ART. IV.—*Cœnopus, the Ancestral Rhinoceros;* by EDWARD L. TROXELL.

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INTRODUCTION.

Until very recent times there were two great groups of extinct rhinoceroses mentioned in the literature, *Acera-therium* Kaup and *Diceratherium* Marsh, and specimens from Lower Oligocene to Middle or Upper Miocene, both in the Old and New World, were classified according to the nasal bones, whether or not they had rugose thickenings designed to support horns. Due to the work of Osborn, Scott, Loomis, Cook, and especially of Peterson, it now appears that the two classes are simply the hornless females and the horned males of a variety of genera. There are, however, two important exceptions to this general rule: (1) the early Oligocene species which did not show the horn rugosities in the males, and (2) those recent animals (excepting *Rhinoceros sondaicus)* in which both males and females may have horns.

Peterson shows that in *Diceratherium cooki* the horns belonged to the mature males alone; the females and young males were hornless. In the Peabody Museum there are horned and hornless specimens of *Diceratherium* from the John Day beds of Oregon. The mature animals may be either, but the very young individuals always have smooth nasals. Osborn (1898) has demonstrated that *Cœnopus tridactylus* also has this sexual distinction, following the discovery by Hatcher (1894) of "*D.*" *pro-avitum* with horns in the males in a very primitive state. The name of *Diceratherium* therefore ceases to have its original sense, all inclusive, and is now limited to one phase of the horned rhinoceroses, the type of which is *D. armatum* Marsh. Other species of "diceratheres" may be, and some are, widely separated in their classification, as will be shown later.

[1] For obvious reasons, space is not given to the publication of all references; the reader is therefore directed to the memoirs by Osborn ("The extinct rhinoceroses", Mem. Amer. Mus. Nat. Hist., vol. 1, 75-164, pls. 12A-20, 1898) and by Peterson ("The American diceratheres", Mem. Carnegie Mus., vol. 7, 399-477, pls. 57-66, 1920), in which detailed descriptions, fine reproductions of all important types, and full bibliographies are published.

Likewise the word *Aceratherium*, heretofore considered to stand for a genus incorporating all aceratheres or hornless rhinoceroses, loses its etymological significance, and by exact definition, based in great measure on the teeth and parts of the skull other than the nasals, comes to be the name of a group which may be and probably is limited to the Old World.

Classification of Species.

Trigonias osborni Lucas 1900. Genoholotype.
Cœnopus mitis (Cope) 1874. Genoholotype.
Cœnopus pumilis (Cope) 1886. Synonym of *C. mitis.*
Cœnopus (*Leptaceratherium*) *trigonodus* (Osborn and Wortman) 1894. Subgenoholotype. Leads to *C. platycephalus.*
Cœnopus trigonodus altus, subsp. nov. Figs. 1, 2.
Cœnopus copei (Osborn) 1898. Leads to *C. tridactylus.*
Cœnopus occidentalis (Leidy) 1851. Inadequate.
Cœnopus tridactylus (Osborn) 1893.
Cœnopus dakotensis Peterson 1920. Synonym of *C. tridactylus.*
Cœnopus tridactylus proavitus (Hatcher) 1894.
Cœnopus tridactylus metalophus, subsp. nov. Fig. 4.
Cœnopus tridactylus avus, subsp. nov. Fig. 5.
Cœnopus platycephalus (Osborn and Wortman) 1894.
Cœnopus platycephalus nanolophus, subsp. nov. Fig. 3.
Cœnopus simplicidens Cope 1891. Of doubtful validity.

Discussion of Genera and Species.

Trigonias Lucas.

The earliest species of the true rhinoceros is made the genoholotype, *Trigonias osborni* Lucas. As summarized by Hatcher (1901), the upper teeth are unreduced, C_1 alone absent, simple superior premolars, P^1 large, P^2 with non-parallel lophs, four digits on the manus. Its geological age is that of the lower Titanotherium beds (lowest Oligocene). The ancestry of the genus is obscure, but it undoubtedly gave rise to *Cœnopus* Cope.

Cœnopus Cope.

Cœnopus is a genus which includes all of the White River (Middle and Upper Oligocene) species; it is based upon the holotype of *C. mitis* (Cope), a fragmentary lower jaw quite indeterminate specifically. The species is usually represented by the paratype maxillary with molars and premolars (No. 6325, A. M. N. H.).

