New Material for the Study of Evolution

A Series of Primitive Rhinoceros Skulls (Trigonias) from the Lower Oligocene of Colorado

By

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INTRODUCTION

While engaged in the search for fossils in Weld County, Colorado, late in the summer of 1919, Messrs. Philip Reinheimer, Chief Preparator of the Department of Palaeontology, and H. D. Boyes located a promising fossil field. The following season, 1920, Director J. D. Figgins sent Messrs. Philip Reinheimer, Frank Howland and Harvey Markman on a prospecting trip in the same general region. Starting in near the Davis ranch, west of Pawnee Buttes, collecting was begun in that area; then camp was moved eastward and work finally resumed in the area above mentioned. While excavating was in progress here, a second fossiliferous deposit was located a short distance away, at a higher level. This proved to be an extraordinarily rich deposit, and one of the most important prehistoric bone-beds ever discovered.

Since that time parties from The Colorado Museum of Natural History have worked the deposit extensively but as yet its limits are not fully determined. It is certain, however, that it extends over a considerable area and fortunately is covered with a sufficient thickness of solid material to protect it from the effects of the elements, erosion, accidental damage and vandalism.

This deposit is in the Lower Chadron formation, which lies unconformably upon the oxidized surface of the Pierre shales, in the same relationship as is observed in the exposures of those formations around the south end of the Black Hills uplift in South Dakota and Nebraska. The evidence appears to be conclusive that the deposit was once the location of a mucky water-hole, or slough, since the matrix is devoid of grit and excavation reveals a clearly defined floor and abrupt margins. In this ancient mud-hole are assembled a great number of *Trigonias* skeletons, numerous others of Titanotheres (*Symborodon*) and Entelodonts (*Archaeotherium*), and a smaller representation of lesser creatures, including bird remains.[1] It is not unlikely that other skeletons will be uncovered as the work of excavating progresses. The rhinoceroses, however, far outnumber the other animals. The abundance of these Oligocene rhinoceroses is in fact comparable to the condition found in the early Miocene beds of the Agate Springs fossil quarries at Agate, Nebraska, and through the efforts of parties from The Colorado Museum of Natural History, a large collection of skulls is available for study.

All but one (or possibly two) of the rhinoceroses so far found in this ancient mud-hole appear to be referable to the genus *Trigonias*

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[1]Wetmore, Alexander. Fossil Birds from the Oligocene of Colorado. Proc. Colo. Mus. Nat. Hist. Vol. VII, No. 2, 1927.

Lucas, a relatively primitive true rhinoceros distinguished by the retention of a reduced canine tooth and three incisors in the upper jaw.

Very wide differences, not only in the form of the skull, length of the premaxillary rostrum, character of the incisors and canines, but specially in the patterns of the upper premolars, are found in the series of skulls already prepared. 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 paleontology, 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[1]: on the other hand, that extensive hybridism between formerly distinct races was actively going on. A study of the comparative measurements of the series reveals the fact that, with regard to certain measurements, the readings do not tend to conform to the symmetrical curve of fluctuating variations but that they tend to group themselves under two or more humps. Such conditions in anthropology are interpretated as indicating the presence in the population studied of more than a single fairly homogeneous race, in other words, the hybridism of widely different hereditary strains. While we thus incline to the hypothesis of extensive hybridism between originally distinct races, for the sake of convenience in describing and cataloguing 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.

The discovery of so large a number of closely related "species" in a single locality and horizon is unusual and a brief review of the geology of the region may be useful, as a means of accounting for such a condition. In eastern Weld County, Colorado, the Chadron represents the first stage of the series of non-marine deposits. Prior to that time, for an unknown period, slow denudation and erosion had been going on over an area east of the Rocky Mountains extending from Montana and the Dakotas to Colorado and Kansas, but we have no other record there of the great hiatus of time, and changes, between the close of the Pierre of the Cretaceous period and the Chadron. We do know, however, that there were large land areas a short distance to the west and probably to the north. Further, we know that mammalian life was abundant in those regions prior to Oligocene times. With the deposition of the Chadron clays and the consequent extension of suitable habitat, it is easily within the realm of probability to assume that extensions of ranges occurred. With these movements in progress, perhaps from more or less distant and previously isolated localities, animals relatively close in relationship but grown apart in divergent characters, might very readily have come in contact through scarcity of food, water, or other prob-

[1]Described especially by Osborn, Mem. Amer. Mus. Nat. Hist., 1898, and Wood, H. E. Some early Tertiary Rhinoceroses and Hyracodonts. 1927 Bulletins of American Paleontology, Ithaca, N. Y.

lomatical causes. Crossing in such an environment would be a logical expectation, but unfortunately the series so far recovered is hardly large enough to be examined for indications of Mendelian inheritance according to the methods of geneticists.

In studying the Colorado series of *Trigonias* we had the advantage of having before us the then unpublished manuscript of the article by H. E. Wood, 2nd, on "Some Early Tertiary Rhinoceroses and Hyracodonts"[1] which enabled us to compare our specimens with the various Oligocene species recognized as valid by him; for which courtesy we desire to express our appreciation and thanks.

We also desire to mention the fact that the highly important material noticed in the present communication has been discovered and made known through the scientific ardor of the Director, Mr. J. D. Figgins, backed by the liberality of Mr. S. N. Hicks, the patron of the expedition that discovered the great fossil quarry in Weld County.

The writers are indebted to Director J. D. Figgins for valuable suggestions, and to Mr. Harvey Markman for drawings of figures and charts, and for painstaking proof reading and checking of manuscript and data. Photographs by Mr. Albert C. Rogers.

Trigonias was established and described by Dr. F. A. Lucas[2] on material from the Lower *Titanotherium* beds in South Dakota, the type species being *T. osborni*. Later, in 1901, Dr. J. B. Hatcher[3] amplified this description. His definition of the genus is: "Dentition, I $^{3}/_{2}$, C $^{1}/_{1}$, P $^{4}/_{4}$, M $^{3}/_{3}$. None of the upper molars are strictly molariform. Skull much elongated and very large in comparison with the size of the skeleton. Manus tetradactyl." All of the complete skulls so far found in this quarry have this dental formula, of which of course the striking feature, in comparison with all later rhinoceroses, is the retention of the three incisors and the canine above, and only slightly greater reduction in the lower jaw. In all the numerous forefeet so far found in the Weld County quarry the manus is still tetradactyl and we have no reason to question at this time that this is the case in all *Trigonias* in that quarry. But it is in the development and construction of the premolars that we find the great diversity and divergence in type among the above-listed characters. This divergence runs all the way from a much more primitive construction than that found in *T. osborni* to complete molarization of all the premolars, advanced as far as the condition found in the Upper Oligocene forms of the genus *Caenopus*. A great diversity of type is also seen in many characters of the skull and jaws but it is the intention to limit the present notes and comparisons chiefly to the dentition.

RELATIONS OF THE DECIDUOUS AND PERMANENT TEETH. HOMOLOGIES OF THE ADULT INCISORS

The material available ranges from examples in which all of the milk teeth are present, with M¹/ barely functional, to dentitions representing advanced age. It is therefore useful in illustrating the succession of both the deciduous and permanent teeth. An item of much interest is the finding of evidence which proves that the prominent lower pro-

[1]Bulletin of American Paleontology, 1927. Ithaca, N. Y.

[2]Lucas, F. A. A New Rhinoceros, *Trigonias osborni*, from the Miocene of South Dakota. Proc. U. S. National Museum, XXIII, No. 1207.

[3]Hatcher, J. B. Some New and Little Known Fossil Vertebrates. Ann. Carnegie Museum, I, 1901.

cumbent tooth is the second incisor ($I/_2$). In a number of specimens a single alveolus is present back of the large incisor, as described by Lucas and Hatcher, but in a young example, No. 1027, two well-developed alveoli are present immediately back of $I/_2$, which in its permanent form had but lately appeared through the bone. Further, the size and position of these alveoli suggest that the tooth generally present is the vestigial canine and that the third lower incisor was the first to be lost by the Rhinocerotidæ. The second lower tooth to be lost, as their evolution proceeded, was the lower canine, and lastly $I\,^2/_1$, leaving $I\,^1/_2$ as the only survivors from the Miocene to Recent rhinoceroses. While the material is not sufficiently complete to warrant final conclusions regarding the order in which the upper incisors are obtained and lost, they consist of deciduous and permanent series, Di. $^2/_2$ being no larger in the juvenile stage than Di. $^1/_1$.[1]

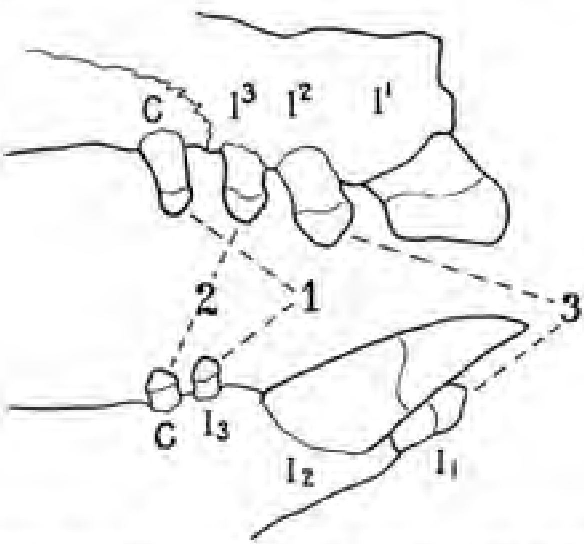


Fig. 1, illustrating the order in which the incisor and canine teeth are lost through evolutionary reduction in various species of *Trigonias* and *Caenopus*. 1, first tooth to be lost. 2, second tooth to be lost. 3, third tooth to be lost.

Not less interesting is the history of $P^1/$. This tooth varies greatly in size, form and development. In some instances it is large and distinctly triangular, or it may be quite elongated and slender. Again, it may be decidedly rounded. The convolutions of the cutting surface range from a primitive type to perfect molarization. The interest attached to this condition is emphasized in view of the evidence that this tooth is not replaced.

From both superficial appearances and dissections the milk teeth are acquired in the following order, reading left to right:

$$\frac{Dp.^3}{Dp._3},\ \frac{Dp.^2}{Dp._2},\ \frac{Dp.^4}{Dp._4},\ \frac{Dp.^1}{Dp._1}$$

[1]According to Wood (1927) in *Subhyracodon* I^3 is lost before C^1. Cf. also Osborn 1898.

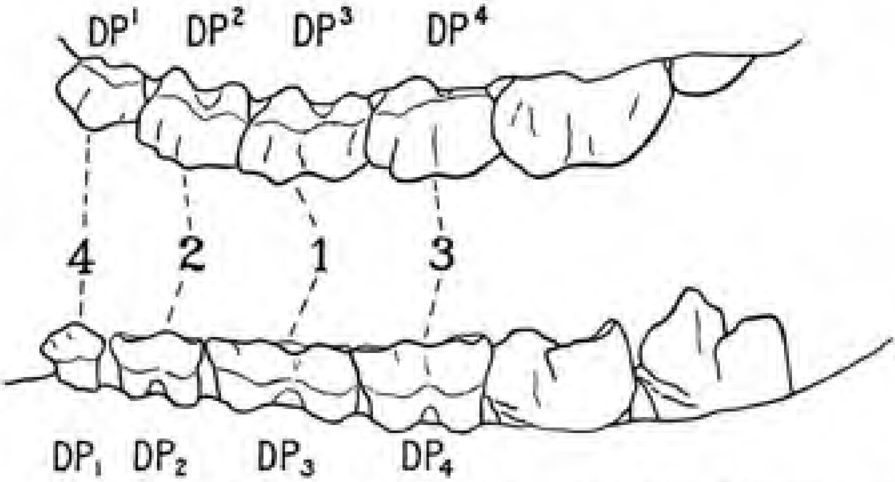


Fig. 2. Illustrating the order in which the deciduous dentition is cut in *Trigonias*, as determined from Colorado Museum of Natural History specimens. Dp^3 and Dp^2, and Dp^1 and Dp^4, are cut practically simultaneously, in pairs.

