

LOWER OLIGOCENE RHINOCEROSSES OF THE GENUS  
TRIGONIAS

BY HORACE ELMER WOOD, 2ND

Gregory and Cook (1928) recently published a very thoughtful and valuable paper on the remarkable *Trigonias* collection from the Lower Oligocene of Weld County, Colorado, now in the Colorado Museum of Natural History at Denver. As their paper presents its material in highly concentrated form, Professor Gregory suggested that I should undertake an evaluation of their results on the basis of my previous work on the genus (Wood, 1927), which covers all known specimens except those at Denver. A several days' visit to Denver in 1928 gave me an opportunity to study the collection described by Gregory and Cook, as well as a number of additional specimens collected too late to be included in their study. I was also privileged to visit the Weld County Quarry.

I wish to acknowledge my indebtedness to Professor W. K. Gregory for his suggestion that I undertake this study, as well as for his helpful criticism; to Mr. H. J. Cook, former Curator of Fossil Vertebrates at the Colorado Museum, for permission to study this material and to visit the "*Trigonias* Quarry," which is leased by the Museum; and to the staff of the Colorado Museum for their assistance during my visit. I am indebted to Dr. Florence Dowden Wood for the drawings, and to Mr. Albert Elmer Wood for assistance in making measurements, and in the partial development of a number of specimens.

The locality of the quarries is twenty-three miles northeast of New Raymer, by road, and fourteen miles north of Stoneham. The two quarries are closely adjoining, in Township 10 North, Range 57 West, Sections 26 (Lower Quarry) and 27 (Upper Quarry). The altitude is about 5000 feet. In an unpublished study of a sample of the Lower Quarry sediment, Mr. Arthur D. Howard finds a high proportion of volcanic shards to other identifiable minerals. Extensive kaolinization has obscured the character of most of the components, but he considers it strongly probable that the material represents an altered tuff. Wanless (1922) reports "occasional fragments of pumice and volcanic glass" throughout the Titanotherium and Oreodon clays of the Big Badlands Oligocene, but this sample would seem to be more predominantly volcanic, as is Wanless' sample from the Oreodon Beds of Lewis Creek, Colorado. There is no possible question that the Weld County Quarry

is of Chadron age. It is probably equivalent to an early phase of the typical Titanotherium Beds of the South Dakota Oligocene.

Gregory and Cook's general conclusion can best be quoted as follows (page 4):

"Indeed, if the series were less complete, were the specimens from different localities or horizons, and had we chanced also to find only the extremes of variation, we should have felt no hesitation, according to widely accepted standards in palaeontology, in describing at least seven 'new species' representing possibly three different genera; but these extreme differences are bridged over by numerous intergrading conditions and combinations of characters, so that one soon gets the impression, on the one hand, that the Weld County series reveals a highly plastic condition of the rhinoceros population from which natural selection might accentuate and stabilize the differences in the premolars so as to give rise to the different 'species' already known from the next higher horizon; on the other hand, that extensive hybridism between formerly distinct races was actively going on. . . . While we thus incline to the hypothesis of extensive hybridism between originally distinct races, for the sake of convenience in describing and cataloging the material we nevertheless designate the various groups or individuals as variants or 'species' realizing full well that these terms in this instance, and perhaps in many others, merely signify a definable set of characters in certain individuals."

This conclusion, which is also illustrated in the series of graphs and tables, certainly accords with the evidence, and serves as a timely warning of the pitfalls of species making. It also is an evidence of the coming period of interpreting paleontologic data in the light of the background furnished by genetics.

Gregory and Cook's first alternative explanation of the causes of the intermingled characters seems the more probable—that incipient speciation was occurring. Some of these types seem to be leading to later and more distinct forms. There is no evidence in the Eocene of any "formerly distinct races" of *Trigonias* which might hybridize to produce the Weld County assemblage. Nor am I able to agree with the apparently implied assumption (page 4) that an area undergoing erosion is thereby less able to support life than one receiving sediments, and that, therefore, there is reason to assume that isolated geographic races of rhinoceroses extended their range with the resumption of sedimentation in the Chadron.

Starting from an essentially similar viewpoint as to the actual situation involved in the Weld County assemblage, Matthew (1930) takes a diametrically opposed view as to the desirability of giving taxonomic recognition to variants of this kind. He writes:

"We should not, in other words, expect to find two or more closely related species living together at the same time, within the same area, and with the same

habitat, causing their remains to be preserved together in the same quarry. We should expect to find that the individuals either intergrade or that the variations are distributed among different individuals in the manner that results from intercrossing of different breeds or strains. . . . This is equally true of the Lower Oligocene rhinoceros *Trigonias*."