In general, the genus is distinguished by the presence of two upper incisors, the absence of the canines (see *Leptaceratherium* below), the presence of rudimentary horn cores or none at all, parallel lophs on P^2, and the tendency toward this arrangement in other premolars in later species.

The generic group is composed of *C. trigonodus* (Osborn and Wortman), and *C. copei* (Osborn), two species which seem to lead respectively to *C. platycephalus*, the terminal member of its line, and to *C. tridactylus*, which probably furnished the source of all later forms, certain possible immigrants excepted.

Cœnopus (*Leptaceratherium*) *trigonodus* (Osborn and Wortman) as a type possesses the upper canine and thus forms the connecting link between this genus and *Trigonias*. This species has a further important primitive feature, a loop uniting the cross lophs of the premolars through the deuterocone and tetartocone, which are so blended as to appear as one element; in this respect also it approaches *T. osborni*, while on the other hand it trends toward *C. platycephalus*, its probable successor.

A new subspecies of *C. trigonodus* is described on a later page in this paper. It illustrates an advanced step in the evolution: has already lost I^3 and C^1, and has developed a very prominent deuterocone on P^4 which envelops the thin sinuous metaloph (Cat. No. 12052, Y. P. M.).

Cœnopus platycephalus (Osborn and Wortman) is typically an Upper Oligocene species, but smaller and more primitive specimens have been reported. Its type is marked by a broad low cranium and nearly obsolete sagittal crest; the species is also noted for the distinct separation of the tetartocone from the metaloph, the great reduction of the latter, the simplicity of the molars, and generally for the large size of the individuals.

A new subspecies will be proposed (Cat. No. 12489, Y. P. M.) which, because of the extreme reduction of the metaloph and the expansion of the deuterocone to occupy the whole inner portion of the larger premolars, is thought to be the termination of its line, and to be in no way related to later genera.

Cœnopus copei (Osborn), although it is barely distinguishable from *C. occidentalis* (Leidy) (heautotype, the holotype being lost), except in size, and although it resembles very much the paratype maxillary of *C. mitis* (Cope), yet should take precedence over either of these because their types are not adequate nor dependable. *C. copei* holds a very important place in taxonomy, since to a large extent it has usurped that of *C. occidentalis,* which is so frequently mentioned in our literature, and stands at the very beginning of that branch of the genus *Cænopus* which gives rise to *C. tridactylus* and probably many of the later genera of American rhinoceroses. Its geological level is the base of the Oreodon beds (early Oligocene).

Cænopus tridactylus (Osborn) is a very important species having a variety of characters which are strongly emphasized in later forms. One is therefore convinced that this is a pivotal point in the racial evolution, and from it there arise two or more lines of descent. Throughout this species the following are notable features: (1) the development of the parallel lophs on the premolars, (2) the greater complication of the enamel of the molars by the presence of cristæ and crochets, (3) the loss of all trace of C^1 and I^3, (4) the reduction to the tridactylous manus, and (5) the first appearance in the males of the thickened and rugose nasals for the support of horns.

The development of horns here is in a very primitive state, but a considerable advance is made in the next stage, *D. armatum,* where the horn supports are much more rugose and elevated, but still widely separated and situated well behind the tips of the nasals.

Other subspecies are chosen to illustrate more fully the variety of forms in *C. tridactylus* and the trend of that species toward the true *Diceratherium,* especially with regard to the simple parallel cross lophs on the premolars. Specimen No. 10254, Y. P. M., is taken as the holotype of one new subspecies, and specimen No. 10251 of another; both are described on a later page.

Description of New Subspecies.

Cænopus trigonodus allus, subsp. nov.

(Figs. 1 and 2.)

Holotype, Cat. No. 12052, Y. P. M. Middle Oligocene (White River beds), Nebraska.

The type material consists of the anterior portion of the face and the larger part of the lower jaws, not including the symphysis. The tooth series (fig. 2) is larger by the length of M^3 than that of the holotype of *C. trigonodus* or of *C. copei.* Other distinctive features consist of the small ridge in front of the protoloph and the great extension of the ectoloph forward on P^1, the reduced tetartocone of P^2 and its union through a broad ridge with the deuterocone, the strong deuterocone of P^3 and more especially of P^4, and the weak metaloph which on P^4 is a thin band so narrow that a wide space is left in front and behind it for the deep fossæ.