Not infrequently $P^1/$ is absent in skulls of advanced age. More often they are greatly reduced through wear but neither in varying ages nor through dissection is there revealed the slightest evidence of a second or "permanent" $P^1/$. Premolar $^1/$ then must apparently be considered in the light of a more or less permanent "milk" tooth and here it may be noted that it appears to be the rule that where $P^2/$ is molarized, $P^1/$ is also of that form, and the reverse, with a single exception in the case of *T. taylori*.

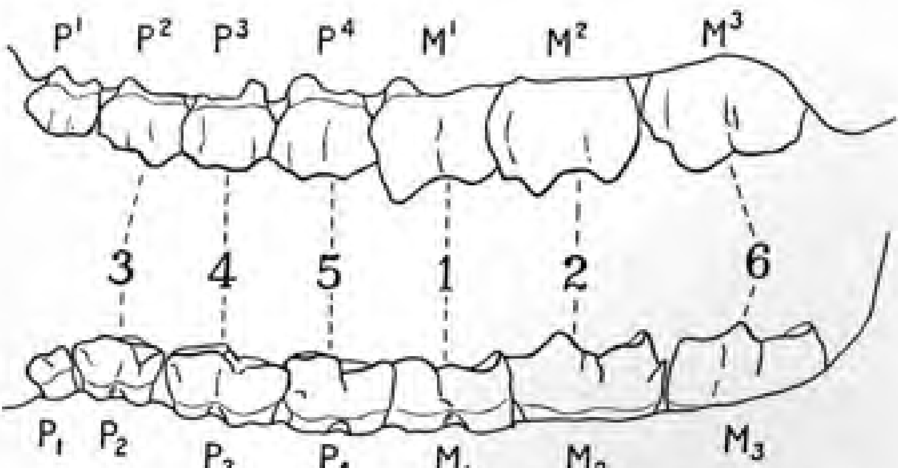


Fig. 3. Illustrating the order in which the permanent dentition is cut in *Trigonias*, as determined from Colorado Museum of Natural History specimens.

VARIATION IN UPPER PREMOLARS

The stages in the transformation of P²/ may be summarized as follows:

Stage 1. Skull F (884). (Plate III, A.) Protoloph of P²/ barely connected with anterointernal side of paracone. Tetartocone well developed, connected with deuterocone by narrow isthmus (left) or broadly (right). Central fossette not open medially. Metaloph incomplete, small, directed forward, not connected with tetartocone.

Stage 2. Skull H (897). (Plate III, B.) Protoloph of P²/ barely if at all connected with anterointernal side of paracone. Deuterocone broadly connected with tetartocone. Hence central fossette not open medially. Metaloph in middle of tooth directed backward, connected with tetartocone.

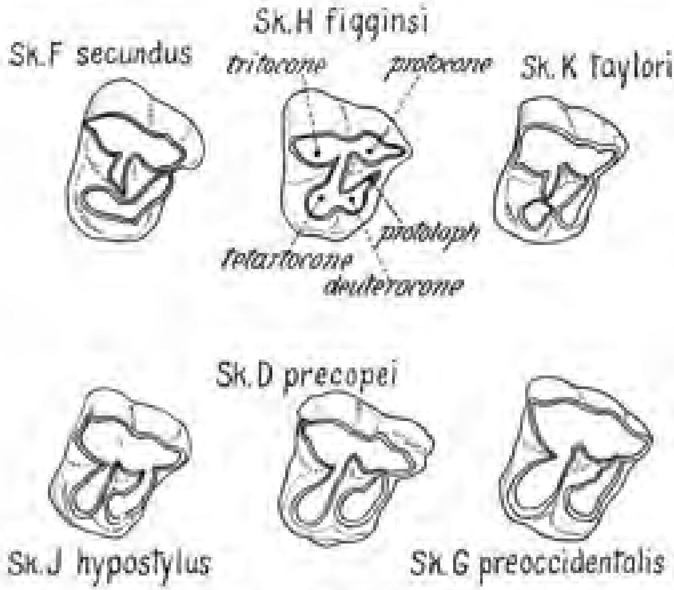


Fig. 4. Second right upper premolars of *Trigonias*, showing range of variations in crown patterns from premolariform to molariform.

Stage 3. Skull K (1029). (Plate V, A.) Protoloph of P²/ barely connected with anterointernal side of paracone. Tetartocone well developed (larger than deuterocone), nearly separated from deuterocone. Central fossette just opening medially. Metaloph small, incomplete, barely connected with the tetartocone, beginning to be directed backward.

Stage 4. Skull J (886). (Plate V, B.) Protoloph of P²/ well connected with anterointernal side of paracone. Tetartocone equal to (right) or larger than (left) deuterocone. Central fossette blocked medially by the slight contact between tetartocone and deuterocone. Metaloph complete, connected broadly with tetartocone, directed backward.

Stage 5. Skull D (414). (Plate VI, A.) Protoloph of P²/ well connected with anterointernal side of paracone. Tooth more elongate

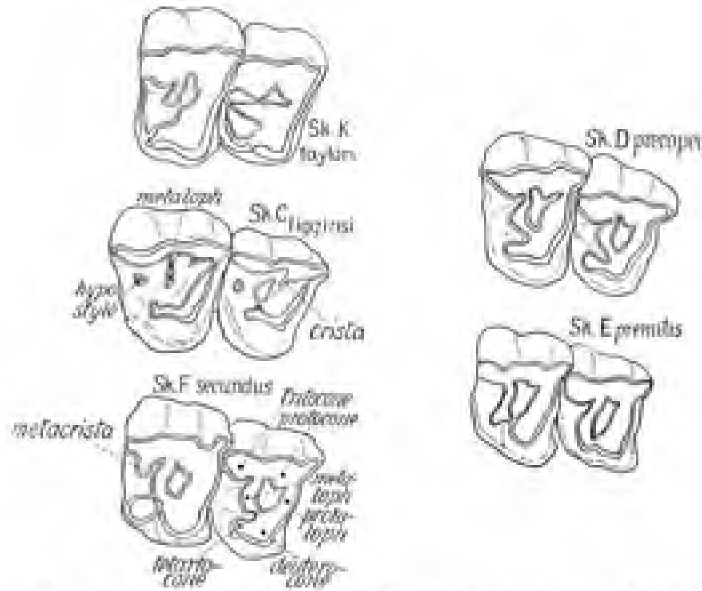


Fig. 5. Third and fourth upper premolars of *Trigonias* showing range of variation.

anteroposteriorly. Tetartocone large, separated from deuterocone. Central fossette valley opening medially by a narrow fissure. Metaloph complete, large, directed backward.

Stage 6. Skull G (878). (Plate VI, B.) Metaloph large, directed backward. Central fossette broadly (right) or narrowly (left) opening medially.

The third and fourth premolars show divergent stages in the process of transformation, from the very simple condition exemplified in *T.* "*secundus*" (Skull F), in which the metaloph is small and still connected with the deuterocone to the almost molariform P⁴/ of ? *C.* "*premitis*" (Skull E), and in the opposite direction to the abortive metaloph of *T. taylori* (Skull K).

The third and fourth premolars also reveal certain variable cusps as follows:

(A) Posterior crista: a loop from posterointernal base of metacone on P⁴/ of Skull *F*. Same but larger on P³/ of Skull J. (Plate V, B.)

(B) Hypostyle: located in posterior fossette, (a) connected with cingulum on left P⁴/ in Skull J, (b) free from cingulum on right.

(C) Tetartoconule: just external to small tetartocone on P³/ left, in Skull F. (Plate III, A.)

CONSPECTUS OF VARIANTS AND SPECIES

1. *Trigonias osborni* var. *figginsi*. Type, Skull H (897), Colo. Mus. Nat. Hist. (Plate III, B.) Pms. agree with skull B (below) except in the following characters:

(3a) Medifossette closed both medially and posteromedially;

(4) Metaloph $P^2/$ connected with tetartocone.

1a. *Trigonias osborni "figginsi."* Referred skull B (422).

(1) All premolars premolariform.
(2) Protoloph of $P^2/$ separated from ectoloph, protocone prominent.
(3) Tetartocone of $P^2/$ not separated from deuterocone; (3a) Medifossette closed medially, open posteromedially; (3b) Metaloph of $P^2/$ not, or imperfectly, molariform, connected with anterior base of tritocone.
(4) Metaloph of $P^2/$ separated from tetartocone.
(5) Metaloph (metaconule) of $P^3/$, $P^4/$, small or moderate.
(6) Metaloph (metaconule) of $P^3/$ separated from tetartocone.
(7) Metaloph (metaconule) of $P^3/$ separated from deuterocone.
(8) Metaloph (metaconule) of $P^4/$ separated from tetartocone.
(9) Metaloph (metaconule) of $P^4/$ separated from deuterocone.
(10) No hypostyle (= metacrista) on $P^3/$, $P^4/$.
(11) Internal cingulum broad or moderate on $P^2/$, $P^3/$, $P^4/$.
(12) Tetartocone of $P^4/$ moderately developed, united with deuterocone.
(13) Pmx. long.
(14) Upper incisors and canines well spaced.
(15) Skull long.
(16) Skull shallow vertically.
(17) Occiput inclined backward.
(18) Zygomata not pitching sharply downward.

1b. *Trigonias osborni "figginsi"* Referred skull C (881), Colo. Mus. Nat. Hist. (Plate IV, B.) Pms as in *figginsi* except in the following characters:

(3a) Medifossette closed both medially and posteromedially.
(3b) Metaloph of $P^2/$ submolariform.
(4) Metaloph of $P^2/$ joined to tetartocone.
(5) Metaloph of $P^3/$, $P^4/$, very small.
(10) Distinct "hypostyles" on $P^3/$, $P^4/$.
(2) Protoloph with poorly developed deuterocone.

2. *Trigonias osborni* var. *secundus.* Type, Skull F (884), Colo. Mus. Nat. Hist. (Plate III, A.) Pms. $^2/$, $^3/$, $^4/$ agree with *T. figginsi* except in the following characters:

(3) Tetartocone of $P^2/$ left, nearly separated from deuterocone; tetartocone of $P^2/$ right, broadly connected with deuterocone.

(3a) Medifossette of $P^2/$ left, nearly open medially by notch between tetartocone and deuterocone.

(7) Metaloph of $P^3/$ touching deuterocone.

(9) Metaloph of $P^4/$ touching deuterocone.

(10) Metacrista on $P^4/$ (right and left) (connected with medial base of tritocone and more correctly regarded as a "metacrista" than as a hypostyle).