"There is every reason to believe on ecologic and other grounds that this series represents one genus and one species thereof, the wide range of variation in structure of the cheek teeth illustrating how little value should be attached to the complex detailed phylogenies with numerous species and many so-called genera, that have been built up on the comparison of numerous fragmentary specimens from various localities." (Matthew, 1931.)

This *Trigonias* material brings up the old question of what is a species, which the geneticist is hardly better able to answer than is the taxonomist. However, from the view-point of convenience, it is certain that some of these specimens are sufficiently different from the rest to require individual mention, and may, therefore, deserve individual designations. Obviously, we cannot be sure whether they would have been sterile *inter se*, or not, nor even whether sexual repugnance existed between them in life. Convenience is the only real criterion, especially in paleontology, for deciding whether or not to give taxonomic recognition to morphologically distinct variants. It is, at least, a tenable point of view that it is legitimate to name any variant sufficiently distinct to require individual discussion.

Study of the entire group of thirty-five skulls (excluding only those with the teeth too worn or too damaged to be of any interest) showed that they are all much of a size, even including the smallest, ?*Caenopus premitis*. Gregory and Cook's measurements confirm this impression. For example, the extremes in length of P<sup>1</sup>-M<sup>2</sup> are 208 mm. and 175 mm. Such extremes for a normal curve of distribution would certainly not warrant specific distinction. Since all members of this assemblage of forms were much of a size, such "speciation" as was occurring was along qualitative, rather than quantitative lines. Again, although the skulls differ somewhat in proportion, the differences are very moderate indeed, particularly when the effects of crushing are allowed for.

Gregory and Cook's ingenious graphs are of considerable interest in showing the extent of variability in various characters, and the degree of correlation between different characters of the various individuals. The distribution of some of these characters seems entirely fluctuating; other characters tend somewhat to separate the individuals into groups. There is, however, always the danger in fitting material into such a formal plan that the verbal definition of a specimen may not give a true impression of its actual character.

By means of this extensive series of specimens, Gregory and Cook were able to settle a number of significant questions regarding tooth succession. They show that in *Trigonias* (and, presumably, in its various relatives) the enlarged lower tusk is the second incisor; that, probably,  $I_3$  is lost before  $C_1$ ; and that there is no succession in the case of the first upper premolar. This has long been regarded as the case with the first lower premolar. The positive demonstration that the lower tusk is  $I_2$  is particularly interesting, in view of the fact that Stehlin (1930) has now definitely established the fact that in at least one European rhinoceros there are two incisors on each side, in front of the lower tusks, so that the enlarged tooth must be  $I_3$  or  $C_1$ . This appeared to be the case in the type of *Epiaceratherium* (*Ronzotherium*) *gaudryi* (Rames), new combination, but some doubt was possible in regard to the interpretation of the right lateral incisor, which might have been considered a retained deciduous tooth. Stehlin's closely comparable specimen (which he calls *Enggyodon* [= *Eggysodon*] sp. and which is probably conspecific with *Epiaceratherium gaudryi*) removes any question. As Stehlin pointed out, the size and erectness of the tooth is more suggestive of a canine than of an enlarged incisor; and there is no precedent for enlarged  $I_3^3$  in rhinoceroses or other perissodactyls (except tapirs). Roman's data (1912), as well as unpublished evidence, would best fit with the view that the enlarged teeth are canines rather than third incisors. Considering all available data, it appears that *Epiaceratherium* belongs to a separate subfamily of true rhinoceroses, paralleling the Amynodontidae, with enlarged canines (or, barely possibly,  $I_3^3$ ), and including the following described forms: *Ronzotherium gaudryi* Rames, *Eggysodon osborni* Roman (not of Schlosser), *Eggysodon pomeli* Roman, *Epiaceratherium bolcense* Abel, and *Epiaceratherium turgaicum* Borissiak. In spite of the general similarity of *Epiaceratherium* to other true rhinoceroses, this line must have split off from them at a very early stage, before  $I^1$  and  $I_2$  began to enlarge. This would add the new subfamily *Epiaceratheriinae* to the seven or so other subfamilies of true rhinoceroses. Matthew (1931) failed to recognize the clear demarkation of *Epiaceratherium* from all other true rhinoceroses, in having  $C_1^1$  enlarged, instead of  $I^1$  and  $I_2$ , but his opinion that it was close to the other Oligocene rhinoceroses was warranted by the data known to him. Further discussion of the relationships and valid species of this group is reserved for a separate paper on the earlier European rhinoceroses.

