NOTES ON THE DECIDUOUS AND PERMANENT DENTITION OF THE HYRACODONTS

LLOYD G. TANNER[1]
LARRY D. MARTIN[2]

ABSTRACT

Study of radiographs and dissections prepared from nearly fifty *Hyracodon* jaws in the collections of the University of Nebraska State Museum have demonstrated the normal presence of the lower premolar one in immature jaws of this genus. This tooth is functional in the young animal but is lost with the deciduous dentition and is not replaced. In the upper dental series permanent premolar one was preceded by a deciduous premolar one, which is also characteristic of the tapirs, but is unusual in the other perissodactyla.

INTRODUCTION

The milk dentition of the Hyracodontinae is unique in several respects from the teeth of other families and subfamilies of the Order Perrisodactyla, and as a result of this, there has been some misinterpretation in the identification of premolars in the deciduous series of the Oligocene *Hyracodon*.

Information has been obtained through the study of a series of over one hundred hyracodont jaws in the University of Nebraska State Museum Study Collection. Fifty of these jaws were either x-rayed or dissected, in order to examine the development of the unerupted teeth.

The dental formulae for juvenile and adult hyracodonts are as follows: juvenile dentition: DI $\frac{3}{3}$, DC $\frac{1}{1}$, DP $\frac{4}{4}$; adult dentition: I $\frac{3}{3}$, C $\frac{1}{1}$, P $\frac{4}{4}$, M $\frac{3}{3}$.

DESCRIPTION OF INCISORS AND CANINES

The deciduous incisors and canines are relatively small, thin teeth, about one half the size of the permanent teeth (Plate I, Fig. b). I^3 and I_3 were developed fully before the M^1 erupted. I_1 and I^1, and I^2 and I_3 followed in short succession after the permanent upper and lower molar one erupted. The canines of both the upper and lower dentition came into place after I^3 and I_3.

DISCUSSION AND DESCRIPTION OF THE LOWER DENTITION

DP_1: (Plate 1, Fig. d) This is a small tooth ranging in size from 9 to 10.5 mm. anteroposteriorly, and the transverse dimension is usually near 6 mm. It

[1] Coordinator of Systematic Collections, University of Nebraska State Museum.
[2] Research Assistant, Department of Geology and University of Nebraska State Museum; field party leader, Division of Vertebrate Paleontology of the Museum.

has a large central protoconid, a small hypoconid and an equally small paraconid. A crescent-shaped facet developed on the posterior one-half of the DP_1 from the occlusial wear with the protocone of DP^1 (Plate 1, Fig. b). DP_1 has two well-developed roots, a strong internal cingulum, and it may or may not have an external cingulum. DP_1 was never replaced, but as the permanent premolars erupted it was translocated anteriorly toward the posterior portion of the diastema where it was pushed off with relatively little reabsorption of the roots (Plate 2, Fig. a). Troxell (1921, p. 39) pointed out the presence of an alveolus for a lower premolar one, on the holotypic ramus of *Hyracodon leidyanus*, but apparently did not realize that it was a consistant feature of hyracodont deciduous dentitions.

DP_2 (Plate 1, Fig. d) The anterior portion of the tooth is narrower than the posterior dimension forming a sub-triangular shaped tooth. It has a shorter anteroposterior dimension than DP_3. It is also characterized by having both internal and external cingula, and a well-developed paraconid.

DP_3: (Plate 1, Fig. d) The DP_3 is the largest of the lower deciduous premolars, it is nearly rectangular in shape, and usually has external and internal cingula. The external cingulum is normally slightly interrupted at the mid-point of the tooth. The hypolophid and metalophid of DP_2 and DP_3 are "L" shaped rather than being rounded as are the other teeth of the deciduous and permanent series.