The tetartocone on $P^4/$, appears to be further differentiated from the deuterocone than in *figginsi* type.

There is an extra cusp on $P^3/$ left, between the tetartocone and the posterior bend of the metaloph.

The dentition of *T. secundus* conforms closely to the measurements and pattern of *T. osborni*, but differs in the presence of a strongly developed metacrista. In premolar characters, it tends to connect *figginsi* and *taylori*. The *secundus* skull is much narrower than *figginsi* and much longer than *taylori*, and shows certain characters tending toward each of these forms.

3. *Trigonias hypostylus*. Type, Skull J (886), Colo. Mus. Nat. Hist. (Plate V, B.) Premolar characters as in *precopei* except:

(1) $P^2/$ slightly less molariform.

(3) Tetartocone of $P^2/$ barely separated from deuterocone; (3a) Medifossette barely opening medially through the narrow fissure between the tetartocone and the deuterocone.

(5) Metaloph of $P^2/$ forming a short, wide, projecting lobe medially.

(7) Metaloph of $P^3/$ separated from deuterocone.

(10) Very large hypostyle on $P^3/$, $P^4/$.

("near the line to *wellsi*". Wood.)

4. *Trigonias taylori*. Type, Skull K (1029), Colo. Mus. Nat. Hist. (Plate V, A.) Differs from *figginsi* in the following characters:

(2) Protoloph of $P^2/$ joining anteromedial base of protocone.

(3) Tetartocone of $P^2/$ nearly separated from deuterocone.

(3a) Medifossette of $P^2/$ beginning to open medially, through notch between deuterocone and tetartocone; (3a') Medifossette nearly closed posteromedially through slight junction of metaloph and tetartocone.

(3b) Metaloph of $P^2/$ submolariform.

(4) Metaloph of $P^2/$ touching tetartocone.

(5) Metaloph of $P^3/$, $P^4/$, very small, abortive.

(11) Internal cingulum reduced opposite deuterocone on $P^2/$, $P^3/$, $P^4/$.

(12) Tetartocone of $P^{3}/$, $P^{4}/$, abortive.

The most striking feature of the premolars is the abortive development of the metaloph and the equally poor development of the tetartocone on $P^{3}/$, $P^{4}/$.

(13) Pmx. very short.

(14) Upper incisors and canines large, crowded.

(15) Skull short and wide.

(16) Skull deep vertically.

(17) Occiput vertical.

(18) Zygomata pitching sharply downward.

5. *Trigonias precopei.* Type, Skull D (414), Colo. Mus. Nat. Hist (Plate VI, A.)

(1) $P^{2}/$ almost molariform.

(2) Protoloph of $P^{2}/$ joined to anteromedial base of protocone (paracone).

(3) Tetartocone of $P^{2}/$ completely separated from deuterocone; (3a) Medifossette open medially by cleft between tetartocone and deuterocone, closed posteromedially; (3b) Metaloph of $P^{2}/$ completely molariform, broadly connected with anteromedial base of tritocone.

(4) Metaloph of $P^{2}/$ broadly connected with large tetartocone.

(5) Metaloph of $P^{3}/$, $P^{4}/$, moderate.

(6) Metaloph of $P^{3}/$ separated from tetartocone.

(7) Metaloph of $P^{3}/$ touching deuterocone.

(8) Metaloph of $P^{4}/$ separated from tetartocone.

(9) Metaloph of $P^{4}/$ touching deuterocone on right P^{4}, separated on left $P^{4}/$.

(10) No hypostyle on $P^{3}/$, $P^{4}/$.

(11) Internal cingulum moderate on $P^{2}/$, $P^{3}/$, $P^{4}/$.

(12) Tetartocone of $P^{4}/$ moderately developed, united with deuterocone.

6. *Trigonias preoccidentalis.* Type, Skull G (878), Colo. Mus. Nat. Hist. (Plate VI, B.) Differs from *precopei* as follows:

(1) $P^{2}/$ fully molariform.

(3) Tetartocone of $P^{2}/$ widely (right) or narrowly (left) separated from deuterocone.

(5) Metaloph of $P^{3}/$ relatively large.

(6) Metaloph of $P^{3}/$ apparently joined to tetartocone.

(8) Metaloph of $P^{4}/$ joined to tetartocone.

(11) Internal cingulum reduced opposite tetartocone on $P^{2}/$, $P^{3}/$, $P^{4}/$.

T. preoccidentalis has the most advanced $P^{2}/$ of all of the Colorado Museum of Natural History series; its $P^{4}/$ is distinctly more advanced than in any of the other variants except "*premitis*."

7. ? *Cænopus premitis.* Type, Skull E (1025), Colo. Mus. Nat. Hist. (Plate IV, A.)

(1) P^2/ less molariform than in *T. precopei.*

(2) Protoloph of P^2/ broadly joined to the internal base of the protocone (= paracone).

(3) Tetartocone of P^2/ not completely separated from deuterocone; (3a) Medifossette closed medially; (3b) Metaloph of P^2/ incompletely molariform; broadly connected with anteromedial base of tritocone.

(4) Metaloph of P^2/ broadly connected with tetartocone.

(5) Metaloph of P^3/, P^4/, well developed.

(6) Metaloph of P^3/ joining tetartocone.

(7) Metaloph of P^3/ separated from deuterocone.

(8) Metaloph of P^4/ large, backwardly directed, broadly joined to tetartocone.

(9) Metaloph of P^4/ separated from deuterocone; (9a) Medifossette of P^4/ opening medially; (9b) Tritocone (metacone) rib on ectoloph very convex and prominent.

(10) No hypostyle.

(11) Internal cingulum reduced opposite tetartocone on P^2/, P^3/, P^4/.

(12) Tetartocone of P^4/ relatively large, barely touching deuterocone.

Remarks. ? *C. premitis* is relatively very advanced in P^4/, less so in P^2/.

Owing to the absence of the front of the maxillæ and the premaxillæ, it is impossible to say definitely that this skull is *not Cænopus.* However, it is extremely probable that if the premaxillæ were present, they would show the presence of the teeth which would place it in the genus *Trigonias.*

UPPER MOLARS

The molars of all variants so far found in the quarry are not strikingly different, but conform rather closely to one type of very simple teeth, with only slight complications started. This generally consists of a poorly developed antecrochet and in some cases the barest suggestion of the crochet. This condition is most noticeable in M^1/ and less so in M^2/. M^3/ in all cases consists of a simple ectoloph and protoloph. The metaloph of M^2/ tends to be shorter in *Trigonias* than in *Cænopus*, comparing the various described forms and those under study. This makes the transverse diameter at the protoloph in *Trigonias* noticeably greater than the transverse diameter of the same tooth through its metaloph; or more strictly at the paracone, whereas in *Cænopus* they are more nearly the same, making a quadrate tooth.

TRIGONIAS OSBORNI Lucas

T. OSBORNI var. FIGGINSI

Type, No. 897 (Skull H), Colorado Museum of Natural History. (Plates I, III, B.) A complete skull. All the permanent cheek teeth are in place and $M^3/$ is already well worn. The diagnostic characters of the premolars are given below. The molars conform to the *Trigonias* type.

Diagnostic Characters.—All premolars premolariform; $P^2/$ with small metaloph usually connected with well developed tetartocone; $P^3/$, $P^4/$ with small metaloph not connected with tetartocone; medifossette opening posteromesially; hypostyle present or absent on $P^2/$, $P^3/$, $P^4/$; $P^1/$ compressed, premolariform; $P^1/$-$M^3/$, 200-205 mm.; $P^1/$-$P^4/$, 90-95 mm.; $M^1/$-$M^3/$, 113-117 mm.; pmx. to occipital condyle, 465 mm.

The paratype, No. 422, Colorado Museum, is a nearly complete skull and lower jaws of an almost mature individual, with all permanent premolars present, but unworn. The second upper premolar is in position and slightly worn. $P^3/$ is fully developed and just coming into full wearing position. $P^4/$ was just pushing the last deciduous tooth out, the latter being removed from one side to show the pattern of the fully formed tooth below, which was nearly ready to become functional. The premolars of this form are more primitive than in any *Trigonias* yet found. They are extremely simple teeth, consisting of the usual ectoloph, a strongly developed protoloph, and a thin, short metaloph, merely suggestive of the development to follow, and situated almost centrally in the teeth. $P^2/$ has the tetartocone and deuterocone nearly equally developed and uniting in a strong crest, the protoloph. In $P^3/$ and $P^4/$ the protoloph is progressively less developed in the region of the tetartocone, with no indentation formed in the enamel to indicate the separation of the loph into two distinct cones, as had already developed in $P^2/$. The metaloph in these teeth is the least developed and most primitive of those found in any known Oligocene rhinoceros. A heavy cingulum extends in a curve around the inside of all three of these premolars, from one end of the ectoloph to the other, but no external cingulum is present.

The comparison (Table V) indicates that although in *figginsi* $M^1/$-$M^3/$ appears to be slightly shorter than in *T. osborni*, the remaining comparative measurements do not diverge sufficiently to warrant specific separation from the evidence of measurements alone. The definition of *T. osborni* adopted by Wood completely covers the characters of *figginsi* in the premolars and molars.

The supposed difference in the longer face of *T. osborni* may well rest on the marked distortion of Hatcher's neotype. According to Wood the nasal incision of *T. osborni* ends vertically above the posterior part of $P^3/$; the same is true in *figginsi* type. The supposed differences in the premolars may be due to the extreme old age of the neotype figured by Hatcher. Hence for the present we may regard *figginsi* as a variant of *T. osborni*.

Troxell has recently described (The American Journal of Science, Vol. II, July 1921) an Upper Oligocene species under the name of "*Cænopus platycephalus nanolophus*, subsp. nov.", a species which appears to be a direct successor to *figginsi*, and in the light of present evidence we are inclined to consider this as not in the *platycephalus* line of ascent, but in a parallel phylum and probably a good species with full specific value.

TRIGONIAS OSBORNI var. SECUNDUS

Type, No. 884 (Skull F), Colorado Museum of Natural History. (Plate III, A.) A nearly complete skull, with exception of occiput.

Diagnostic characters.—All premolars premolariform; $P^2/$ with small metaloph not, or barely, connected with tetartocone; $P^3/$, $P^4/$ with small metaloph touching deuterocone; hypostyle variable on $P^3/$, $P^4/$; $P^1/$ compressed, premolariform; $P^1/$ to $M^3/$, 180 mm.; $P^1/$ to $P^4/$, 82; $M^1/$ to $M^3/$, 103; pmx. to occipital condyle, 478.

Skull long and moderately slender, with long thin nasals and long premaxillæ, with posterior incisors relatively small, spread well apart, and nearly functionless. Zygomatic arches sloping, not square-shouldered. General proportions of skull much less brachycephalic and angular than in *T. taylori* and more nearly like the typical *T. osborni;* but its premolar characters tend to connect it with *taylori.* Though the occiput is largely restored, it was evidently narrow, and of the backward-sloping type.

TRIGONIAS HYPOSTYLUS, sp. nov.

Type, No. 886 (Skull J), Colo. Mus. Nat. Hist. (Plate V, B.) A complete skull, somewhat crushed, but not badly distorted. Skull broad and flattened, with relatively straight top. Occiput very low, short and reduced in size,—ending almost vertically or slightly anterior to back of condyles. Zygomatic arches wide and bow-shaped, in a sweeping curve. Nasals moderately long, ending above tip of premaxillæ. $I^2/$, $I^3/$ and canine small, well spaced and functionless.