*Generic definition of Trigonias:* Primitive, hornless, dolichocephalic, true rhinoceroses with functionally tetradactyl manus, known only from the Chadron

Formation (= Titanotherium Beds, Lower Oligocene) of Colorado, Nebraska, and South Dakota.<sup>1</sup> The nasals and premaxillaries are elongate, and the latter are closely appressed and may be more or less suturally connected.  $I^1$ ,  $C_0^{1-2}$ ,  $P^4$ ,  $M^3$ . Of the front teeth, only  $I^1$  and  $I_2$  are functionally important.  $P^1$  is relatively large. In the more primitive members of the genus, the protoloph of  $P^2$  has an unusually low connection with the ectoloph for a true rhinoceros, a situation suggesting *Hyrachyus*.  $P^4$  is never fully molariform, the hypocone being principally attached to the protocone, and separated from the metaconule by a valley.  $M^3$  may retain a trace of the posterior buttress. (See Wood, 1927, pp. 198-215, for additional data and discussion.)

Gregory and Cook's summary of the morphological divergences of the *Trigonias* Quarry material requires some modification (page 5). "This divergence runs all the way from a much more primitive construction than that found in *T. osborni* to complete molarization of all the pre-molars, advanced as far as the condition found in the upper Oligocene forms of the genus *Caenopus*." I should state the case as follows: This divergence runs from a primitive stage of *T. osborni* to virtually complete molarization of the second and third premolars and marked progress in the last, comparable to upper Middle Oligocene species of *Subhyracodon*. On page 5, by a misprint, *Trigonias* is defined as having none of the upper "molars" strictly molariform, when, of course, "premolars" is intended. I disagree slightly with the authors as to the relative primitiveness of the different stages of premolar evolution shown in their figure 5. Taking into account the general trends of rhinocerine evolution, I should arrange them in the following order (in relation to the characters shown in these figures only): K, C-diverging in one direction, then after K, on the main line, D, and F, then, a marked advance, E.

It will be observed that I group these specimens somewhat differently from Gregory and Cook. Another worker might handle them still differently; this is, however, the set of cubbyholes which seems to me to permit the most natural arrangement of the specimens. The divergences in possible viewpoints show the intergrading character of most of the material. In general, I prefer to take a position more conservative than that of Gregory and Cook, but less so than that of Matthew.

<sup>1</sup> Dal Piaz (1929) mentions *Trigonias ombonii* from Monteviale, Italy, of which the description is apparently to appear shortly. If, as seems almost certain, this name refers to the material which I saw in Padua in 1927, it has no significant relation to *Trigonias*, but belongs in *Epiaceratherium*.

### *Trigonias osborni osborni* Lucas

Figures: Lucas, 1900, 1 and 2, (fig. 1 reproduced in Scott's "Land Mammals," fig. 177); Hatcher, 1901, Pl. I, figs. 1 and 2, Pls. II-IV; Troxell, 1921, p. 46, fig. 3; Cockerell, 1923, p. 275; Wood, 1927, figs. 20-28; Gregory and Cook, 1928, Pls. I and III.

Synonymy: *Trigonias osborni* Lucas, 1900; *Caenopus platycephalus nanolophus* Troxell, 1921; *Trigonias osborni fignisi* Gregory and Cook, 1928; *Trigonias osborni secundus* Gregory and Cook, 1928.

The characters of *T. osborni* have been fully discussed elsewhere (Wood, 1927). I disagree with Gregory and Cook that *T. nanolophus* (Troxell), Troxell, fig. 3, 1921, is probably a good species. It seems to me, as I indicated in 1927 (p. 213-214), to be almost identical with Lucas' type specimen of *T. osborni osborni*, allowing for the difference in the amount of wear.

The type of *Trigonias osborni fignisi* Gregory and Cook, Cat. No. 897-H, Colorado Museum (Gregory and Cook, Pl. I and IIb) appears to be inseparable from the type of *Trigonias osborni* Lucas (Wood, 1927, figs. 20-21) and becomes, therefore, a synonym. The stated differences from Hatcher's referred specimens (Hatcher, Pl. I, II, and IV, and Wood, figs. 22-24) can be explained by crushing and extensive tooth wear. I<sup>1</sup>, C<sup>1</sup> and P<sup>1-1</sup> seem very similar to Lucas' type. The only difference observed is that the outer attachment of the protoloph of P<sup>2</sup> of "fignisi" seems lower, as the dentine areas of the protoloph and ectoloph are still separate. However, they would coalesce on further wear. Skull C (Cat. No. 881, Colorado Museum, Gregory and Cook, Pl. IVB), referred to *T. osborni fignisi*, seems to belong in *Trigonias hypostylus*.

The following Colorado Museum specimens seem to be definitely referable to *Trigonias osborni osborni*: Cat. Nos. 420, 421, 879, 888-E, 892-H, 897-H (type of *T. "fignisi"*), 935 (which, however, has some peculiar features), 1024 (cf., however, *T. preceper*), 1051, and 1052.