DP_4: (Plate 1, Fig. d) This tooth is very molariform, smaller than DP_3, and has an external cingulum which thins at the midpoint of the tooth. The ectoloph is discontinuous, and the hypolophid is continuous with the internal cingulum. Since the DP_4 is very molariform it may be confused with the unworn M_1. Wood (1927, Plate 13, Figs. 12 and 13), for example, interpreted two lower jaws to have the series "DP_2-M_1." However, the anterior alveolus shown in his illustration is for the DP_1. The corrected series would therefore be DP_1 (alv.) -DP_4. Butler (1952) also states that the corrected series for these specimens should be DP_1 - DP_4.

The ramus in young hyracodonts lacks calcification relative to that of the mature jaws. The juvenile jaw in all cases observed is expanded, to make room for the developing teeth, at a point near the posterior portion of the jaw. There are three or four mental foramina which extend from the posterior edge of the DP_3 to the anterior of DP_1. (This number is usually reduced to one or two upon maturity.) One of the youngest rami in the collection (Plate 1, Fig. a) has a depth posterior to DP_3 of 16 mm., which is less than one-half the depth the ramus would probably have had upon maturity.

The sequence of tooth replacement in the hyracodonts was observed through the use of x-rays (Martin, 1967) and dissections. In the case of the deciduous teeth, no specimens of very young jaws were available for study which could be used to determine the time at which the DP_1 erupted. DP_2 and DP_3 erupted prior to the DP_4.

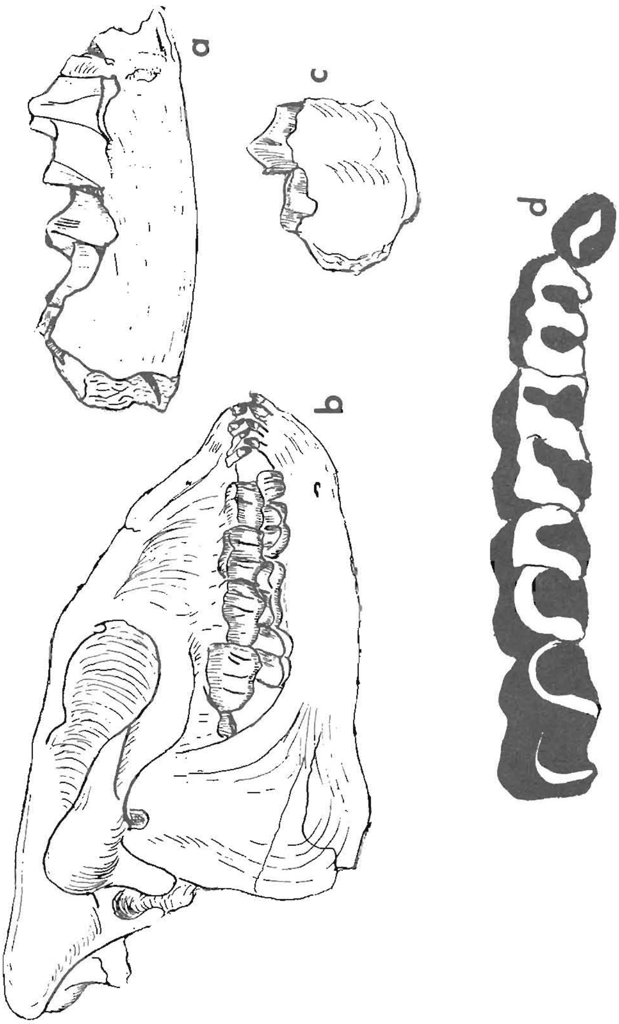

PLATE 1

Fig. a. Immature *Hyracodon* ramus U.N.S.M. 11031 showing $DP_3 - DP_4$. x 1.

Fig. b. The skull and lower mandible of an immature hyracodont U.N.S.M. 11036 showing the deciduous incisors, as well as $DP^1 - DP^4$, a trace of M^1 just erupting, and $DP_1 - DP_4$. x ½.

Fig. c. A hyracodont M_1, and its crypt U.N.S.M. 11075, weathered out of the ramus. x 1.

Fig. d. $DP_1 - M_1$ of *Hyracodon* U.N.S.M. 11077. x 1.