Diagnostic Characters.—$P^2/$ submolariform, with large metaloph broadly connected with the large tetartocone; medifossette barely opening medially; $P^3/$, $P^4/$ with small metaloph, not, or but slightly connected with deuterocone; large hypostyles; $P^4/$ more molariform, with large metaloph broadly connected with large tetartocone and incipient protoloph-deuterocone, well separated from metaloph-tetartocone; $P^1/$ to $M^3/$, 181 mm.; $P^1/$ to $P^4/$, 84; $M^1/$ to $M^3/$, 102; pmx. to occipital condyle, 474.

T. hypostylus differs widely from the preceding species in the advanced characters of the premolars. In over-all measurements (Tables I, II) it approaches on the one hand, *T. osborni*, and on the other, *T. precopei*, but differs from the former in the advanced stage of $P^2/$ and in the strong development of the hypostyles; from the latter in detailed dimensions and in the less advanced stage of the premolars.

TRIGONIAS PRECOPEI, sp. nov.

Type, No. 414 (Skull D), Colo. Mus. Nat. Hist. (Plate VI, A.) A complete adult skull, lacking only the incisors and canines, for which alveoli are present.

Diagnostic Characters.—$P^2/$ submolariform; $P^3/$, $P^4/$, with moderate metaloph barely if at all connected with deuterocone; medifossette nearly or quite closed medially; no hypostyles; $P^1/$ apparently progressive; $P^1/$ to $M^3/$, 183; $P^1/$ to $P^4/$, 87; $M^1/$ to $M^3/$, 105; pmx. to occipital condyle, 451.

Premolar $^1/$ small, almost vestigial. $P^2/$ is completely molarized, with protoloph and metaloph equally and almost identically developed. In $P^3/$ the protoloph is strongly and heavily developed. The deuterocone is large and situated nearly centrally in relation to the anteroposterior diameter of the tooth, making the outline of the tooth more nearly trigonal than quadrate, as in $P^2/$. The tetartocone is connected with the deuterocone but is a nearly independent smaller cone, crowded into the posterointernal surface of the tooth, so that it interrupts the cingulum at that point. The metaloph is a thin angular crest, connected narrowly at its tip with the protoloph on the internal face of the deuterocone.

The construction of $P^4/$ is essentially the same as that of $P^3/$ but with smaller and less independently developed tetartocone. A strong cingulum is developed around the whole internal side of all these premolars. With the exception of $P^1/$, which appears to have a great deal of individual variation in *Trigonias*, in skulls otherwise very similar the premolar-molar dentition of this species is so nearly identical to that found in *Cænopus* (*Subhyracodon*) *copei*[1] that no one, seeing only these teeth, would hesitate a moment to call it that species. But when we reach the strongly developed canine and three functional incisors, we realize that we have a condition ideally typifying what might be expected in the direct ancestor of *Cænopus* (*Subhyracodon*) *copei*.

In certain respects this form recalls *T. osborni secundus*, the chief difference being the more progressive $P^3/$ and the absence of a metacrista on $P^4/$. An objection to its being truly ancestral to *Subhyracodon copei* lies in its larger size.

TRIGONIAS PREOCCIDENTALIS, sp. nov.

Type, No. 878, (Skull G). Colo. Mus. Nat. Hist. (Plate VI, B.) A complete adult skull lacking only the incisors and one canine, with entire premaxillæ and alveoli for missing teeth.

Diagnostic Characters.—$P^2/$ molariform; $P^3/$, $P^4/$ with larger metaloph, directed backward and connected with tetartocone; the latter still connected with deuterocone so as partly to block the medial exit of the medifossette; $P^1/$ very progressive with small distinct protoloph and large metaloph-tetartocone; $P^1/$ to $M^3/$, 208 mm.; $P^1/$ to $P^4/$, 95; $M^1/$ to $M^3/$, 117; pmx. to occipital condyle, 470.

The whole grinding series of teeth in this species, from $P^1/$ to $M^3/$, is so nearly identical with those of *Cænopus* (*Subhyracodon*) *occidentalis*, figured by Osborn in Fig. 5, Plate XIII, of his memoir on "The Extinct Rhinoceroses" (1898), that were only these teeth preserved in the specimen at hand, anyone would without hesitation refer them to that species. They are strikingly alike from one end of the series to the other. The most noticeable difference is that the molars are relatively larger than in *T. preoccidentalis* in relation to the premolars. But, as in the case of *T. precopei*, we find a great difference again in the front teeth, all three incisors and the canine being present, instead of only the first two incisors as is found in *C. occidentalis*. Again we have here the ideal ancestor of the Upper Oligocene tridactyl *C. occidentalis* in a tetradactyl Lower Oligocene *Trigonias*, so far as tooth characters may

[1]Osborn, H. F., 1898. The Extinct Rhinoceroses. Mem. Am. Mus. Nat. Hist., Vol. 1, Part III.

be concerned. As these have been considered dependable by all paleontologists, they are taken as a basis for the present differentiation and descriptions. When completely associated skeletal materials are prepared for study, comparison of them will prove illuminating to many problems, as preliminary examinations now make obvious. An objection to this species as being truly ancestral to *Subhyracodon occidentale* lies in its larger size.

TRIGONIAS TAYLORI, sp. nov.[1]

Type, No. 1029 (Skull K), Colo. Mus. Nat. Hist. (Plates II, V, A.) A complete skull and jaws of a fully adult animal, with teeth in advanced wear and premaxillae complete but with the first upper incisors absent.

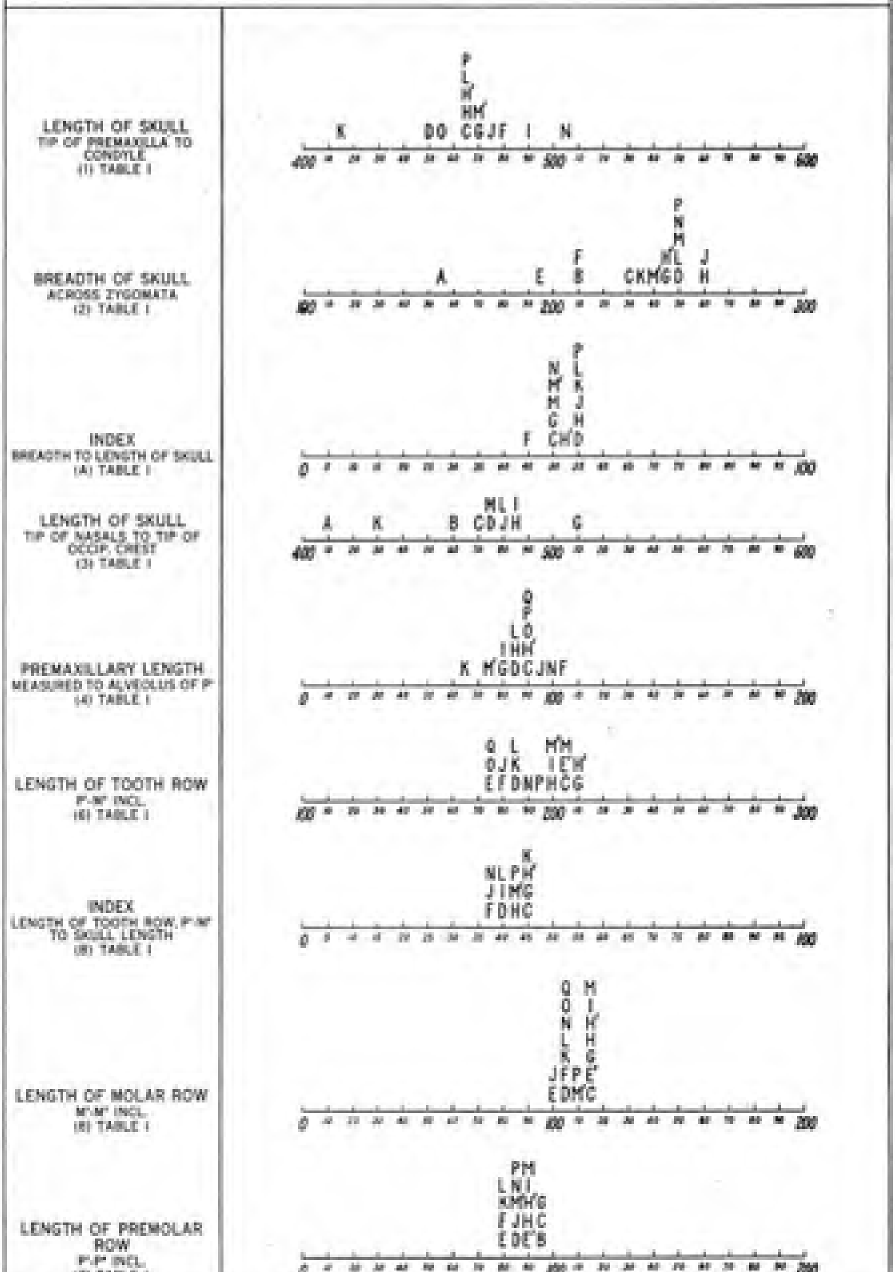
Diagnostic Characters.—$P^2/$ more or less transitional; with narrow metaloph just touching tetartocone; $P^3/$, $P^4/$, with abortive metaloph, widely separated from deuterocone and tetartocone, the latter small; hypostyle absent on all premolars; $P^2/$ very wide; $P^4/$ wider, but premolariform; $P^1/$ to $M^3/$, 185 mm.; $P^1/$ to $P^4/$, 80; $M^1/$ to $M^3/$, 107; pmx. to occipital condyle, 415.

In some ways this is the most remarkable skull so far found in the Weld County series. Unlike all other known *Trigonias* skulls, it is short, wide and deep, brachycephalic in type, with a number of marked peculiarities when compared with the other described forms, or with any skulls so far found. As we are limiting the discussion in this paper to a comparison of the teeth, only a few of the more striking features will be noted; but those given above as to the dental pattern, while different, would not in themselves suggest the degree of differences that actually exist. The general conformation of the skull is strongly suggestive of a type that could have led up readily to such a later development as we find in *Peraceras* in the late Miocene and Lower Pliocene. The back of the skull is very much elevated but the occiput ends *anterior* to the condyles, whereas in the other described species it extends backward, in most types to a very marked degree. The whole basi-cranial region is crowded and the external auditory meatus is nearly closed below; the wide and slender occipital condyles are, on the outside, slightly overlapped by the paroccipital processes of the exoccipital; these, in turn, by the postglenoid processes, which are peculiarly wide, angular and backward-sloping. The zygomatic arches have the same type of sharp elbow-angulation that is so marked in *Peraceras*. One of the most striking features is the development of a remarkable pair of heavy rugose knobs in the frontal over the orbits, quite unlike the rudimentary horn development in other known Oligocene Rhinocerotidae, either in position or in size. The nasals curve rather sharply downward, extending over a pair of rugged premaxillae, thick and short, with the three incisors and canines crowded together; all functional teeth, more comparable to the condition found in horses than in rhinoceroses! This crowding is so marked that $I^2/$ and $I^3/$ are both forced transversely in the jaw. The posterior edge of the second incisor turns outward, while the anterior edge of the third turns out. Unfortunately, the first upper incisor is absent on both sides, but from the alveoli it is obvious that they were relatively smaller than is usual in *Trigonias*. This, together with the

[1] Named in honor of Mr. Frank Mansfield Taylor, President of the Board of Trustees, Colo. Mus. Nat. Hist., Denver, Colo.