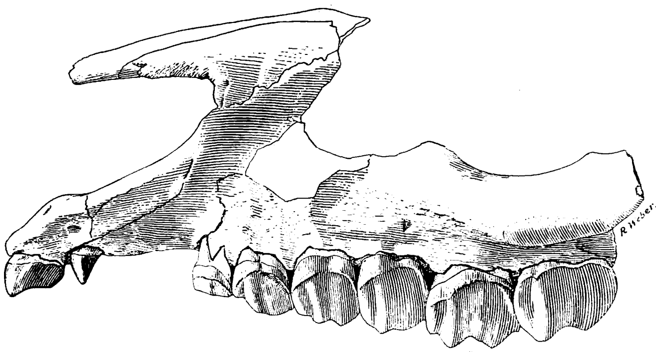

FIG. 1.—*Cœnopus trigonodus allus,* subsp. nov. Holotype. Side view of skull. × 1/3.

The cingula are weak around the bases of the deuterocones, but on the molars the cingula are discontinuous across the bases of the protocones and hypocones. Irregular tubercles and ridges obstruct the entrance to the medifossette or central valley. There are no sharp secondary folds on the molars, but the antecrochet is prominent.

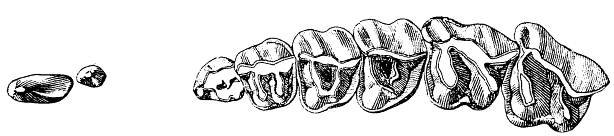

FIG. 2.—*Cœnopus trigonodus allus,* subsp. nov. Holotype. Molar-pre-skull. × 1/3.

I^{1-2} are present, but the third incisor and the upper canine are obsolete. The nasals are smooth, slightly expanded over P^1, and notched. There is a broad, shallow depression in front of the orbit.

The specimen is from layers later geologically than *C. trigonodus* but about the same age as *C. copei.*

Cœnopus platycephalus nanolophus, subsp. nov.

(FIG. 3.)

Holotype, Cat. No. 12489, Y. P. M. Middle or Upper Oligocene, Colorado.

This new subspecies is founded on a holotype consisting of the permanent upper molars and premolars of a young individual. The new name has reference to the dwarfed condition of the metaloph. It represents an undescribed species of rhinoceros near *C. platycephalus* but because of its incompleteness is ranked as a subspecies.

The tetartocone in each premolar except P^1 is closely joined to the deuterocone, and in P^4 these constitute a single element. P^2 varies from the others in having a groove on the outer side defining the two cones, which in this case are united to form a continuous loop of the inner lophs. On P^1 the metaloph is large and curves backward to enclose the postfossette; the protoloph is short and straight, while the ectoloph is broad and heavy and occupies the greater part of the tooth.

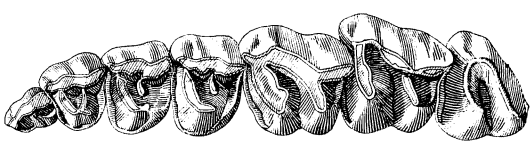

FIG. 3.—*Cœnopus platycephalus nanolophus*, subsp. nov. Holotype. Molar-premolar series. × 1/3.

In most species of *Cœnopus* the anterior side of the larger premolars is greatly lengthened by having a prominent protocone antero-exteriorly, and a tritocone so subdued that this part of the ectoloph is smooth exteriorly, as in the molars. In the specimen under discussion, however, the equal prominence of the two outer cones gives this side of the tooth a squared form; the ectoloph is at right angles to the anterior and posterior sides of the tooth. The premolars (except P^1) are thus subquadrate, with the inner sides rounded. The parastyle and metastyle are separated by grooves from the prominent exterior cones.

The anterior cingulum is strong on each tooth except P^1 but it does not encircle the inner border completely. On

P^4 the postero-interior cingulum rises high on the tetartocone, and forms a veritable cusp or cone; it descends sharply on the inner side and becomes broken along the base of the deuterocone. On P^3 it becomes an integral part of the tetartocone, and on P^2, antero-interiorly, the cingulum blends with the deuterocone, rising high on the side to do so. The posterior cingulum of each molar is much less extended than is usual in the rhinoceroses of this time, so that not only is the hypocone a smooth rounded base, but the median valley also is uninterrupted by cusp or cingulum, in this respect differing from *C. platycephalus*. The postfossette is very small on M^{1-2} and on M^3 is entirely lacking. The antecrochet on the molars is low and broad, while an inconspicuous crista is present on each of the larger premolars.

