc.	Upper	[1] Elasmotherium sibericum			" antiquitatis	" sivalensis. " palæindicus.
Pleistoc.	Middle				" merckii	
Pleistoc.	Lower					
Pliocene.	Upper			C. etruscus C. platyrhinus		
Pliocene.	Middle			C. leptorhinus		
Pliocene.	Lower	Aceratherium incisivum	Teleoceras goldfussi	C. schleiermacheri. [1] C. steinheimensis.	" neumayri " pachygnathus	
Miocene.	Upper	A. tetradactylum.	T. brachypus	C. steinheimensis		
Miocene.	Middle	A. tetradactylum.		C. simorrensis. C. sansaniensis		
Miocene.	Lower ? Diceratherium douvillei	A. platyodon	T. aurelianensis.			
Oligocene.	Upper " minutum	A. lemanense				
Oligocene.	Middle					
Oligocene.	Lower [1] Ronzotherium velaunum [1] " gaudryi	A. filholi				
	Geographical Districts: Europe, America.	Europe, Asia, America.	Europe, America.	Europe, Asia.	Europe, Africa.	Asia.

[1] Incertæ Sedis.

CONCLUSIONS.

This phylogeny leaves many species untouched and unsettled. It certainly contains both errors and omissions, and I set it forward mainly as a *method of solution of the Rhinoceros problem.*

1. It disregards homoplastic or convergent characters, which are often entirely misleading.
2. Great stress is laid upon exactness as to stratigraphical or geological succession, the neglect of which has been a fertile source of error.
3. According to our present knowledge, none of the six phyla can be connected by European stem forms, as in the phylogenies previously attempted.
4. The newer hypothesis of foreign (African or Asiatic) invasion into Europe of certain phyla has at present more in its favor than the older hypothesis of the derivation of all Upper Tertiary from Lower Tertiary types of Europe.
5. It is a fact that the earliest known members of each phylum show substantially all its fundamental characters; subsequent modifications are adaptive and may be more or less convergent to other phyla.
6. Generic, specific, and subfamily terms are simply our symbols for clear thinking and description. If the hypothesis of six or more distinct phyla is correct, and these breeds or races have been distinct since the Middle, and in some cases since the Early Tertiary Period, then the actual remote relationships of the individual members of said phyla will be most truthfully and clearly expressed both by the revival of certain disused generic names, and by the use of subfamily names.