GRAPH 1. VARIABILITY OF SKULL MEASUREMENTS AND INDICES

RELATIVE INDIVIDUAL AGE OF SKULL INDICATED BY SEQUENCE OF LETTERS



Data taken from Table I (pp. 20-21).

See page 28 for explanation of graphs.

Key to principal skulls: (B) *T. osborni* var. *figginsi*; (C) *T. osborni* var. *figginsi*; (D) *T. precopei*; (E) ?*Caenopus premitis*; (F) *T. osborni* var. *secundus*; (G) *T. preoccidentalis*; (H) *T. osborni* var. *figginsi* type; (K) *T. taylori*.

larger size and with the presence of functional teeth behind it, points to a primitive condition, all of these teeth showing marked and heavy wear.

The zygomatic arches rise considerably above the top of the small braincase at their posterior tips. Premolar two nears complete molarization, with the deuterocone and tetartocone distinct; the metaloph still slightly more slender than the protoloph and just becoming connected with the tetartocone, a structural stage not shown in other types illustrated herewith. P²/ has the protoloph developed in a long heavy curve extending around the whole inner side of the tooth, broadly expanded at the deuterocone. There is no suggestion of the tetartocone and the wearing crest ends confluently with the cingulum on the posterior side of the tooth, near the middle, transversely. The ectoloph is wide and heavy and the metaloph very short but relatively wide. P³/ is almost identical in pattern to P²/ but very pinched and crowded and correlated with the excessively short face, so that its transverse diameter greatly exceeds the anteroposterior measurement. M¹/ is relatively small and crowded. The molar patterns are closely comparable to those of the other species.

The lower jaw is remarkably curved and heavy and the coronoid process actually curved forward over the molars at an angle of 15 degrees, a character correlated with the extremely brachycephalic skull. The incisors, both upper and lower, and the canines in this skull are much heavier than represented in the other types described.

? CÆNOPUS PREMITIS, sp. nov.

Type, No. 1025 (Skull E), Colo. Mus. Nat. Hist. (Plate IV, A.)

Diagnostic Characters.—P²/ submolariform but with large metaloph partly directed forward and connected through tetartocone with deuterocone; P³/ submolariform, much as in P²/; P⁴/ very progressive with well formed, backwardly directed metaloph-tetartocone and anteroposteriorly elongate ectoloph; no hypostyles; P¹/ wide, apparently progressive; size extremely small: P¹/ to M³/, 175 mm.; P¹/ to P⁴/, 80; M¹/ to M³/, 98.

This skull has the most advanced molarization of the premolars so far found in any *Trigonias*. In characters they are very close to *Cænopus mitis* and the type is the smallest form yet found of *Trigonias*, as well as the most advanced. The grinding teeth are of far more uniform size than in any of the other *Trigonias* types with which we have to deal from this quarry, all of the others so far found, regardless of type or structure of teeth, having noticeably large molars and premolars that taper in size more rapidly from the molars forward. In this type the protoloph and metaloph are of nearly equal size and are parallel in P²/ but connected between the deuterocone and tetartocone. The same description holds for P³/, save that the metaloph is slightly reduced in size but almost independent from and parallel to the protoloph. The difference between the teeth of *Cænopus premitis* and those of its successor in the genus *Cænopus*, after which it is named, is again very slight and, as in the cases of the last two described species, larger differences are apparent in the skulls of all these forms. As with *T. precopei* and *T. preoccidentalis* this species is larger than its supposed successor (Wood).

TABLE I

COMPARATIVE MEASUREMENTS OF THE COLORADO MUSEUM SERIES OF *TRIGONIAS* SKULLS[1]

		1027 (A)	897 (H) *T. osborni* var. *figginsi* type	422 (B) *T. osborni* var. *figginsi*	881 (C) *T. osborni* var. *figginsi* (?)	951 (I) *T. osborni* var. *figginsi* ref'd	876 (M) *T. osborni* var. *figginsi* ref'd
(1)	Length of skull, premaxilla to condyle incl.		465		463	488	
(2)	Breadth of skull across zygomata	157	258	208	228		248
(A)	Index of breadth, $\frac{\text{breadth} \times 100}{\text{length}}$		55		49		
(3)	Length, tip nasals to tip occipital crest	410	483	460	470	485	477
(4)	Premaxillary length, measured to alveolus of P^1		85		92	80	
(5)	Premaxilla, length, to canine suture		51		49	47	
	P^2-M^3 est.		178		185	180	184
(6)	P^1-M^3		200		205	201	205
(B)	Index $\frac{P^1\text{-}M^3 \times 100}{\text{pmx.-cond.}}$		43		44	41	
(7)	P^1-P^4		90	93	95	91	90
	P^2-P^4 est.		68		75	79	69
(8)	M^1-M^3		113		117	115	117
(C)	Index $\frac{P^1\text{-}P^4 \times 100}{M^1\text{-}M^3}$		79		81	79	77
(9)	P^1 a.p. (antero-posterior)	21	22	18	20	21	21
(10)	P^1 tr. (transverse)	16	18	15	19	15	19
(D)	P^1 index $\frac{\text{tr.} \times 100}{\text{a. p.}}$	76	81	83	95	71	90
(11)	P^2 a. p.		20	20	19	20	20
(12)	P^2 tr.		28	27	27	29	32
(E)	P^2 ind. $\frac{\text{tr.} \times 100}{\text{a. p.}}$		140	135	142	145	160
(13)	P^3 a. p.		23	22	23	23	22
(14)	P^3 tr.		37	32	34	35	39
(F)	P^3 ind. $\frac{\text{tr.} \times 100}{\text{a. p.}}$		160	145	148	152	177
(15)	P^4 a. p.		25	25	25	25	26
(16)	P^4 tr.		41	37	36	38	45
(G)	P^4 ind. $\frac{\text{tr.} \times 100}{\text{a. p.}}$		164	148	144	152	173
(17)	M^1 a. p.	37	34	31	35	30	33
(18)	M^1 tr.	43	44	39	44	40	50
(H)	M^1 ind. $\frac{\text{tr.} \times 100}{\text{a. p.}}$	116	129	125	125	133	151
(19)	M^2 a. p.		41	35	33	40	41
(20)	M^2 tr.		50	45	49	48	{r 53 / l 51}
(I)	M^2 ind. $\frac{\text{tr.} \times 100}{\text{a. p.}}$		122	128	129	120	129r
(21)	M^3 a. p.		38		37	41	42
(22)	M^3 tr.		49		44	46	48
(J)	M^3 ind. $\frac{\text{tr.} \times 100}{\text{a. p.}}$		129		119	112	114

	888 (E')	892 (H')	878 (G) *T. precoccidentalis*	879 (P)	420 (M')	882 (N)	884 (F) *T. osborni* var. *secundus*	1024 (L)	1029 (K) *Trigonias taylori*	886 (J) *T. hypostylus*	414 (D) *T. precopei*	953 (O)	880 (Q)	1025 (E) ? *C. premitis*
(1)		466	470	465	470	504	478	463	415	474	451	453		
(2)		244	243	252	239	248	210	249	234	262	251			196
(A)		52	51	54	51	49	44	54	56	55	55			
(3)			510					480	430	479	475			
(4)		88	80	88	76	98	105	85	65	95	84	88	90	
(5)			50	50			49	39	45	54	43	53	44	
P^2-M^3 est.			186	180	179		161	168	168	162				159
(6)	206	210	208	197	198	191	180	185	185	181	183	173	177	175
(B)		45	44	42	42	38	38	40	44	38	40			
(7)	92	92	95	85	87	84	82	80	80	84	87			80
P^2-P^4 est.							63		64	62				
(8)	117	115	117	109	111	104	103	107	107	102	105	107	105	98
(C)	78	80	81	78	78	80	79	75	75	82	83	67	66	81
(9)			22	19	17		19	17	17	19				16
(10)			15	17	16			15	16	15				15
(D)			68	89	94			88	94	79				93
(11)	20	20	21	18	17	20	18	18	19	20	18	17	18	17
(12)	29	32	30	30	28	29	30	27	28	21	28		25	26
(E)	145	160	143	167	165	145	166	150	147	105	155		139	153
(13)	21	23	26	21	22	21	21	20	22	21	21	20	19	20
(14)	36	38	38	35	34	35	35	35	35	35	36	33	31	31
(F)	171	165	146	167	155	167	167	175	159	166	171	165	163	155
(15)	22	25	22	24	23	22	24	23	21	23	23	22	21	23
(16)	39	41	40	41	41	38	38	40	39	38	42	37	37	35
(G)	177	164	181	171	178	173	158	174	185	165	182	161	176	152
(17)	35	37	34	34	34	28	31	31	37	33	30	30	35	30
(18)	43	44	49	45	44	44	41	44	47	40	43	43	41	36
(H)	122	119	144	132	129	157	132	142	127	121	143	143	117	120
(19)	39	40	41	33	36	38	37	38	39	36	38	37	38	34
(20)	52	52	54	52	48	47	45	50	50	45	49	50	42	39
(I)	133	130	131	157	133	123	121	131	128	125	129	135	110	114
(21)	40	41	40	37	40	36	35	47	48	34	34	34	35	31
(22)	46	47	49	44	46	45	41	44	48	45	43	46	43	38
(J)	115	114	122	119	115	125	117	94	109	132	126	135	123	122

[1]The sequence of capital letters, (A) to (Q), indicates the relative individual ages as indicated by the degrees of wear of the cheek teeth.

SUMMARY

The wide variation in premolar patterns and in measurements among the Colorado Museum of Natural History series of *Trigonias* indicates that at the time of deposition of the Titanotherium beds in the Weld County locality there were already at least seven definable stages of premolar evolution:

(1) *Trigonias osborni* var. *figginsi* (Skulls H, C, B): all premolars premolariform; $P^2/$ with small metaloph usually connected with well developed tetartocone; $P^3/$, $P^4/$ with small metaloph not connected with tetartocone; medifossette opening posteromedially; hypostyle present or absent on $P^2/$, $P^3/$, $P^4/$; $P^1/$ compressed, premolariform; $P^1/$ to $M^3/$, 200-205 mm.; $P^1/$ to $P^4/$, 90-95 mm.; $M^1/$ to $M^3/$, 113-117; pmx. to occipital condyle, 465.

(2) *Trigonias osborni* var. *secundus* (Skull F): all premolars premolariform; $P^2/$ with small metaloph not or barely connected with tetartocone; $P^3/$, $P^4/$ with small metaloph touching deuterocone; hypostyle variable on $P^3/$, $P^4/$; $P^1/$ compressed, premolariform; $P^1/$ to $M^3/$, 180 mm.; $P^1/$ to $P^4/$, 82; $M^1/$ to $M^3/$, 103; pmx. to occipital condyle, 478.

(3) *Trigonias hypostylus* (Skull J): $P^2/$ submolariform, with large metaloph broadly connected with the large tetartocone, medifossette barely opening medially; $P^3/$, $P^4/$, with small metaloph, not or but slightly connected with deuterocone; large hypostyles; $P^1/$ more molariform, with large metaloph broadly connected with large tetartocone and incipient protoloph-deuterocone, well separated from metaloph-tetartocone; $P^1/$ to $M^3/$, 181; $P^1/$ to $P^4/$, 84; $M^1/$ to $M^3/$, 102; pmx. to occipital condyle, 474.