There is an unusually long sharp crista on the right P<sup>3</sup> (but not on the left P<sup>3</sup>) of *T. osborni osborni*, Cat. No. 1050 R, reaching from the ectoloph across to the protoloph and forming a small basin, as in certain hyrachyids. This resemblance, of course, is entirely due to parallelism. Otherwise, this specimen is commonplace. Neither P<sup>2</sup> is quite molariform. Left P<sup>2</sup> has a fully developed metaloph, closely united with the protoloph. The hypocone of right P<sup>2</sup> is about equally connected with the protoloph and the metacone.

A young individual, Cat. No. 422 (B), Colorado Museum, has more primitive P<sup>2</sup>s than any other specimen of *Trigonias*, or, for that matter, than any other true rhinoceros which I have seen (fig. 2). It does not seem advisable to separate it, however, from the *T. osborni osborni* group. The second upper premolars have hardly advanced beyond the third and fourth, so that they suggest the condition in *Hyrachyus*. The connection between the ectoloph and protoloph of P<sup>2</sup> is very low and the median valley opens to the rear over the low wind-gap between the hypocone and the metacone. The hypocone, although defined from the protocone by a deep internal groove, is essentially a portion of the protoloph. The tooth is slightly worn; previous to this wear, the tips of the protocone and hypocone would apparently have been slightly separated. Both of the P<sup>3</sup> and the right P<sup>4</sup> are in place. The left dP<sup>4</sup> had not yet been replaced. P<sup>2</sup> and P<sup>4</sup>

are generally like P<sup>3</sup>, except that the wind-gap is lower in P<sup>3</sup> than in P<sup>2</sup>, and the median valley of P<sup>4</sup> is completely open to the rear. The hypocone is only slightly

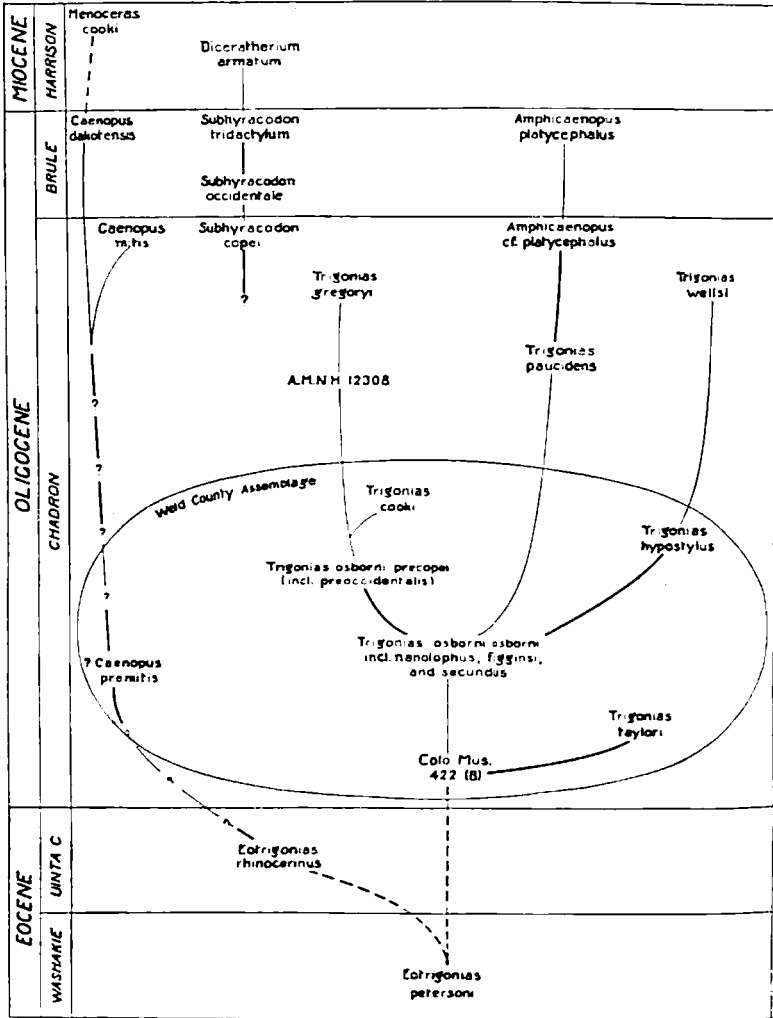


FIG. 1. Phylogenetic chart of the genus *Trigonias* and related American forms

defined in P<sup>3</sup> and not at all in P<sup>4</sup>. On the right, P<sup>4</sup> and M<sup>3</sup> are cutting the gums; left M<sup>3</sup> had not yet erupted.

Cat. No. 1055 (W) Colorado Museum. appears to be a primitive member of *T. osborni osborni*, with certain peculiar features. Both of the P<sup>2</sup>s have a wide gap

to the rear between the metaconule and the hypocone. Both of the  $P^3$ 's are normal, and similar except for the hypostyle on left  $P^3$ ; right  $dP^4$  is not yet replaced. The left  $dP^4$  has either a twinned metaconule, or a hypostyle misplaced to the front. Except as noted, hypostyles are not present. This individual shows some tendencies toward *Trigonias hypostylus*.