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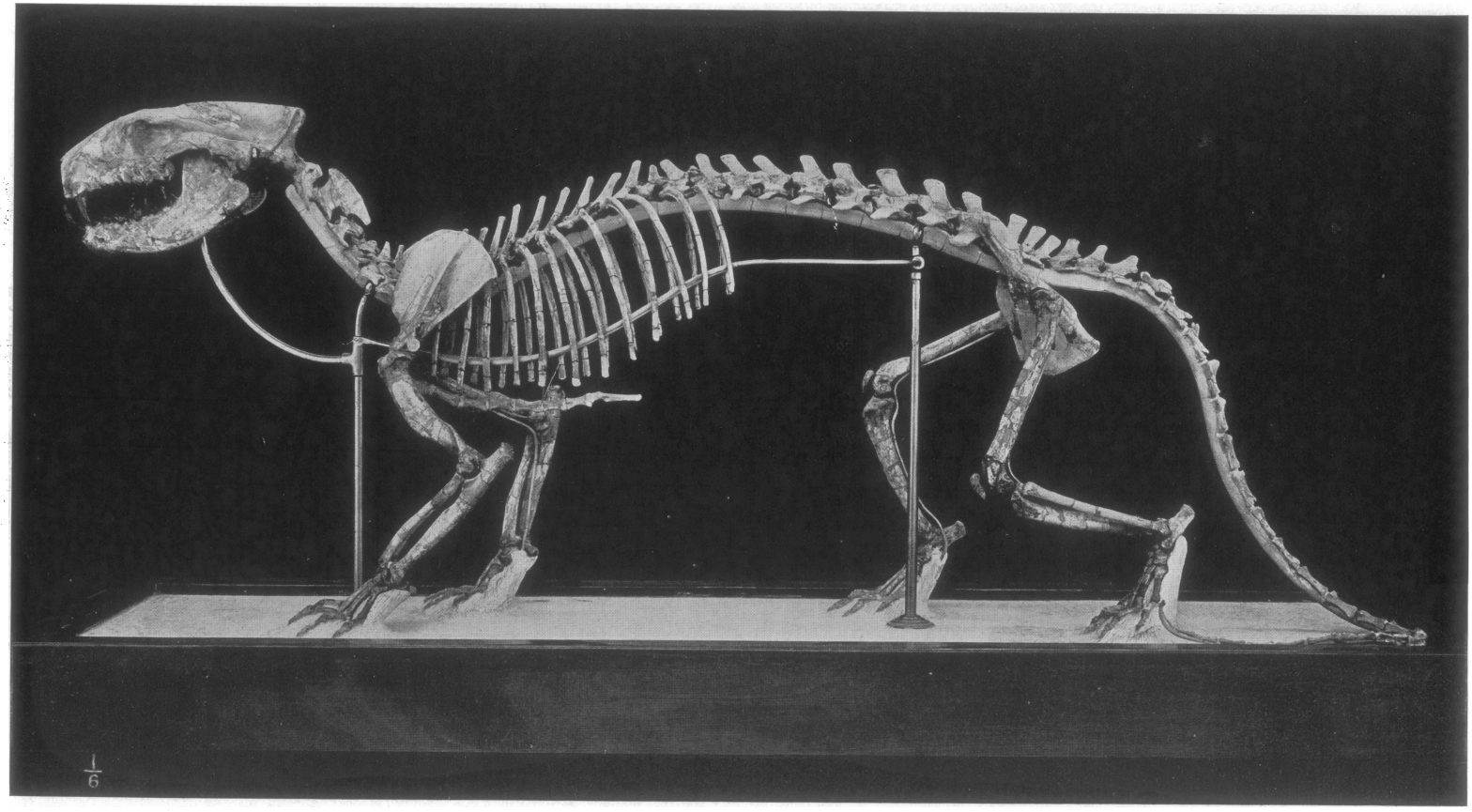
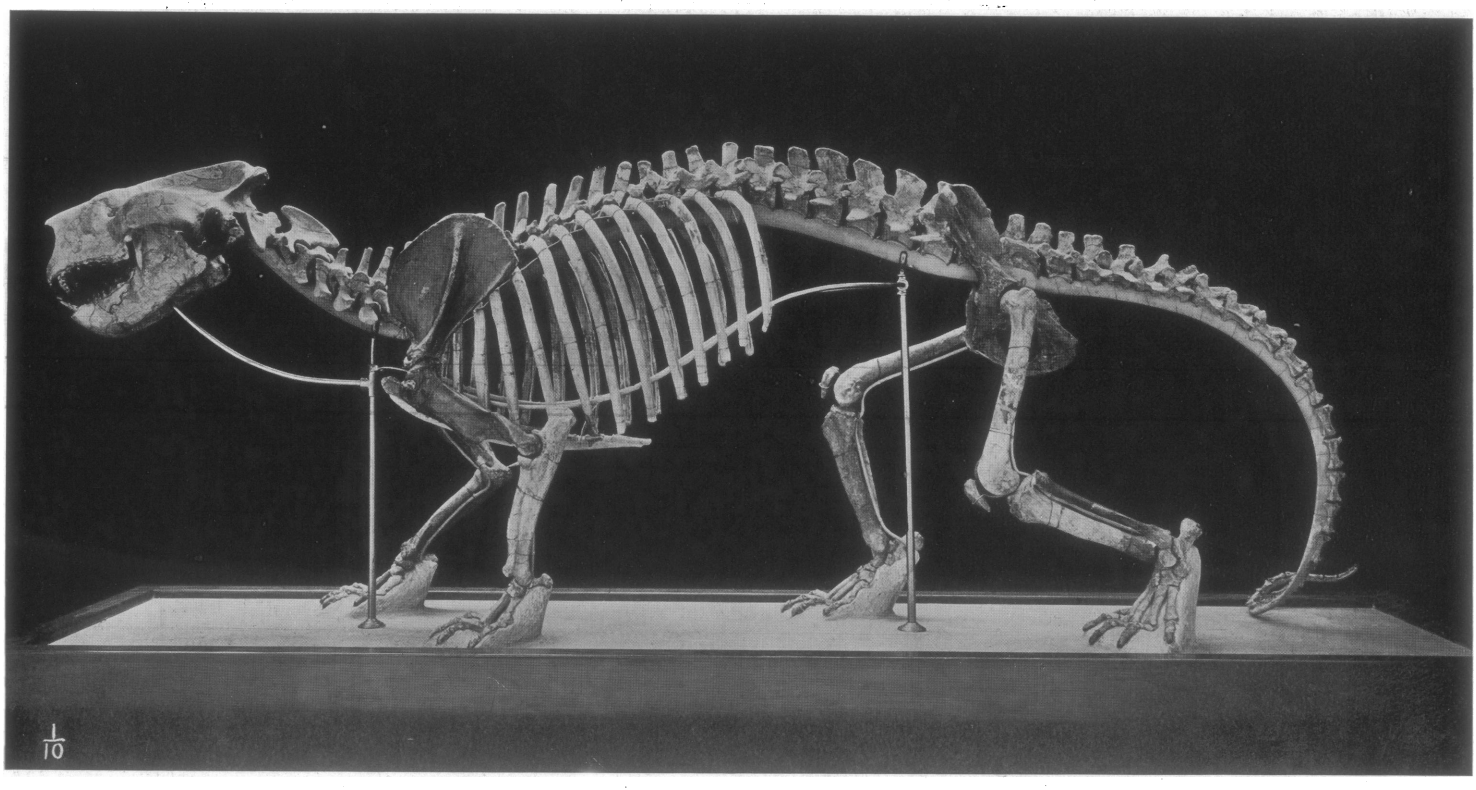


Oxyæna lupina, Mounted Skeleton in the American Museum. One Individual.



Patriofelis ferox, REMOUNTED SKELETON IN THE AMERICAN MUSEUM. INCLUDING PARTS OF TWO INDIVIDUALS.