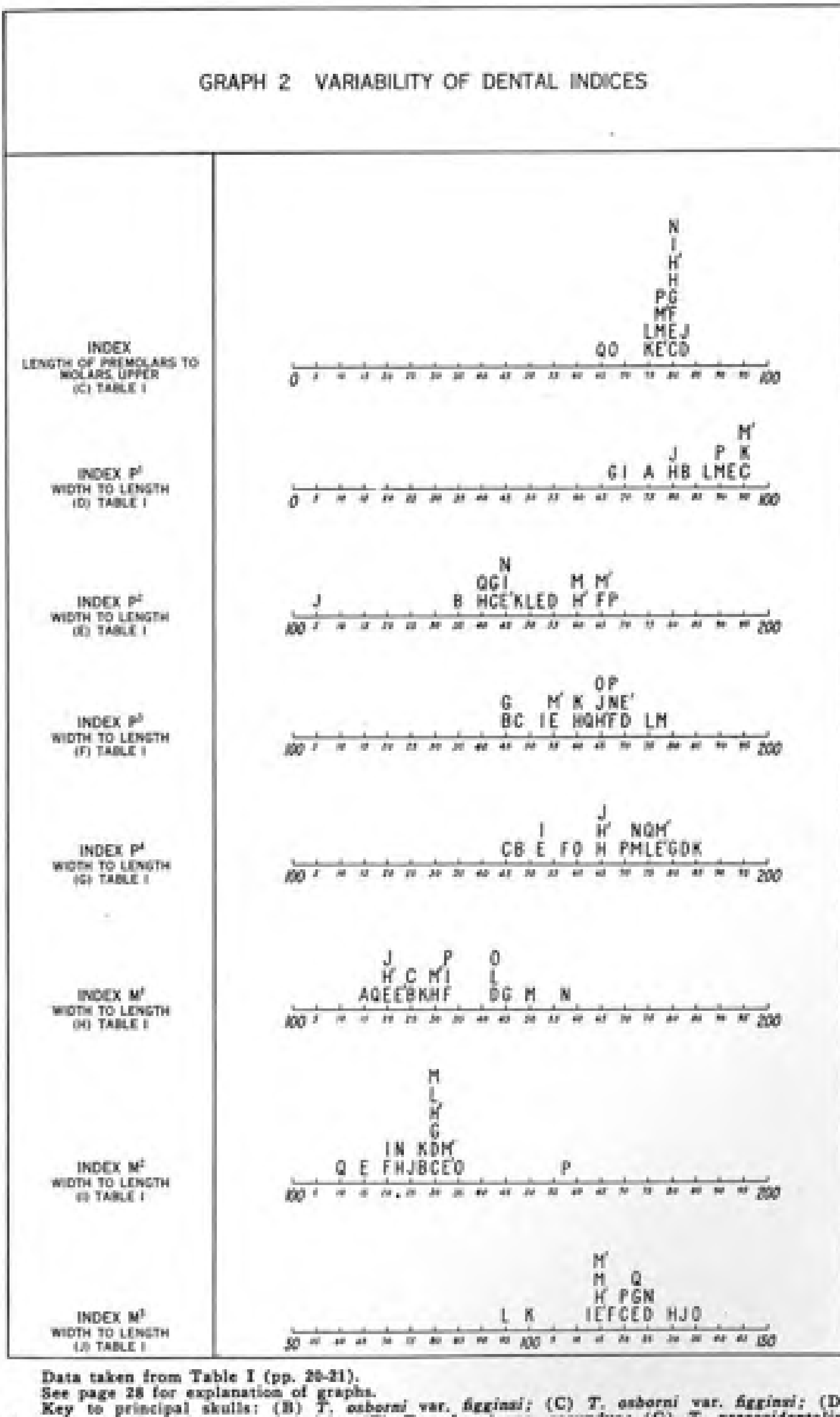
(4) *Trigonias precopei* (Skull D): $P^2/$ submolariform; $P^3/$, $P^4/$ with moderate metaloph barely if at all connected with deuterocone; medifossette nearly or quite closed medially; no hypostyles; $P^1/$ apparently progressive; $P^1/$ to $M^3/$, 183 mm.; $P^1/$ to $P^4/$, 87; $M^1/$ to $M^3/$, 105; pmx. to occipital condyle, 451.

(5) *Trigonias preoccidentalis* (Skull G): $P^2/$ molariform; $P^3/$, $P^4/$, with larger metaloph, directed backward and connected with tetartocone; the latter still connected with deuterocone so as partly to block the medial exit of the medifossette; $P^1/$ very progressive with small distinct protoloph and large metaloph-tetartocone; $P^1/$ to $M^3/$, 208; $P^1/$ to $P^4/$, 95; $M^1/$ to $M^3/$, 117; pmx. to occipital condyle, 470.

(6) *Trigonias taylori* (Skull K): $P^2/$ more or less transitional; with narrow metaloph just touching tetartocone; $P^3/$, $P^4/$, with abortive metaloph, widely separated from deuterocone and tetartocone, the latter small; hypostyle absent on all premolars; $P^4/$ very wide; $P^1/$ wider but premolariform; $P^1/$ to $M^3/$, 185 mm.; $P^1/$ to $P^4/$, 80; $M^1/$ to $M^3/$, 107; pmx. to occipital condyle, 415.

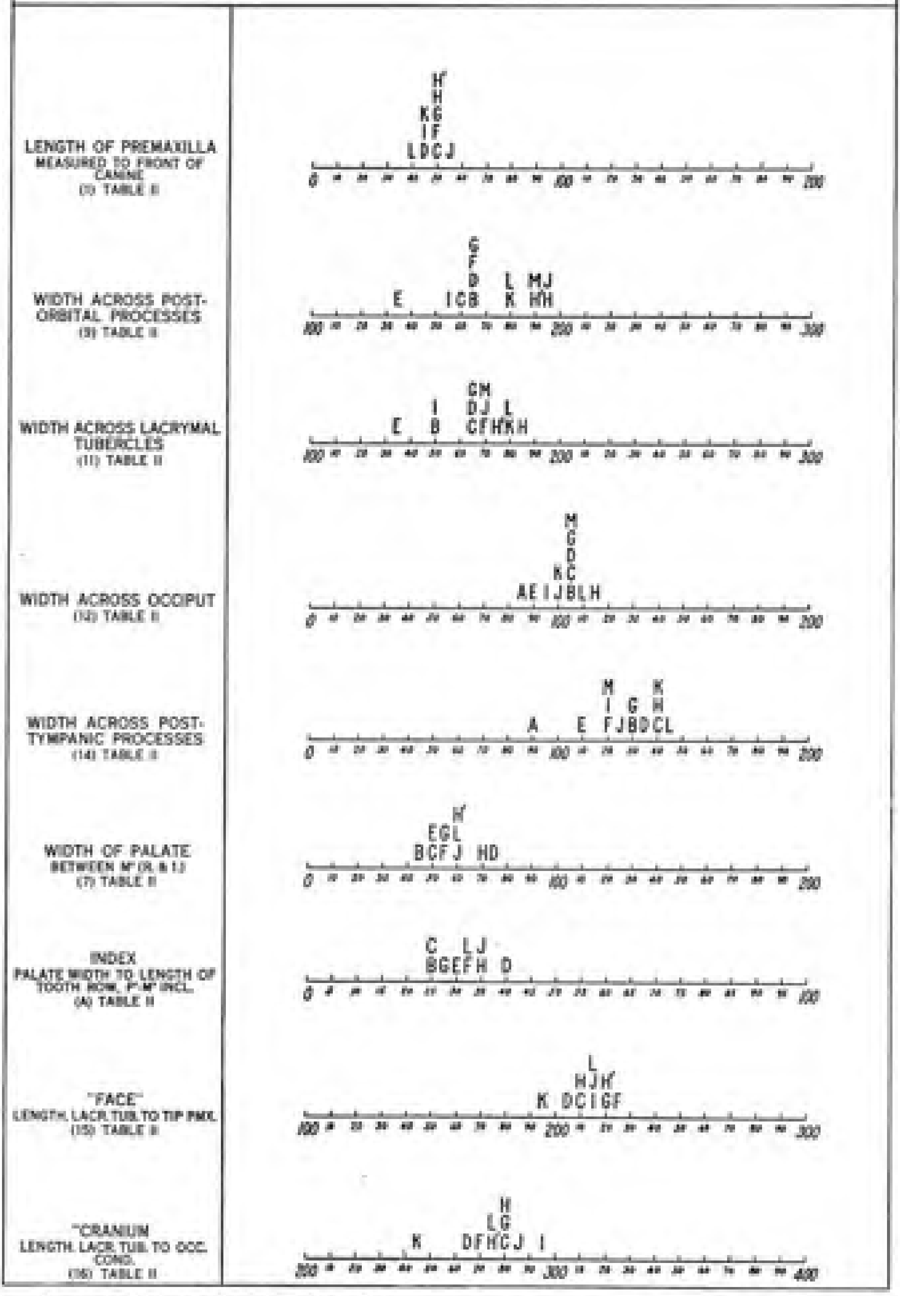
(7) ? *Caenopus premitis* (Skull E): $P^2/$ submolariform, but with large metaloph partly directed forward and connected through tetartocone with deuterocone; $P^3/$ submolariform, much as in $P^2/$; $P^4/$ very progressive with well formed, backwardly directed metaloph-tetartocone and anteroposteriorly elongate ectoloph; no hypostyles; $P^1/$ wide.

(Continued on page 28)



Data taken from Table I (pp. 20-21).
See page 28 for explanation of graphs.
Key to principal skulls: (B) *T. osborni* var. *figginsi*; (C) *T. osborni* var. *figginsi*; (D) *T. precopei*; (E) *?Caenopus premitis*; (F) *T. osborni* var. *secundus*; (G) *T. preoccidentalis*; (H) *T. osborni* var. *figginsi* type; (K) *T. taylori*.

GRAPH 3. FREQUENCY CURVES OF PRINCIPAL MEASUREMENTS OF TABLE II



See page 28 for explanation of graphs.