Cat. No. 421, Colorado Museum, appears to be referable to *T. osborni osborni*. Left  $P^2$  is a little unusual, since the hypocone is transversely elongated, although its dentine is not yet quite confluent with that of the metaconule. Left  $P^3$  is peculiar, since it has twinned metaconule and metacrista, connected at their tips and enclosing a small basin.

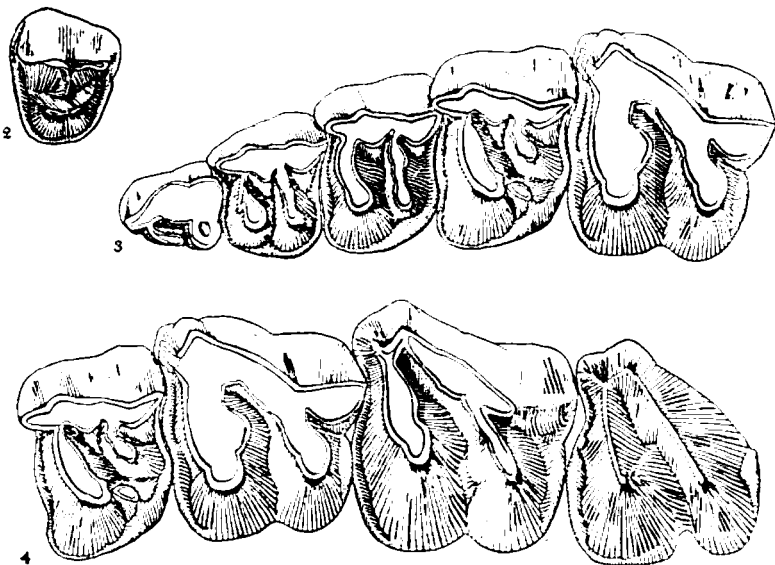


FIG. 2. Right  $P^2$  of Cat. No. 422, B, Colorado Museum, *Trigonias osborni* cf. *osborni*,  $\times \frac{1}{2}$ .

FIG. 3. Left  $P^1$ - $M^1$  of holotype of *Trigonias cooki*, new species, Cat. No. 1053, U, Colorado Museum  $\times \frac{1}{2}$ .

FIG. 4. Left  $P^4$ - $M^3$  of holotype of *Trigonias cooki*, new species, Cat. No. 1053, U, Colorado Museum  $\times \frac{1}{2}$ .

Cat. No. 955, Colorado Museum, is a progressive variant of *T. osborni osborni*. It is a young individual, with  $dP^4$  still in place. The protoloph and metaloph of  $P^1$  are complete and nearly parallel, and accessory internal cuspsules occur in front of the protoloph.  $P^2$  is unworn and almost fully erupted. The protoloph and metaloph are fully separate, nearly down to the level of the cingulum. The metaloph seems to hook to the rear more than usual. The protoloph has almost no connection with the ectoloph. In  $P^3$ , the hypocone is defined from the protocone by a faint, internal groove only. The metaconule is widely separate from the hypocone, leaving a posterior opening to the median valley.



Cat. No. 1026, Colorado Museum, here regarded as referable to *T. osborni osborni*, has the transverse lophs of P<sup>2</sup> separate nearly to the level of the cingulum. The metaloph of right P<sup>1</sup> forms (with the protoloph) a nearly continuous antero-posterior ridge, not at all connected with the ectoloph. P<sup>3</sup> is very progressive for *T. osborni*; it is more progressive than in *T. osborni precopei*. The hypocone is as high as the protocone, well separated from it at the crown, and connected with the metaconule almost as much as with the protoloph, enclosing a V-shaped basin. The dP's had not yet been replaced. This specimen is quite progressive, but its features do not require taxonomic recognition. P<sup>2</sup> of this specimen follows alternative 3b in its metamorphosis (Wood, 1927, p. 238); that is, the hypocone joins the metaconule before it has separated from the protocone, completely enclosing the median valley. This is the course apparently followed by P<sup>2</sup> in the *Trigonias osborni* group, although P<sup>2</sup> of Cat. No. 421, Colorado Museum, suggests the alternative possibility that the hypocone may have been an isolated cusp for a time, before joining with the metaconule.

#### *Trigonias osborni* var. *secundus* Gregory and Cook

The authors make, here, for the first time, a much-needed distinction between the hypostyle, a separate independent cuspule, appearing in the post-fossete, and their "metacrista" (new term), a projection mediad from the metacone.

