Dental Ontogeny of Juvenile *Pliauchenia Magnifontis* (Mammalia, Camelidae) From the Miocene Of South Dakota

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ABSTRACT

Specimens of a single population of juvenile camelids from the Big Spring Canyon locality, Bennett County, South Dakota, reveal stages of dental development for the first time. Ontogenetic development can be traced with stages of tooth eruption refined by substages of occlusal wear. The youngest individuals represented in the sample possess deciduous premolars. From this population, two stages of the development of the upper dentition are apparent: 1) Stage UA with deciduous premolars and M1/, but not M2/, erupted and worn and the posterior valley of M1/ is not enclosed posteriorly by wear and 2) Stage UB in which the M2/ is also erupted and worn and DP4/ shows great wear. Stage UA is subdivided into Substages UA1 and UA2. Substage UA1 is demarked by a poorly developed connection of the external crescents of DP4/ and the area of wear surfaces less than the area of intervening valleys. Stage UA2 is represented by the advanced states of the characters mentioned above for UA1. Stage UB is represented by only two specimens and thus could not be refined into substages.

The lower dentition exhibits similar stages, although, due to overlapping occlusion, they appear to be slightly delayed in their timing relative to those of the upper dentition. Development of wear and eruption of the lower dentition is divided into two stages: Stage LA, with the eruption of all teeth up to the M/1 and the continued presence of an anterior valley on DP/4 and Stage LB, defined by eruption and first wear of M/1 and the disappearance of the anterior valley of DP/4.

These developmental stages of tooth wear and eruption in conjunction with dental count may eventually prove useful in taxonomic assignment of isolated juvenile camelid specimens.

INTRODUCTION

In 1942, J. T. Gregory described the vertebrates then known

ACKNOWLEDGEMENTS:

We would like to thank Dr. John Bolt and Mr. William F. Simpson of the Field Museum of Natural History, Chicago, Illinois, for making available the specimens used in this study.

from the Clarendonian (Miocene) Big Spring Canyon locality in Bennett County, South Dakota. A principal component of the local fauna were camelids, and Gregory described four genera. Two genera, *Procamelus* and *Pliauchenia,* were relatively well represented (e.g. Martin, 1985a), whereas *Protolabis* and *Megatylopus* or *Alticamelus* were poorly known. The latter is known only by post-cranial elements and the former by a juvenile skull and a cervical vertebra. In addition, seven specimens of juveniles were described only as "immature *Procamelus* and *Pliauchenia.*" Gregory noted that inadequate information was available concerning juvenile camels to allow their assignment to taxa based on adult specimens. Subsequent authors have encountered the same problem, and most juveniles have therefore gone unassigned. A collection of juveniles from a discrete horizon described herein may prove useful in providing a baseline of morphological parameters, which change with ontogeny, necessary to delineate young camelids.

One of us (Martin, 1985b:43-45) chronicled the history of a collection of fossil vertebrates at Big Spring Canyon. Of the collections, the one made under the direction of Dr. Paul McGrew in 1939 from a single horizon high on the western side of the canyon provides the sample considered in this contribution. Derivation from a single horizon of relatively complete cranial elements with similar preservation suggests that a single population was sampled.

All specimens, which are housed at the Field Museum of Natural History, University of Chicago, appear to represent *Pliauchenia magnifontis.* This camelid is advanced in several characteristics compared to other camelids from the locality. These specimens do not possess the double-rooted P1/ and full complement of upper incisors characteristic of *Protolabis* (Webb, 1969). It might be noted that these diagnostic features were not preserved on the skull that Gregory (1942) questionably assigned to *Protolabis.* The series of Field Museum specimens appear too small to be either *Megatylopus* or *Auchenia* and possess arched nasals and llama buttresses on the lower molars (Harrison, 1979). The collection most closely resembles *Procamelus grandis,* but differs in the absence of P2/ either as a deciduous or permanent premolar, P3/ completely formed, palate not constricted anterior to P3/, and llama buttresses on lower molars (Gregory, 1942; Harrison, 1979).

ONTOGENETIC DEVELOPMENT AND STAGES

INTRODUCTION

Despite the relative homogeneity of the sample of *Pliauchenia magnifontis* it is also a small one. Ontogenetic stages, however, can be determined from this sample with the use of descriptions of wear features on the teeth and the equivalent state of tooth

eruption. The specimens used in this paper were divided into two ontogenetic stages for the upper teeth (labeled UA and UB) and two stages for the lower teeth (LA and LB). These stages are primarily descriptive of the state of tooth eruption and not so much the wear. Based on the degree of occlusal wear, Stage UA was subdivided into two substages.