An unusual feature is seen on these premolars, in that the postfossette is larger than the medifossette and the two are confluent, due to the short metaloph; the median valley opens backward instead of inward and this, together with the dominance of the deuterocone, constitutes the chief feature of the subspecies. The type of the subspecies is about five sixths the size of that of C. *platycephalus*.

Cænopus tridactylus metalophus, subsp. nov.

(Fig. 4.)

Holotype, Cat. No. 10254, Y. P. M. Probably Middle Oligocene, Rushville, Nebraska.

The holotype of this new subspecies shows a strong tendency to have the cross lophs of all the premolars parallel and unconnected. The form of these lophs would

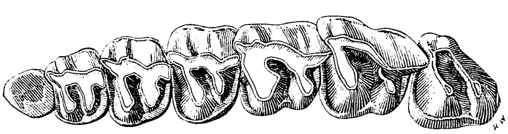

Fig. 4.—*Cænopus tridactylus metalophus*, subsp. nov. Holotype. Molar-premolar series. × 1/3.

seem to link it with *C. tridactylus* (Osborn) and remotely with *Diceratherium* Marsh. There is evident a close similarity to the skull of *C. proavitus* Hatcher in the form of the wide area between the parietal ridges on the sagittal crest. These ridges for a considerable distance are almost straight, converging at an angle of about 30° up to a point 8 or 9 cm. from the occiput, whence they run uniformly parallel. The occiput rises well above the plane of the face.

Both the proto- and metalophs are straight; the latter are especially thin and the terminating cones are not intimately connected with the strong postero-internal cingulum. The metaloph does not increase the length of its surface with wear, but with advanced age it may unite with the protoloph, at a point, however, scarcely more than halfway along the latter. The tetartocone, though small, is not recessive; it stands near the outer edge of the tooth crown, thus giving the great length to the metaloph.

The deuterocone, as it terminates the protoloph, swings forward, away from the tetartocone, in decided contrast to the *C. trigonodus* or *C. platycephalus* type of premolar, in which it curves backward, envelops the central part of the tooth and sometimes even the metaloph itself. The cingula are interrupted for short distances on the protocones and hypocones of the first and second molars, but the one is continuous on the protocone of the third molar. On P^4 there is a small crista. The antecrochet is prominent on the molars, giving a strong curve forward to the median valley. There is a small groove running up the protocone.

The slender premaxillaries supported the first incisor teeth only, which were found separated from the skull. The nasals, extending out to the ends of the premaxillaries, are unusually slender. This is commonly considered a sexual difference, but it is here presumed to be a feature of the earlier stages of the evolution, for no Middle Oligocene forms are known to have the rugose horn supports.

This specimen is probably one of the progenitors of *C. tridactylus* which leads ultimately to the parallel-lophed rhinoceroses of the Great Plains, where in each succeeding stage the enamel folding becomes more and more complicated. *C. tridactylus* is longer in the tooth series by the length of M^3; *C. copei* is shorter by that amount.

Cœnopus tridactylus avus, subsp. nov.

(Fig. 5.)

Holotype, Cat. No. 10251, Y. P. M. Upper Oligocene (Protoceras beds), South Dakota.

Cœnopus tridactylus avus, subsp. nov., is very probably a true form of this species, but as a subspecies shows a decided trend toward *Diceratherium armatum* (see fig. 6.) The type material consists of the skull of a young animal still retaining the last milk tooth, Dp^4, and having the last molar uncut. The first three premolars (P^4 is also uncut) are notable for the parallel, separate lophs, uniting only with wear. The metaloph is at first longer, but because of the extended base of the deuterocone, the protoloph soon surpasses it in length. P^1 has two parallel, backward curving crests, but the metaloph does not encircle a lake (postfossette) as does Osborn's paratype (1898, pl. 13). On the larger premolars, small sharp

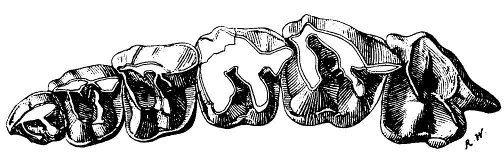

Fig. 5.—*Cœnopus tridactylus avus,* subsp. nov. Holotype. Premolars and first and second molars. × 1/3.

folds appear on the ectoloph, and on P^3 (left) one has an unusual position behind the metaloph. On P^2 and P^3 (right), there is a fold in the anterior angle between the two lophs.