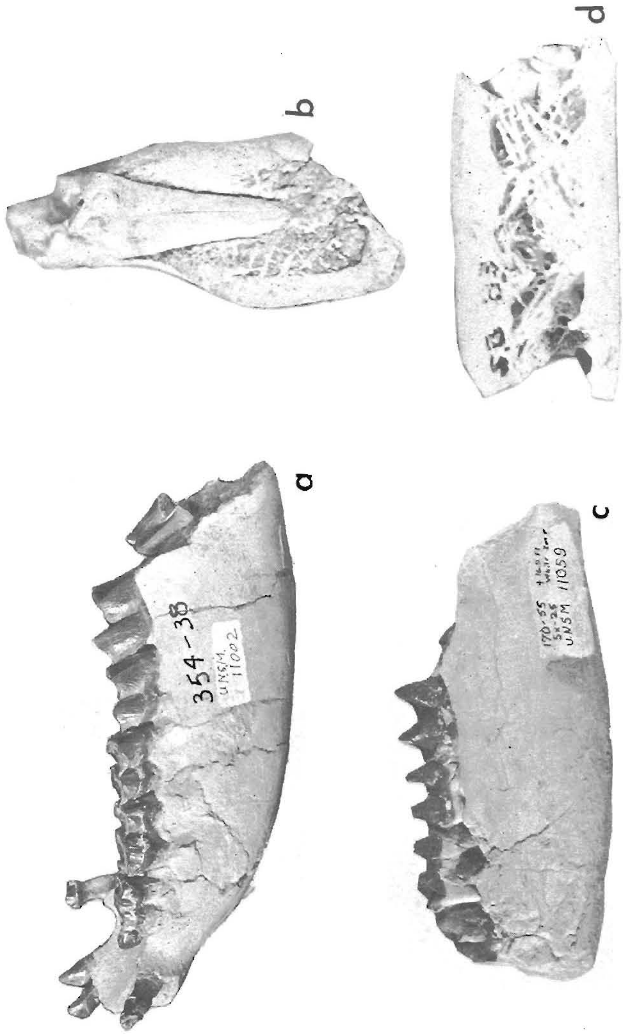

PLATE 2

Fig. a. An immature *Hyracodon* ramus U.N.S.M. 11002 with M_3 about to erupt. The fully erupted teeth are DP_1 – M_2. x ½.

Fig. b. A section through a *Hyracodon* ramus U.N.S.M. 11077 showing the relationship of the tooth roots to the trabecular bone tissue. (not to scale).

Fig. c. A *Hyracodon* ramus U.N.S.M. 11059 with DP_4 – M_2 erupted and P_3 – P_4 erupting simultaneously. DP_4 is resting on the crown of P_4. x ½.

Fig. d. A ventral section of a *Hyracodon* ramus U.N.S.M. 11078 showing the trabecular bone tissue just above the mandibular canal. (not to scale).