THE STAGES

Stage UA — This stage represents the youngest age of the animals based on the eruption and, to some extent, masticatory wear on the upper teeth. In this stage, the deciduous premolars and the M1/ are fully erupted and the posterior valley of M1/ is not enclosed posteriorly by wear (henceforth, "wear" = exposed dentine). The M2/ is only partially erupted at best and is unworn. Based on specifics of wear, Stage UA is subdivided into Substages UA1 and UA2.

Substage UA1 — Specimens of Substage UA1 are united by only a couple of features of wear. For instance, the area of the central valleys on M1/ is generally greater than that of the wear surfaces. Also, there is a poorly developed connection between the labial crescents of DP4/. Substage UA1 is represented by specimens P 15859, P 26365, P 26371, P 26383, P 26368, P 26381o., and P 26381L, in order of increasing wear. The beginning of this substage is most closely represented by P 15859, which exhibits the following state of wear: 1) the DP3/ is only moderately worn and only on the posterior side, 2) DP4/ has all occlusal surfaces worn, central cavities deep, and crescents still with a high amount of arch, and 3) the M1/ has all occlusal surfaces worn except for the posterior one-quarter, the labial crescents (anterior and posterior) are not continuous past the mesostyle, the posterior valley is not enclosed posteriorly by wear, and anteriorly it almost reaches to the mesostyle.

The end of Substage UA1 is here represented by P 26381L. In this specimen, a right M1/, the area of wear surface is only slightly less than or equal to the area of the valleys. The posterior end of the tooth is distinctly open, wear extends all the way out the parastyle (probably the mesostyle also, judging from P 26381o.), and the anterior valley appears smaller than the posterior because of the greater amount of wear surrounding it than surrounds the posterior. The DP3/ of P 26368, which is the DP3/ that exhibits the most wear, shows wear all along its length.

Substage UA2 — Substage UA2 represents the advanced states of wear for the features mentioned in UA1. This substage includes specimens P 26381n, P 26381k, P 26381m, P 26366, and P 25381q. The beginning of this substage is represented by P 26381n, a DP4/, in which the valleys are greatly reduced in size, little shearness re-

mains to the occlusal surfaces, and the posterior end is well enclosed by wear. The M1/, however, is not represented in any specimen preceding the wear stage of P 26366. In this specimen, there is no enclosure of the posterior end, all wear surfaces are definitely connected, and the valleys are somewhat less in area than the surfaces of wear. The crescents, however, still retain relatively high arches. For the purposes of this paper, P 26366 also represents the later end of Substage UA2 as the M1/ of P 26381q does not present a significant advance in development from P 26366.

Stage UB — This stage of development of the upper dentition is advanced over stage UA in that the M2/ is also fully erupted and worn and the DP4/ shows a minimal high degree of wear. Because there were only two specimens remaining in this sample to assign to this stage, it was not subdivided. The earlier representative of this stage is P 26369, in which the DP4/ has almost no dorsoventral arch remaining on the anterior crescents and little on the posterior, the wear surfaces of the lingual cusps are finally continuous, and the anterior valley is an elongate slit. On M1/, wear extends all the way out each of the styles, the posterior end of the posterior valley is now enclosed, and the anterior and posterior wear surfaces are connected. In M2/, the area of the valley is still greater than that of the wear surfaces, and the parastyle is apparently not entirely worn (part of it is damaged). The later part of Stage UB is represented by P 15869. In this specimen, the crown morphology of DP4/ is missing except for a small amount of enamel representing the posterior valley. Also, there is no arch to the anterior crescents, very little arch to the posterior crescents, and the wear surface at the far anterior end (parastyle) almost extends down to the base of the enamel. The wear of M1/ and M2/ is only slightly advanced over that of P 26269, however. The anterior and posterior crescents of M2/ are not connected and wear does not extend very far out the parastyle. The anterior end of M1/ blends into the posterior end of DP4/ with the virtual disappearance of their intervening enamel walls. With the addition of more specimens from this locality, the development of wear of the DP4/ may prove useful in subdividing Stage UB. The next logical stage of development of the upper dentition would have been the loss of DP4/ and the eruption of P4/, but as there were no representative specimens in this sample, the stage was not formulated.