The holotype is Cat. No. 884-F, Colorado Museum, Gregory and Cook, Pl. IIIA. This variety seems very doubtfully distinct from *T. osborni osborni*. It might be used to indicate the more primitive specimens of *T. osborni*, with P<sup>2</sup> definitely premolariform, that is, with the hypocone connected with the protocone and partly separated from the metaconule. This is shown to be a doubtful basis for varietal distinction, however, by Cat. No. 1051-S, Colorado Museum, in which the right P<sup>2</sup> agrees with advanced specimens of *T. osborni osborni*, while the left P<sup>2</sup> agrees with *T. osborni secundus*. In Cat. No. 884 (F), Colorado Museum, the holotype of *T. osborni secundus*, the metaloph is the only transverse crest on P<sup>1</sup>. The only sign of a protoloph is a basal cingulum in the right position to give rise to it. P<sup>2</sup> has the hypocone demarked from the protocone, but connected to it. The median valley escapes over a "wind-gap" between the metaconule and the protocone. In P<sup>3</sup> and P<sup>4</sup>, the hypocone is less demarked, the metaconule is attached to the protocone, and the lowest point in the divide, in an unworn tooth, would probably have been between the metaconule and the hypocone. The left P<sup>3</sup> has an accessory cusp, probably an outwardly-displaced hypocone. Both P<sup>4</sup>s have metacristae, the only distinctive subspecific character that could be considered definitely valid, since it is present on both sides. This hardly seems a sufficient basis to establish a new variety. The right P<sup>4</sup> has the hypocone attached only to the rear of the metaconule. This seems, at first glance, a very distinctive character, but with a little less wear it would appear as an isolated cusp, as in Cat. No. 12308, A.M.N.H., or, with a little more wear, every distinctive feature of the pattern would be obliterated. I do not feel that this variety can justifiably be established on this specimen; particularly in view of the character of Cat. No. 1051 (S), Colorado Museum, described below.

In Cat. No. 1051 (S), Colorado Museum, the median valleys of the right and the left P<sup>3-4</sup> open to the rear, as in *T. osborni osborni*. In the right P<sup>2</sup>, the transverse lophs are fully separate to below the level of the cingulum, so that the tooth

is molariform; in the left P<sup>2</sup>, the hypocone, although a definite cusp, is attached to the protocone, and there is a "wind-gap" between the hypocone and metacornule. The left premolars had previously been covered with matrix so that their character had not been observed. The P's have two lophs, the protolophs much lower than the metalophs and looping around against them. On the whole the left P<sup>2</sup> could best be referred to *T. osborni secundus*, while the right P<sup>2</sup> resembles *T. osborni* or *T. precopei*. It would, then, seem reasonable to regard *T. osborni secundus* as being merely an aggregation of the more primitive individuals of *T. osborni osborni*. The Colorado Museum specimens of this general category are: Cat. Nos. 884 (F), the type; 422 (B), referred by Gregory and Cook to *T. figginsi*; 876 (M); 880; 951 (I); and 1051 (S), all of which intergrade with *T. osborni osborni*.

### *Trigonias osborni precopei* Gregory and Cook Gregory and Cook, 1928, Pl. VIIA.

Synonymy: *Trigonias precopei* Gregory and Cook, and *Trigonias preoccidentalis* Gregory and Cook. The holotype is Cat. No. 414, D, Colorado Museum (Gregory and Cook, Pl. VIIA). This form can only stand as, at most, a progressive variety of *T. osborni*, rather than as a distinct species. The lophs of P<sup>2</sup> are fully separate, as in some individuals of *T. osborni osborni*. The metaconules of P<sup>2</sup> and P<sup>4</sup> are a little more closely attached to the protocone than in *T. osborni osborni*. These characters make it legitimate to regard this form as a progressive phase of *T. osborni*. The resemblance to *Subhyracodon copei* in premolar pattern, observed by Gregory and Cook, is unquestionable, but the interpretation of this resemblance is another matter. Certainly, this is the only known form, whether of *Trigonias* or of anything else, that seems even faintly plausible as an immediate ancestor of *Subhyracodon* in general and *S. copei* in particular. On the other hand, it is materially larger than the earlier species of *Subhyracodon*, and retains the full *Trigonias* complement of front teeth, whereas the Lower Oligocene species of *Subhyracodon* have already completely lost I<sup>1</sup> and C<sub>1</sub>, and frequently, C<sup>1</sup> also. The question whether *Trigonias osborni precopei* gave rise to *Subhyracodon copei* should be kept open until more data come to hand. I, personally, doubt that it did.