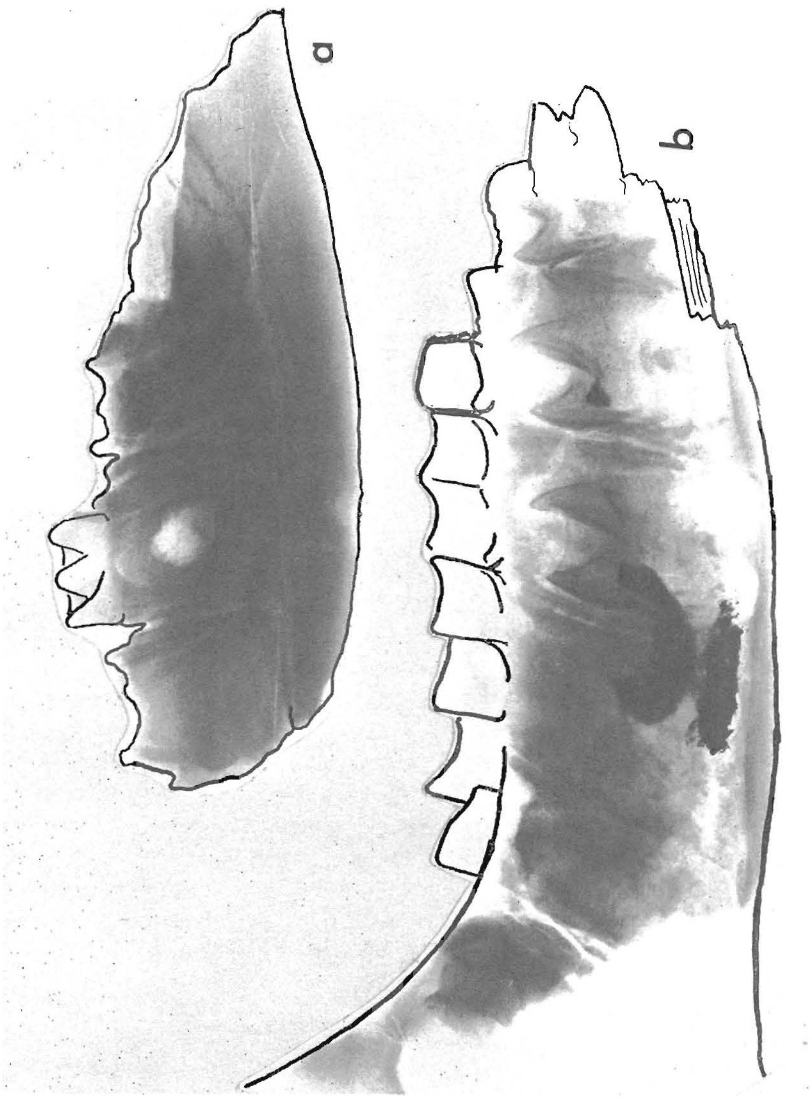

PLATE 3

Fig. a. A logitronic print of a x-ray of an immature *Hyracodon* ramus U.N.S.M. 11050. DP_4 was present on the original specimen but did not print and was later sketched in as is also true for the erupted teeth in the following figures of x-ray negatives. The crypt for P_4 is visible while that for P_3 is not yet evident. x 1.

Fig. b. A print of a x-ray of a *Hyracodon* ramus U.N.S.M. 11053 showing P_{2-4} migrating upwards directly under DP_{2-4}. M_{1-2} are erupted and M_3 can be seen in its crypt in the ascending ramus. x 1.

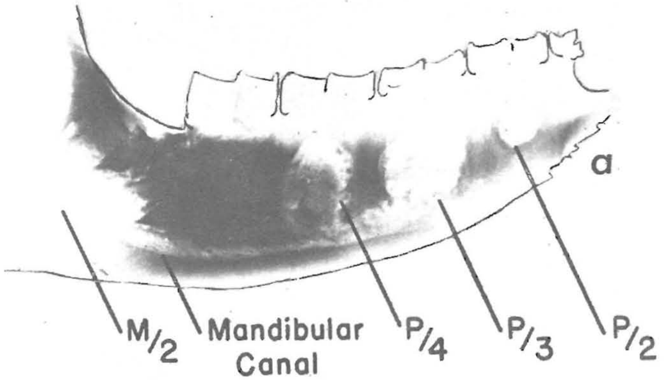

PLATE 4

Fig a. A x-ray of a right ramus of *Hyracodon* U.N.S.M. 11077 showing the crypts for $P_{3\text{-}4}$ well formed and P_2 beginning to be evident. $DP_1 - M_1$ are present on the original specimen and are sketched in. x ½.

Fig. b. $DP^1 - DP^4$ of *Hyracodon* U.N.S.M. 11022. x 1.

Fig. c. The maxilla below the teeth illustrated in Fig. 6 dissected to show the $P^1 - P^4$. x 1.