Key to principal skulls: (B) *T. osborni* var. *figginsi;* (C) *T. osborni* var. *figginsi;* (D) *T. precopei;* (E) ?*Caenopus premitis;* (F) *T. osborni* var. *secundus;* (G) *T. preoccidentalis;* (H) *T. osborni* var. *figginsi* type; (K) *T. taylori.*

TABLE II

COMPARATIVE MEASUREMENTS OF THE COLORADO MUSEUM SERIES OF *TRIGONIAS* SKULLS

		1027 (A)	887 (H) *T. osborni* var. *figginsi* type	422 (B) *T. osborni* var. *figginsi*	881 (C) *T. osborni* var. *figginsi* (?)	851 (I) *T. osborni* var. *figginsi* ref'd.	876 (M) *T. osborni* var. *figginsi* ref'd.	892 (H')	878 (G) *T. preoccidentalis*	884 (F) *T. osborni* var. *secundus*	1024 (L)	1029 (K) *T. taylori*	886 (J) *T. hypostylus*	414 (D) *T. precopei*	1026 (E) ? *C. premitis*
(1)	Length of premaxilla, to front of canine		51		49	47		49	50	49	39	45	54	43	
(2)	Length of diastema, canine to P^2		29	33	41	25		21	23	37	35	21	35	38	
(3)	Diastema, canine to I^1		6		0	1		3	5	4	4	0	7	4	
(4)	Diastema, I^1 to I^2		3		0	2		2	0	3	1	0	4	0	
(5)	Diastema, I^2 to I^3		5		0	2		5	3	2	1	0	2	0	
(6)	Canine, relative size		large	small	very large	int.		int.	small	small	small	very large	minute	large	
(7)	Width of palate between M^1 (r. & l.)		70	45	50	cr.	cr.	61	57	57	62	cr.	62	73	52
(A)	Index:[1] palate width × 100 / length, P^2 to M^3		35	24	24				27	32	33		34	40	30
(8)	Length of skull, tip nasals to tip occipital crest	410	483	460	470	485	477		510		480	430	479	475	
(9)	Width across postorbital processes	Im.	195	163	161	155	191	191	164	165	178	178	195	167	137
(B)	Index:[2] width across postorb. pr. × 100 / length, tip. nas. to tip. occ.	Im.	40	35	34	32	40		32		37	41	41	35	
(10)	Width across zygomata	157	258	208	228	cr.	248	244	243	210	249	234	262	251	196
(11)	Width across lacrymal tubercles		183	148	163	151	170	175	166	168	178	180	170	167	137
(12)	Width across occiput	85	116	103	103	96	102		104		112	100	102	103	89
(13)	Height, condyles to occip. crest	133	130	134	130	153	129		134		135	142	121	125	113
(14)	Width across post-tympanic processes	91	140	132	140	122	119		130	118	146	139	124	135	109
(C)	Index:[3] width occ. × 100 / height occ.	48	89	76	74	55	66		67		82	73	67	86	69
(15)	"Face"—lacr. tub. to tip. pmx.		209		210	217		221	220	225	217	195	217	203	
(16)	"Cranium"—lacr. tub. to occ. cond.		280		280	293		272	282	272	275	243	285	267	
(D)	Index:[4] face length × 100 / cran. length		75		75	74		81	78	83	79	80	76	76	
(17)	Lacrymal tubercles, above M^2		85						72			90	72		45
(18)	Lacrymal tubercles, above M^3			58	69	75	72			77	77			62	

[1]Percentage of palate width to palate length; width measured between M^1/; length, from P^2/ to M^3/ inclusive.

[2]Percentage of width to length of skull; width measured across postorbital processes; length, from tip of nasal to tip of occipital crest.

[3]Percentage of width of occipital crest to its height; width measured at narrowest point below flare of crest; height, from base of condyles to highest point.

[4]Percentage of "facial" length to "cranial" length; "face" measured from lachrymal tubercles to tip of premaxilia; "cranium", from lachrymal tubercles to occipital condyles.

GRAPH 4. FREQUENCY CURVES OF PREMOLAR CHARACTERS

(SEE TABLES III AND IV)

Character			
P^4 METALOPH	E′ I N U D H′ M′ T C H K R W B F J Q V (18) FREE FROM TETARTOCONE	S L (2) INTERMEDIATE	O NEOTYPE (HATCHER'S) G E X (4) JOINED TO TETARTOCONE
P^3 METALOPH	H K S E′ J R W C I Q V B H′ M′ T (15) FREE FROM TETARTOCONE	F D (2) INTERMEDIATE	L O NEOTYPE G N X E M U (8) JOINED TO TETARTOCONE
P^2 METALOPH	E′ J N S X E H′ M′ R V D H L Q U C G K O T (20) COMPLETE MOLARIFORM	I (1) INTERMEDIATE	M NEOTYPE F B W (4) NOT MOLARIFORM
P^3 (GENERAL)	H F U C W B S (7) ELONGATE PREMOLARIFORM	K T J R I M′ G M (8) INTERMEDIATE	V L E (3) SHORT SUBMOLARIFORM
P^4 HYPOSTYLE	W V J C (4) PRESENT	INCIPIENT	E′ I M′ S E H′ M R X D H L Q U B G K N T (19) ABSENT
P^3 HYPOSTYLE	W V J C (4) PRESENT	INCIPIENT	E′ K N T E I M′ S D H′ M R X B H L O U Q (19) ABSENT
P^2 HYPOSTYLE	V (1) PRESENT	INCIPIENT	E′ H′ M R W E H L Q U C G J N T B F I M′ S X (21) ABSENT
P^4 INTERNAL CINGULUM	F J N S W D H′ M′ R V C H M Q U B G J O T X (21) STRONG	E′ (1) INTERMEDIATE	K E (2) ABSENT OPPOSITE PROJECTING DEUTEROCONE
P^3 INTERNAL CINGULUM	F I N T D H′ M′ S X C H M R W B G J O V (19) STRONG	E′ (1) INTERMEDIATE	Q L K E U (5) NEARLY ABSENT OPPOSITE PROJECTING DEUTEROCONE
P^4 TETARTOCONE	M′ K E′ U B T (6) SMALL	H′ Q H N D M C I S (9) INTERMEDIATE	J G X F V E O (7) LARGE
P^2 TETARTOCONE	L (1) < DEUTEROCONE	H′ N W F M T E K R B I O (12) = DEUTEROCONE	G Q X E′ M′ V D J U C H S (12) > DEUTEROCONE

See page 28 for explanation of graphs.

Key to principal skulls: (B) *T. osborni* var. *figginsi*; (C) *T. osborni* var. *figginsi*; (D) *T. precopei*; (E) ?*Caenopus premitis*; (F) *T. osborni* var. *secundus*; (G) *T. preoccidentalis*; (H) *T. osborni* var. *figginsi* type; (K) *T. taylori*.

TABLE III

VARIATIONS IN PREMOLAR AND MOLAR CHARACTERS

	897 (H) T. osborni var. figginsi type	422 (B) T. osborni var. figginsi type	881 (C) T. osborni var. figginsi (?)	951 (I) T. osborni var. figginsi ref'd	870 (M) T. osborni var. figginsi ref'd	888 (E')	892 (H')	878 (G) T. precoci-dentalis	420 (M')	882 (N)	884 (F) T. osborni var. secundus	1024 (L)	1029 (K) Trigonias taylori	886 (J) T. hypostylus	414 (D) T. precopei	953 (O)	880 (Q)	1025 (E) ?C. premitis	1050 (R)	1051 (S)	1052 (T)	1053 (U)	1054 (V)	1055 (W)	1056 (X)
P4																									
Metaloph free from tetartocone	√	√	√	√	?	√	√		√	√	√		√	√	√		√		√		√	√	√	√	
Metaloph joined to tetartocone								√								√		√							√
Metaloph intermediate												√								√					
Incipient crista		O	√	√		O	√		√	O		O	O	√	√	√	O	O	O	O	O	√	√	O	O
Hypostyle present			√								?			√		?							√	√	
Hypostyle absent	√	√		√	√	√	√	√	√	√		√	√		√		√	√	√	√	√	√			√
Antecrochet on protoloph		O		√		O	O		√	?			O	√		?	O		O	O	O	O	O	O	O
Internal cingulum strong	√	√	√	√	√	Int.	√	√	√	√	√	?		√	√	√	√		√	√	√	√	√	√	√
Internal cingulum absent opposite projecting deuterocone												?	√					√							
Tetartocone small		√				√			√			?	√						Absent		√	√		Absent	
Tetartocone intermediate	√		√	√	√		√			√		?			√		√			√					
Tetartocone large								√			√			√		√		√					√		√
P3																									
Metaloph free from tetartocone	√	√	√	√		√	√		√				√	√			√		√	√	√		√	√	
Metaloph joined to tetartocone					√			√		√		√				√		√				√			√
Metaloph intermediate											√				√										
Incipient crista	√	O	√	√		√	√				√	O	O	√	√	?	O		√	O	O	√	?	O	O
Hypostyle present			√					?			?			√		?							√	√	
Hypostyle absent	√	√		√	√	√	√	?	√	√		√	√		√		√	√	√	√	√	√			√
Antecrochet on protoloph		O	O	?		O	?		?			O	O	l √ r O	O	?	O	O	O	O	O	O	O	O	O
Internal cingulum strong	√	√	√	√	√	Int.	√	√	√	√	√			√	√	√			√	√	√		√	√	√
Internal cingulum nearly absent opp. projecting deuterocone												√	√				√	√				√			

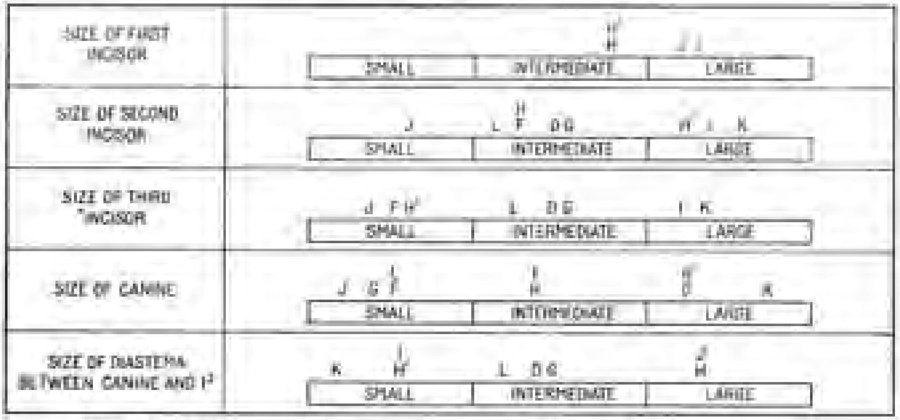
(Continued from page 22)

apparently progressive; size extremely small; P^1/ to M^3/, 175 mm.; P^1/ to P^4/, 80; M^1/ to M^3/, 98.

Further preparation of the material already in hand will doubtless reveal more intermediate conditions and different combinations of characters.

A highly important fact revealed by the Colorado Museum of Natural History series of *Trigonias* is that the upper premolars were in an extremely variable state, some of them retaining the conditions of earlier known stages (*Eotrigonias*), others clearly foreshadowing the most advanced stages seen in *Cænopus* and other genera of succeeding horizons.

This highly plastic and variable state seems to indicate that hybridism has played an important role in the evolution of the group, throws new light on some probable causes of changes observed in their structure, and suggests that hybridism has been a far more important factor in natural evolution than has been generally admitted.[3]



Graph 5. Variability in size and relative position of upper incisors and canines.

EXPLANATION OF GRAPHS

In Graphs 1, 2 and 3 (pp. 18, 23 and 24) the skulls are designated by letter and grouped upon the base line according to actual measurements, or where index figures are involved, according to percentages. The method of Graphs 4 and 5 (pp. 26 and 28) which deal with characters that are difficult or impossible to express in units of measurement, differs only in the substitution of a more flexible basis of comparison for the numerical scales used in the other graphs.

These frequency curves reveal grouping tendencies indicating stability in some characters, and in others varying degrees of scattering or fluctuation, which is suggestive of instability. It is well to note in this connection that the employment of a larger scale in the drawing of the graphs would reveal more prominently the divergent tendencies in smaller measurements, where only a few millimeters are involved, as in the case of tooth proportions.

For further interpretation and inferences, see Page 4 of the text.