Stage LA — The lower dentition exhibits similar stages in eruption and the development of wear, but the timing of both appears to lag behind that of the upper dentition, primarily because of the nature of the occlusion of the upper and lower dentitions. A correlation between the upper and lower stages, at least in the earlier phases, can be made with P 15859, which consists of both upper and lower dentitions. As with the upper dention, P 15859 is a representative of the first stage, in this case LA. In specimen P 15859, the wear of the DP/4 and DP4/ are approximately equivalent, yet the M1/ is essentially fully erupted whereas the M/1 has not even breached the dorsal surface of the jaw. Stage LA is defined by the complete eruption of all teeth up to, but not including, the M/1. Specimens in Stage LA also have the anterior valley remaining on DP/4. Specimens assigned to this stage include P 26381b, P 15859, P 26381d, P 26378, P 26376, P 26336, P 26381c, and P 26381a. Despite the number of representative specimens, there are no features of wear that can be used to separate the specimens into substages. There is some difference in the degree of wear on DP/3, but if specimens with wear on the anterior one-third are separated from those without, there would only be one specimen in the latter group. Judging from P 15859, which is young enough so that the M/1 is only barely visible, the anterior one-third of DP/3 wears soon. Similarly, the posterior and middle crescents of DP/4 are probably not always connected, but the DP/4 is always so advanced in wear by the time M/1 erupts that any divisions between the posterior and middle crescents has disappeared. All of the specimens mentioned above have at least minimally continuous wear surfaces on the DP/4.

The beginning of this stage is represented by P 26381b. In this specimen, the DP/3 is unworn on the anterior one-third, and the area of wear on DP/4 is only slightly greater than that of the valleys. Also on DP/4, the wear surfaces are connected, and the posterior valley is just barely open posteriorly. The later extreme of Stage LA is here represented by P 26381c, in which the anterior one-third of DP/3 is distinctly worn, but not strongly connected to the wear on the rest of the tooth. Also, the posterior valley of DP/3 is almost gone. The DP/4 has wear surfaces of much greater area than the valleys, fully connected crescents, and an enclosed posterior valley. The anterior valley, though small and slit-like, is still present.

Stage LB — Stage LB is represented by specimens in which the M/1 is fully erupted and worn. The state of eruption and wear of M/2, M/3, and DP/4 are unknown beyond the initial representative of this stage because there are no specimens in this sample in which more than one of these teeth are preserved. Specimens placed in this group are P 15869, P 26381f, and P 26381g. In the representative of the initial phase of this stage, P 15869, the M/1 has almost completely erupted, but the M/2 is not yet visible. The DP/3 is missing, and the DP 4 is well-worn with the anterior valley worn away and the other two virtually slit-like. All styles are fully worn. On M/1, there is wear on all parts of all crescents, but the posterior end is not quite enclosed. Also, the wear surfaces of the anterior and posterior lingual crescents are not quite connected

past the metastyle, but the valleys are already of distinctly less area than the wear surfaces. There are no specimens of M/1 or M/2 to indicate their condition in the later part of this stage. Because of the greater amount of lag in the times of eruption between the lower molars and the uppers, the logical beginning of the next stage might have been at the eruption and initial wear of M/2 or the loss of DP/4 and eruption of P/4, whichever comes first. However, because there is no specimen to represent the next stage, it is not known which happens first in *Pliauchenia.* In *Procamelus,* the M/3 erupts just before the P/4, and the M/2 is apparently fully erupted before the DP/4 is shed.

CONCLUSION

The primary purpose of this investigation is to provide a baseline for the comparison of juvenile fossil camelids. Successive ontogenetic stages of a single population from a discrete geographic area and horizon based upon tooth eruption, a trait primarily controlled genetically, and substages based upon wear, a trait partially controlled by environment, provide the first such baseline. Later comparison with additional juvenile populations will resolve the parameters of taxonomic, dietary, and temporal differences and may illustrate evolutionary changes. Once a series of baselines for various species from different horizons is established, identification of isolated juvenile specimens may result.

The Clarendonian camelids from Big Spring Canyon may be differentiated on the basis of size and incisor and premolar configuration. None of the juvenile specimens observed possess evidence of either permanent or deciduous P2/, suggesting that the characteristic is usually important in taxonomic determination, even of juveniles.

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