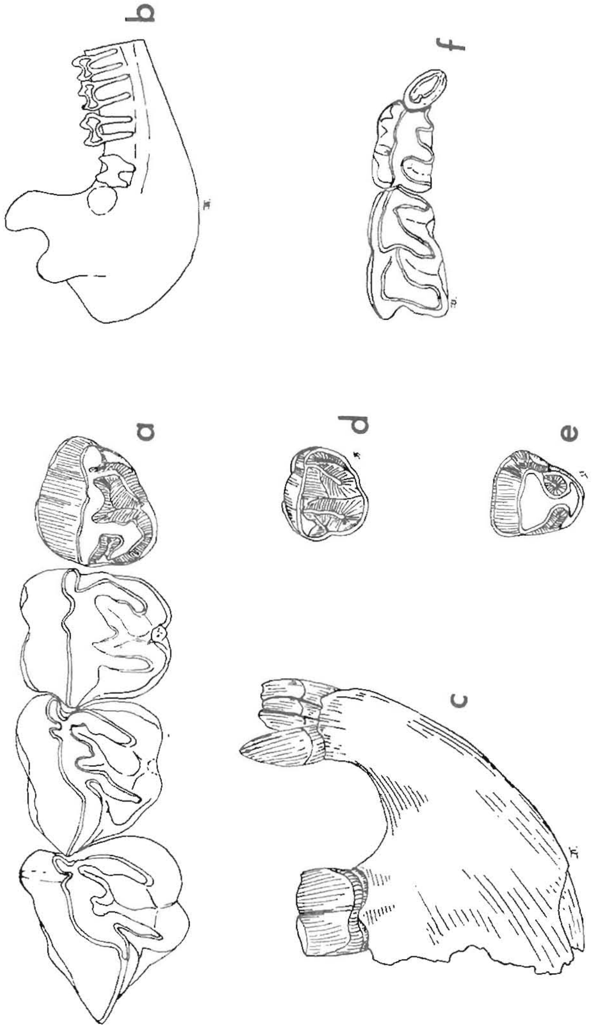

PLATE 5

Fig a. DP_{1-4} of *Hyracodon* U.N.S.M. 11026. This specimen is from the large size group of deciduous dentitions. x 1.

Fig. b. X-ray of *Dendrohyrax* showing positions of developing molars. x 1.

Fig. c. Anterior portion of a mandible of *Hyracodon* with an enlarged canine. (not to scale).

Fig. d. DP_1 of *Hyracodon* U.N.S.M. 11076. This specimen is from the small size group of deciduous dentitions. x 1.

Fig. e. P_1 of *Hyracodon* U.N.S.M. 11001. x 1.

Fig. f. Left DP_{1-3} of *Hyracodon* U.N.S.M. 11002 showing pronounced interstitial wear between DP_1 and DP_3. x 1.

The M_1, before its eruption, occupied a crypt formed by the reabsorption of the surrounding trabecular bone tissue (Plate 2, Figs. b and d), and during this time the unerupted M_1 is enclosed in a shell of compacted bone tissue. (Plate 1, Fig. c, shows an M_1, which has been weathered out of its ramus, prior to collection, but is still surrounded by this shell of compacted bone.) The bud of the M_1 before translocation, is tilted only slightly in comparison to the tooth germs of the other molars. The positions of the permanent molars and premolars prior to eruption are very similar to the unerupted teeth of hyracoids (Plate 4, Fig. a and Plate 5, Fig. b).

The M_2 began to form prior to the eruption of M_1 and by the time roots had begun to form under the M_1, the roots of the deciduous premolars had nearly reached their greatest length. Following the eruption of the M_1, a small oval crypt formed, approximately posterior to the center line of the ramus, and under the DP_4 (Plate 3, Fig. a), also, at this stage, reabsorption of the DP_4 roots began. The same procedure took place under the DP_3 and at nearly the same time (Plate 4, Fig. a). Further development of these deciduous teeth followed as the ventral borders of the crypts extended gradually downward until they rested on the top of the mandibular canal. Also during these processes the crypt for the P_2 was being formed, and it too extended to the top of the mandibular canal. In this study no evidence has been found which would indicate that a crypt ever formed under the DP_1. The crypts are at first oval-shaped then gradually become heart-shaped, with the apex between the roots of the deciduous premolars, reabsorbing the roots on either side (Plate 4, Fig. a).