I am unable to regard *Trigonias preoccidentalis* Gregory and Cook (Gregory and Cook, Pl. VIB), based on Cat. No. 878, G, Colorado Museum, as a valid form. It seems to be a synonym of *T. osborni precopei*. The main differences are due to the greater amount of wear suffered by the type of *T. preoccidentalis*, for which, it seems to me, the authors do not allow sufficiently. If the type of *T. osborni precopei* were worn down, it would have an identical pattern. Cat. No. 1056, X, Colorado Museum, is just a shade less worn than Cat. No. 878, and shows exactly transitional patterns on the left P<sup>3</sup> and the right P<sup>4</sup> while the right P<sup>3</sup> and the left P<sup>4</sup> are identical with Cat. No. 878. Minor differences exist in size, in the attachment of the metaconule of P<sup>4</sup> to the protocone instead of to the hypocone, and in the partial interruption of the internal cingulum by the hypocone of P<sup>2</sup>, but they hardly seem to require taxonomic recognition. In any case, this is not the ancestor of *Subhyracodon occidentale*, as the name would suggest, since the derivation of the latter from *S. copei* is adequately demonstrated (Wood, 1927

and 1929a). The individuals referable to *T. osborni precopei* are: Colorado Museum Cat. Nos. 414 (D), the type of *precopei*; 1026; 1056 (X); and 878 (G), the type of *preoccidentalis*.

### *Trigonias taylori* Gregory and Cook

Gregory and Cook, 1928, Pls. II and VA.

The holotype is Cat. No. 1029 (K), Colorado Museum. Although the peculiarities of this skull may have been slightly accentuated by post-mortem crushing, this could only explain a minor part of its peculiar features. I should be tempted to consider this individual as an achondroplastic mutant, paralleling similar mutants observed in goldfish, bull-dogs, man, and the Austrian cave bears. It should be observed that it, as well as *T. wellsi* and *T. hypostylus*, are slightly less progressive, as to premolar metamorphosis, than the typical *T. osborni osborni*, and may have been derived from some slightly more primitive stage. *T. taylori* certainly deserves specific rank if it is regarded as a race, and not merely as an abnormal individual, since it is at once primitive in some features, and aberrant in others.

### *Trigonias hypostylus* Gregory and Cook

Gregory and Cook, 1928, Pl. VB

The holotype is Cat. No. 886, J, Colorado Museum. The chief specific character is the presence of hypostyles on  $P^2$  and  $P^4$  (Gregory and Cook, Pl. VB). The transverse lophs of  $P^2$ , though distinct, unite well above the cingulum, as in Cat. Nos. 1054 (V) and 881 (C), referred to this species. The hypostyles of  $P^2$  become confluent, after some wear, with the ectoloph; those of  $P^4$  are still very distinct from the ectoloph.  $LP^3$  has an accessory cusp between the metaconule and the protocone, occupying the posterior outlet of the median valley.

Skull C (Colorado Museum, Cat. No. 881), referred by Gregory and Cook to *T. osborni figginsi* (Pl. IVB), should be placed in *T. hypostylus*, chiefly because of its agreement with the type of the latter in the presence of hypostyles on  $P^2$  and  $P^4$ . The two are close to the same size, and, in any case, every one of these Colorado specimens is within the probable range of specific variation in size of every other specimen, and hence their size characters are not especially significant.  $P^2$  differs from the type in the fact that the protoloph trends more to the rear and is more closely connected to the metaloph. In  $P^2$ , the hypocone and metaconule are closer together and the hypostyle is a shade smaller than in the type. The hypostyle of the right  $P^4$  is a high conical cusp. That of the left  $P^4$  is crescentic, nearly connecting with the metastyle and metaconule, so that further wear would make it appear even more like a backwardly swinging metaconule than do  $P^2$ - $P^4$  of Cat. No. 1054, V, Colorado Museum. The right  $P^2$  has a small metaconule, the left  $P^2$  a tiny one.

The exact character of a third specimen, probably referable to *T. hypostylus*, Cat. No. 1054, V, Colorado Museum, is in doubt, due to extreme wear. Hypostyles may have been present on both  $P^2$ s and on left  $P^4$ , or these may have been metacristae, or this appearance may have been due to the metaconule looping around all the way to the rear. This last is the case on the right  $P^4$ , which certainly did not have a hypostyle.

Another individual suggesting intergradation between *T. osborni* and *T. hypostylus* is Cat. No. 1055, W, Colorado Museum. A hypostyle is present on the left P<sup>3</sup>. There are no hypostyles on the left P<sup>2</sup>, or the right P<sup>2-3</sup>. The left P<sup>4</sup> has what may be called either an accessory metaconule or a misplaced hypostyle.

*Trigonias hypostylus* is an ideal ancestor for *Trigonias wellsi* Wood. In view of the close general resemblance of *T. hypostylus* to *T. osborni*, and of the partly intergrading specimens described above, the two forms would appear to be closely related. On this basis, I now feel that I formerly gave *T. wellsi* somewhat too long a line of independent ancestry (Wood, 1927, fig. 1).