Cristæ and crochets may be seen on the molars, and the latter, especially on M^1, have encroached so far on the median valley as to isolate a small lake (medifossette). On the protoloph of M^1, two vertical valleys, anterior and posterior, partly separate the protocone from its protoconule; the posterior valley emphasizes and sets off the moderate antecrochet. The inner cingula are broken across the bases of the protocone and hypocone, and are peculiarly offset where the two ends join in the median groove.

Not only in size but in the general form of the skull does this specimen resemble *C. tridactylus*; it has the rising and double parietal ridges extending into the sagittal crest. The nasal bones are long and slender,

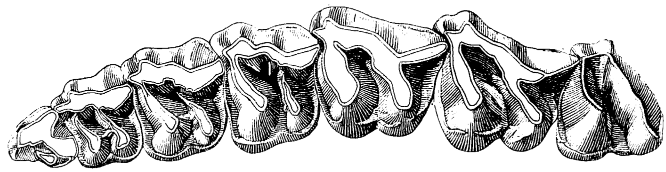

FIG. 6.—*Diceratherium armatum* Marsh. Holotype. Molar-premolar series. × 1/3. (See Peterson 1920 for reproduction of complete skull.)

slightly wide over P^1, where there appear actual shoulders or barbs resembling in this feature *C. copei.* Another specimen in the collection, Cat. No. 12059, Y. P. M., has the broad thick nasals, presumably of the male, but they do not show the rising protuberances so typical of the later *Diceratherium.*

Measurements of New Subspecies and also of D. armatum.

	C. allus No. 12052 Y. P. M. mm.	*C. nanolophus* No. 12489 Y. P. M. mm.	*C. metalophus* No. 10254 Y. P. M. mm.	*C. avus* No. 10251 Y. P. M. mm.	*D. armatum* No. 10003 Y. P. M. mm.
Molar-premolar length ...		205	194		254
Premolar series, length...	98	98	98	111	129
Molar series, length		115	102		139
P^4, width, base	37	39	39		50
P^4, length, center	27	28	26		34
M^1, width, ant.	37	43	39	44	53
M^1, length, center	33	38	33	38	44
M^2, width, ant.	39	48	40	45	56
M^2, length, center	38	41	35	39	50
M^3, width, ant.		43	39		50
M^3, length, inner side.....		39	35		48

SUMMARY.

With further study of the great family of rhinoceroses it becomes evident that they can not be classified on the presence or absence of horns, a sexual variation; the female and young dicerathere had no horns; probably the male acerathere had them, at first in an incipient stage.

The genus *Cænopus* Cope includes nearly a dozen distinct species and subspecies, representing a long line of ungulate evolution extending throughout the Oligocene. Clearly separated from the Hyracodontidæ and Amynodontidæ, this gave rise to all later forms, including the modern genera of rhinoceroses.

Four new subspecies are proposed: *Cœnopus allus* is noted for its strong protoloph and weak metaloph; *C. nanolophus* is so named from the dwarfed or incomplete metaloph on the premolars and the large posterior fossa. *C. metalophus* reverses the conditions of the others mentioned and has a metaloph as long as the protoloph and the two are parallel. This is probably one of the progenitors of *C. tridactylus*. *C. avus,* although a valid subspecies of *C. tridactylus,* yet shows a very definite similarity to *Diceratherium* Marsh and is ancestral to it. It is notable for the parallel cross lophs, complicated enamel bands, and its late Oligocene age.

SCIENTIFIC INTELLIGENCE.

I. Chemistry and Physics.

1. *A Recalculation of the Atomic Weights.*—Dr. Frank Wigglesworth Clarke, chemist of the U. S. Geological Survey, has now published the fourth edition, revised and enlarged, of this important work in the form of a volume of 418 quarto pages. The data of atomic weight determinations are presented very fully and the various ratios, with the exception of some that appear to be undoubtedly inaccurate, are calculated in connection with their mathematical probable errors. Then the available ratios are combined, with weightings according to their probable errors, in order to find the atomic weights. The author admits certain deficiencies in this mathematical method of calculation, due to the effect of constant errors in the determinations, such as the effect of impurities in the substances weighed, but it appears that his method is the best one available. A final table of atomic weights is presented in which the greater part of these constants are carried out to five figures. The table varies in this last respect from that of the International Committee, and there are also other appreciable variations in the two tables. For instance, Clarke gives 27.039 for aluminium, while the International Tables give 27.1, and it is interesting to observe that Richards has found, just recently and too late for Clarke's use in the work under consideration, that this atomic weight is probably about 26.96.