The development of P_3 and P_4 occurred before that of P_2 (Plate 4, Fig. a). This process of tooth formation commenced after the eruption of the M_1, but before the roots completely formed on that molar. The last two premolars appear to have formed almost simultaneously and migrated upward together (Plate 3, Fig. b). As these teeth approached the upward limit of the dentary line they took their places nearly at the same time (Plate 2, Fig. c). In other words, by the time the M_1 and M_2 have erupted and the M_3 is formed (except for the roots) the roots of DP_2 through DP_4 have been almost completely reabsorbed, finally as the M_3 started to erupt, the permanent premolars also commenced to extrude: The P_3 and P_4 came into place almost at this same time. According to the evidence at hand, either of these teeth may have come into place prior to the other; P_2 is the last of the premolars to be replaced in the series.

UPPER DENTITION

The premolars of the upper dentary are more molariform than are the permanent premolars, and the medial valleys of these teeth are open. DP^1 is replaced (Plate 4, Figs. b and c), and the DP_1 is nearly one-half larger at the anteroposterior and transverse dimensions than the permanent P^1, and is triangular shaped. It has a hook-shaped metaloph which is often more elaborate in design than the metaloph of the P^1. The DP^1 occludes against the DP_1 and DP_2 and the large posteriorly directed protoloph of the DP^1 wears against the posterior portion of the DP_1, forming a crescent-shaped facet on the tooth. DP^1 is lost with the deciduous dentition and P^1 may or may not have a protoloph, if one is present, it is usually small.

In most cases DP^2 and DP^3 had a style developed on the anterior edge of the medial valleys and both had well-developed cristae. DP^4 is the largest tooth in the deciduous series and also has the medial valley open. The first three deciduous premolars all erupt at nearly the same time and DP^4 is the last to take its place.

SUMMARY AND CONCLUSIONS

Very little previous work has been done on tooth replacement in the hyracodontids. Sinclair (1922, Fig. 6) does illustrate a very worn upper cheek-dentition of *Hyracodon* with DP^{1-4}. Wood, when discussing the Hyrachyidae suggests that DP $\frac{1}{1}$ are not replaced in that family nor in *Hyracodon* (Wood, 1934, p 263). Very little opposition has been offered to this view although the possibility of the replacement of the DP^1 has been considered (Butler, 1952). That this situation should have been maintained for such a long period of time is strange, as we have shown in this study that the DP^1 and P^1 are very disimilar teeth (Plate 5, Figs. a and e). The presence of the P^1 beneath the DP^1 has been demonstrated by both x-ray negatives and dissections (Plate 4, Figs. b and c). The upper deciduous cheek-teeth of *Hyracodon* very clearly show that they belong to the same tooth series as the molar teeth, as they are all more molariform than their replacements. The development of the permanent premolars was very rapid as was pointed out by Sinclair (1922, p. 75) and most of it took place after the eruption of M^1.

The lower dentition is exceptional in the presence of a large functional DP_1 which is not replaced, but is lost with the deciduous dentition. This tooth is absent from most Tapir and Rhinoceros dentitions, and when present is usually vestigial. In *Hyracodon* the DP_1, along with the larger DP^1 contributes a significant portion of the grinding surface in the mouth of the young animal. The molar teeth are formed in the ascending ramus as in the hyracoids (Plate 5, Fig. b) and moved down and then up into place behind the previously erupted teeth. The ramus apparently grows enough in length to accomodate these teeth until the eruption of M^3, at which time the tooth row is translocated forward and the DP_1 is pushed off the ramus in a manner similar to that of the proboscidia. This causes a large amount of interstitial wear on the deciduous premolars (Plate 5, Fig. f). The mandible grows in depth very rapidly before the eruption of M_1. This translocation can be