### *Trigonias cooki*, new species (figs. 3 and 4)

The holotype is Cat. No. 1053, U, Colorado Museum (figs. 3 and 4). The name is given in recognition of the work done on fossil rhinoceroses by Mr. Harold J. Cook. The cheek teeth are very advanced for a member of the genus *Trigonias*—even more advanced than *Trigonias gregoryi*, although not nearly as large as the latter. Its closest resemblances are with *T. gregoryi*, of which it may be considered a collateral ancestor. The skull has about average proportions for this material. Such crushing as occurred was dorso-ventral. The right and the left P<sup>1</sup>-M<sup>3</sup> are present, the premaxillaries and front teeth having been lost. P<sup>1</sup> is of normal type, with both transverse lophes looping to the rear, internally. P<sup>2</sup> and P<sup>3</sup> have parallel transverse lophes, fully formed, and separate down to the level of the cingulum. P<sup>2</sup> is very similar to P<sup>2</sup> of *T. gregoryi*, but P<sup>3</sup> is much more advanced so that this form seems to be barred from direct ancestry to *T. gregoryi*. The internal cingulum of P<sup>3</sup> is nearly interrupted by the protocone; the internal cingulum of P<sup>2</sup> is complete; that of P<sup>4</sup> is nearly interrupted by the hypocone. None of the cheek teeth have external cingula. M<sup>1-2</sup> have no internal cingula. M<sup>3</sup> has a poorly marked internal cingulum on the protocone, and a strong posterior cingulum rising externally into a small cuspule. A faint depression and swell mark the position of the lost posterior buttress. P<sup>4</sup> has an oval hypocone attached to the posterior flank of the protocone, and separated from the metaconule by a wide valley, so that the median valley opens widely to the rear. The right P<sup>4</sup> has the inner tip of the metaconule incipiently twinned. The median valleys of M<sup>2-3</sup> have wide "flood plains." The protocone of M<sup>1</sup> is well set off from the protoconule, both anteriorly and posteriorly. The protocone of M<sup>2</sup> is faintly defined anteriorly, and fairly well to the rear. That of M<sup>3</sup> is faintly defined to the rear, with only a bare trace anteriorly. The left M<sup>3</sup> has a small cuspule on the anterior cingulum, which is not represented on the right M<sup>3</sup>.

*Trigonias cooki*, new species, Cat. No. 1053, U, Colorado Museum

	Right mm.	Left mm.
Nasals to occipital crest.....	465	464
Across zygomas.....	241	
Occiput, above condyles.....	112.5	113
Between P <sup>2</sup> s.....	47.5	
Between M <sup>3</sup> s.....	58.0	
P <sup>1</sup> -M <sup>3</sup> .....	203.5	203.0
P <sup>2</sup> -M <sup>3</sup> .....	184	184

tion. The question as to just what taxonomic recognition should be given to the different strains has been answered in diametrically opposed fashion by Gregory and Cook, and by Matthew, without any serious difference of opinion as to the actual facts involved. I have taken a somewhat intermediate position, solely on the basis of convenience, and without any mystical views as to what constitutes a "real" species in paleontology. This view is expressed in diagrammatic form on the phylogenetic chart (fig. 1). One new species, *Trigonias cooki*, is described, and three other forms are reduced to synonymy.

2. Matthew (1931) apparently regards the genus *Trigonias* as ancestral to all other true rhinoceroses. This view seems unduly simplified. At the most, *Trigonias* may be directly ancestral to a very few European and to most American forms. Some of the evidence for this has already been published (Wood, 1927, 1929a, 1929b), and more will appear later. *Trigonias* is, however, the most primitive true rhinoceros which is fully documented.

3. Matthew's views as to the phylogeny of the rhinoceroses are interesting and suggestive, but they seem to be an over-simplification of the actual situation. In several respects, such as the miscellaneous and diverse group of European and American genera which he lumps as "*Caenopus*" (including *Epiaceratherium*!), he can hardly be correct. Discussion and criticism of his views in regard to the relationships of the later rhinoceroses is reserved for the future.

4. Stehlin has proved that the tusks of the European genus *Epiaceratherium* are not I<sup>1</sup> and I<sub>2</sub>, but are probably C<sub>1</sub>. The doubt which he apparently feels as to the identity of the tusks of the American rhinoceroses is definitely negated by the known *Trigonias* material. As the tusks of other true rhinoceroses are closely comparable morphologically with those of *Trigonias* and differ definitely from those of *Epiaceratherium*, the latter genus would seem to be the aberrant form. The *Epiaceratheriinae* should be considered a distinct subfamily, paralleling the *Amynodontidae* in their tusks, while remaining typically rhinocerotid in their cheek teeth and body structure.

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