[3] Dr. W. D. Matthew has long held this view.

TABLE IV VARIATIONS IN PREMOLAR AND MOLAR CHARACTERS (Continued)	897 (H) *T. osborni* var. *figginsi* type	422 (B) *T. osborni* var. *figginsi*	881 (C) *T. osborni* var. *figginsi* (?)	951 (I) *T. osborni* var. *figginsi* ref'd	876 (M) *T. osborni* var. *figginsi* ref'd	888 (E)	892 (H')	878 (G) *T. preoccidentalis*	430 (M')	882 (N)	884 (F) *T. osborni* var. *secundus*	1024 (L)	1029 (K) *Trigonias taylori*	886 (J) *T hypostylus*	414 (D) *T. precopei*	953 (O)	880 (Q)	1025(E) ?*C. premitis*	1050 (R)	1051 (S)	1052 (T)	1053 (U)	1054 (V)	1055 (W)	1056 (X)
P^4																									
Metaloph complete and molariform	√		√	Int.		√	√	√	√	√		√	√	√	√	√	√	√	√	√	√	√	√		√
Metaloph not molariform		√			√						√													√	
Hypostyle present	O	O	O	O	O	O	O	O	O	O	O	O		O		?	O	O	O	O	O	O	√	O	O
Tetartocone larger than deuterocone	√		√			√		√	√					√	√		√			√		√	√		√
Tetartocone equal to deuterocone		√		√	√		√			√	√		√			√		√	√		√			√	
Tetartocone smaller than deuterocone												√													
Protoloph barely connected with ectoloph	√	√	√					√					√		√				√	√			√	√	
P^3																									
Elongate, premolariform	√	√	√								√									√		√		√	
Intermediate				√	√			√	√				√	√	?				√		√				
Short, submolariform												√						√					√		
M^1																									
Metastyle proj. distinct	√				√						√	√	√	√		√			?	?	?	?	?	?	
Metastyle proj. intermediate				√				√		√					√			√							
Metastyle proj. vestigial to absent			√			√	√		√								√								√

TABLE V

COMPARATIVE DENTAL MEASUREMENTS

T. OSBORNI Type, and *T. OSBORNI* var. *FIGGINSI*

	T. osborni var. *figginsi*	*T. osborni*[1]
P¹/-M³/	200-205	183 est.
P²/-M³/	178-185	161 -188
P¹/-P⁴/	90- 95	91 est.
P²/-P⁴/	68- 75	61 - 79
M¹/-M³/	111-117	102 -109.5
P¹/ a. p. (anteroposterior)	18- 22	21 - 23
P¹/ tr. (transverse)	15- 19	17
P²/ a. p.	19- 20	20 - 22.5
P²/ tr.	27- 29	24+- 31
P³/ a. p.	22- 23	20 - 27
P³/ tr.	32- 37	33 - 40
P⁴/ a. p.	25	21.5- 26.5
P⁴/ tr.	36- 41	37.5- 40
M¹/ a. p.	31- 35	28.5- 34
M¹/ tr.	39- 44	41 - 43
M²/ a. p.	35- 41	36 - 39
M²/ tr.	45- 50	44.5- 48
M³/ a. p.	37- 41	34.5- 38
M³/ tr.	44- 49	44 - 45

[1]Measurements from Wood, *op. cit.*

TABLE VI

COMPARATIVE MEASUREMENTS OF LOWER JAWS

	T. osborni var. *figginsi* No. 951 (I)	*T. taylori* No. 1029 (K)
I/₂ to back cond.	380	340
I/₂ to back M/₃	246	237
P/₁ to M/₃	200	190
P/₁ to P/₄	82	80
M/₁ to M/₃	115	108
Depth beneath post. border M/₃	62	71
Height cond. above base	169	176
Symphysis to angle	400	394
Height coronoid above angle	215	217
Length symphysis	90	87
Depth of ramus below P/₂	62	56
Depth of ramus below M/₂	80	70

Note. No other lower jaws were found positively associated with the skulls herein described, therefore no other lower jaw measurements are given.

TABLE VII

COMPARATIVE MEASUREMENTS OF TRIGONIAS, CÆNOPUS,[1] SUBHYRACODON[1], AND AMPHICÆNOPUS[1]

	Trigonias taylori Skull K	*T. precopei* Skull D	*T. procidentalis* Skull G	*T. osborni* var. *figginsi* Skull H	*T. osborni* A. M. N. H.	*T. paucidens*	*T. nanolophus*	*T. wellsi*	*T. gregoryi*	?*Cænopus premitis*	*C. mitis*	*Amphicænopus platycephalus*	*Subhyracodon copei*	*S. trigonodus*	*S. occidentale*	*S. metalophum*
Pmx. to cond.	415	451	470	465	500+	504	...	596	...	?400		...	406	434		
$P^{1}/$ to $M^{3}/$	185	183	208	200	183	201	207	258	250	175	...	241	158	174	182	
$P^{1}/$ to $P^{4}/$	80	87	95	90	90	91	95	118	114	80	69	116	76	82	85	
M^{1} to M^{3}	107	105	117	113	102 109	115	116	142	139	98		136	84	100	100 106	103 108
	787[2]	826	890	868	875 882	911		1114	...	753		...	724	790		

[1]Measurements from Wood, *op. cit.*

[2]These totals, although derived from non-homologous measurements, afford a convenient magnified view of the size differences between the several forms.

TABLE VIII ANALYSIS OF COMPARATIVE MEASUREMENTS	Pmx. to cond.	Transv. zyg.	P^1 to M^3	P^2 to P^4	M^1 to M^3
T. taylori type (K)	Very short	Within limits of *T. osborni*	Practically same as in *T. osborni* referred	Much smaller than *T. osborni*; far smaller than *wellsi*; perhaps equals *paucidens*	About the same as *T. osborni*
T. osborni var. *figginsi* rf'd. (B)	Unknown	Slightly smaller than *T. osborni*	Unknown	Unknown	Unknown
T. osborni var. *figginsi* type (H)	Distinctly shorter than *T. osborni*; far shorter than *T. wellsi*	Wider than in *T. osborni*; about the same as in *T. paucidens*	Larger than *T. osborni*; much smaller than *T. wellsi*, *gregoryi*, etc.	Smaller than *T. osborni*; about equals *paucidens*	Considerably larger than *T. osborni*; about equals *paucidens*
T. osborni var. *figginsi* (?) (C)	Distinctly shorter than in *T. osborni*	Narrower than in *T. osborni*, *T. paucidens*	Larger than *T. osborni*; much smaller than *wellsi*; about equals *paucidens*, *nanolophus*	About equals *T. osborni*, *T. paucidens*	Considerably larger than *T. osborni*; about equals *paucidens*
T. osborni var. *secundus* (F)	Shorter than *T. osborni*	Slightly narrower than *T. osborni*	About same as in *T. osborni*; much smaller than *wellsi*	Decidedly smaller than *T. osborni*	
T. procopei type (D)	Much shorter than *T. osborni*, etc.	Not very different from *T. osborni*	Same as in *T. osborni*; much smaller than *T. wellsi*, etc.	Decidedly smaller than *osborni* and most others	About equals *T. osborni* far smaller than *T. wellsi*
T. hypostylus (J)	Much shorter than *T. osborni*, etc.	Wider than in *T. osborni*, *T. paucidens*	Same as in *T. osborni*	Decidedly smaller than *T. osborni*	About equals *T. osborni*
T. prooccidentalis (G)	Distinctly shorter than *T. osborni*	Not very different from *T. osborni*; less than *T. paucidens*	Larger than *T. osborni*; about the same as in *T.* mut. *hypostylus*; *T. paucidens*, *T. nanolophus*	About the same as *T. osborni*	Slightly larger than *T. osborni*; about equals *paucidens*
? *Cænopus premitis* (E)	Shortest of all	Extremely small	Much smaller than *T. osborni* or the rest	Far smaller than *T. osborni*	Smallest of all

Plate I. TRIGONIAS OSBORNI VAR. FIGGINSI. Type No. 897 (Skull H).
Right side of skull, slightly less than 15/32 natural size.

Plate II. TRIGONIAS TAYLORI. Type No. 1029 (Skull K).
Right side of skull, slightly less than half natural size.

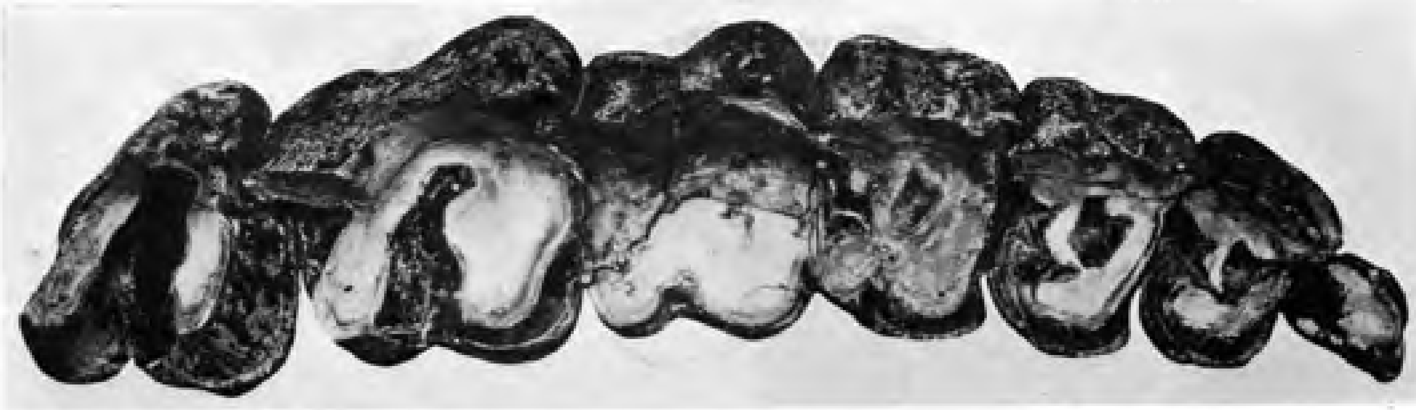


Plate III A. TRIGONIAS OSBORNI VAR. SECUNDUS. Type No. 884 (Skull F).
Right upper molar-premolar teeth, slightly more than natural size.

Plate III B. TRIGONIAS OSBORNI VAR. FIGGINSI. Type No. 897 (Skull H).
Left upper molar-premolar teeth. Natural size.

Plate IV A. ?CAENOPUS PREMITIS. Type No. 1025 (Skull E).
Right upper molar-premolar teeth, slightly less than natural size.

Plate IV B. TRIGONIAS OSBORNI "FIGGINSI". Referred skull No. 881 (Skull C).
Right upper molar-premolar teeth, slightly less than natural size.

Plate V A. TRIGONIAS TAYLORI. Type No. 1029 (Skull K).
Right upper molar-premolar teeth, slightly more than natural size.

Plate V B. TRIGONIAS HYPOSTYLUS. Type No. 886 (Skull J).
Right upper molar-premolar teeth, slightly less than natural size.

Plate VI A. TRIGONIAS PRECOPEI. Type No. 414 (Skull D).
Right upper molar-premolar teeth. Natural size.

Plate VI B. TRIGONIAS PREOCCIDENTALIS. Type No. 878 (Skull G).
Right upper molar-premolar teeth. Natural size.