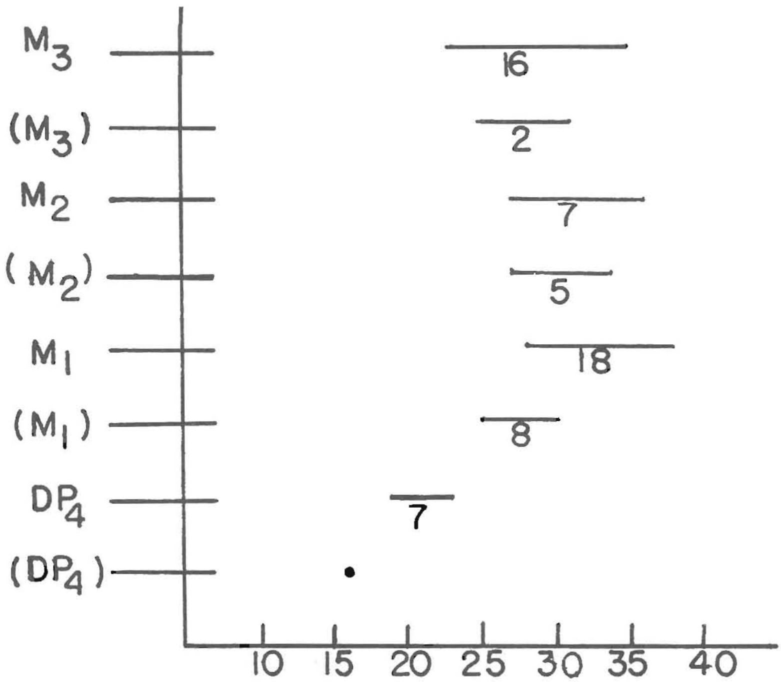

PLATE 6

Graph showing relative increase in depth of *Hyracodon* rami in millimeters measured posterior to DP_3 until the eruption of M_3 and then the dimension is taken posterior to the P_3. The horizontal lines indicate the total range in depth, and the sample size is given below the lines. A single dot means a sample of one specimen. The measurements are taken as each tooth is beginning to erupt = ( ) and after full eruption. A decrease in depth is shown during the eruption of M_3 at which time the tooth row is translocated forwardly towards the thinner portion of the ramus.

shown graphically by plotting the depth of the ramus below the posterior edge of DP_3 at the time of eruption of each of the following teeth (Plate 6). This dimension shows a decline when P_3 is used as the tooth row has moved anteriorly with eruption of M_3 and the ramus tapers in that direction.

We have at the present time noted few characters which might be due to sexual dimorphism in *Hyracodon*. However, certain specimens which share the same cheek-tooth pattern may differ in the size of the lower canines. We presume that the larger canines belong to males (Plate 5, Fig. c), although this probably cannot be proved. The deciduous dentitions can be readily separated into groups of large and small size (Plate 5, Figs. a and d). These size groups roughly correspond to the stratigraphic horizon of the specimens, with the larger being later in time. Their exact relationship to the various described species of *Hyracodon* have not been worked out, but they do lend additional support to the concept that more than one species is involved. This is contrary to the view presented by Scott (1941, p 841) that the several species of *Hyracodon* which have been erected are variants of H. *nebraskensis* (Leidy). Radinsky (1967, p. 30) concurred with Scott and lists H. *nebraskensis* as the "type and sole species." Specific differences can also be observed in the permanent dentition and in the skull leading the writers to believe that there are at least four or five separate species of *Hyracodon* present in the Oligocene (Tanner, 1965, p. 45).

Radinsky (1966, p. 633) includes the Hyrachyinae as a subfamily of the tapiroid family Helaletidae. The Hyrachyinae probably gave rise to the hyracodontids independently from the rhinocerotoidea and if the Hyrachyinae is included with the tapirs so should the hyracodontids which are tapir-like in the presence of DP^1, as well as in the form of their canines and incisors, be included in the Tapiroidea.

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