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(MAMMALIA, DINOCERATA) FROM THE LATE PALEOCENE AND
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ANN ARBOR

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SYSTEMATICS AND EVOLUTION OF *PROBATHYOPSIS* (MAMMALIA, DINOCERATA) FROM THE LATE PALEOCENE AND EARLY EOCENE OF WESTERN NORTH AMERICA

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Abstract.—*Probathyopsis* is the only genus of Dinocerata known from the late Paleocene and earliest Eocene of North America. *Bathyopsoides* and *Prouintatherium* are junior synonyms. North American *Probathyopsis* and Asian *Prodinoceras* are included in Prodinoceratidae Flerov 1957, a primitive family differing from Uintatheriidae in retaining three upper incisors in each premaxilla, in lacking cranial horns, and in retaining a distinct neck on the astragalus. Two (possibly three) species of *Probathyopsis* are known. *P. harrisorum* Patterson is a species of larger individuals from the late Tiffanian and early Clarkforkian land-mammal age. *P. praecursor* Simpson is a species of smaller individuals from the middle and late Clarkforkian land-mammal age. *Probathyopsis? lysitensis* Kelley and Wood from the late Wasatchian land-mammal age is poorly known and it may belong in either *Probathyopsis* or *Bathyopsis*. *Probathyopsis harrisorum* and *P. praecursor* are both sexually dimorphic, with male specimens being about 10% larger in linear dimensions than their female counterparts. Trends in the evolution of Clarkforkian *Probathyopsis* include diminution in tooth size and body size of both sexes, and shortening of the neck with elongation of the ectal facet on the astragalus.

INTRODUCTION

The mammalian order Dinocerata is known from the late Paleocene through middle Eocene of Asia and North America. Dinoceratans are interesting for several reasons: their origin is obscure, their dental and cranial specializations are distinctive, and known dinoceratans are discontinuously distributed in the Eocene fossil record, suggesting ecological specialization. The most impressive dinoceratans were huge animals from the middle Eocene, browsing herbivores with large tusks and three pairs of cranial horns (Marsh, 1885). These are of interest historically as a focus of the highly publicized feud between nineteenth century American paleontologists Edward Drinker Cope and Othniel Charles Marsh (Wheeler, 1960).

The earliest North American dinoceratan, *Probathyopsis*, appears in the fossil record in the latter part of the Tiffanian land-mammal age (*Plesiadapis simonsi* zone or biochron Ti-5 in the system of range-zones described by Gingerich, 1976, 1983). Dinoceratans are often thought to have originated in South America (Simpson, 1935; Paulo Couto, 1952; McKenna, 1979), and their sudden appearance in North America in association with arctostyloid notoungulates and metacheiromyid edentates supports this idea. *Probathyopsis* may have originated from a South

American stock, traversing Central America and invading middle latitudes of North America from lower latitudes during late Paleocene climatic warming (Gingerich, 1985). *Probathyopsis* ranged through all of the Clarkforkian land-mammal age (*Plesiadapis gingerichi*, *P. cookei*, and *Phenacodus-Ectocion* zones of Rose, 1981, or biochrons Cf-1 to Cf-3 of Gingerich, 1983), and it may have survived into the late Wasatchian land-mammal age as well.

Probathyopsis is a rare but consistent faunal element in Clarkforkian faunas, comprising approximately 1.3% of the fauna known to date: 38 of 2837 catalogued specimens in University of Michigan collections from the Clark's Fork Basin, Wyoming. *Probathyopsis* appears to have become extinct, locally at least, at the Clarkforkian-Wasatchian boundary: no dinoceratans have ever been found by University of Michigan field parties in the early Wasatchian land-mammal age of the Clark's Fork Basin despite the recovery of over 10,000 specimens from that interval. Dinocerata reappear in Wyoming in the late Wasatchian of the Wind River Basin (Kelley and Wood, 1954; Stucky, 1984), and three specimens are known from the late Wasatchian of the central Bighorn Basin (UM 86621, USGS 12765 and YPM 22954). Dinoceratans of the family Uintatheriidae (*Bathyopsis*, *Eobasileus*, *Tetheopsis*, and *Uintatherium*) are more common in Bridgerian and Uintan faunas in North America (Wheeler, 1961). No dinoceratans are known in North America from stratigraphic intervals younger than the Uintan land-mammal age.

In revising the order, Wheeler (1961) listed several Paleocene taxa, *Probathyopsis praecursor*, *P. successor*, *P. newbilli*, and *Bathyopsoides harrisorum* without critical discussion. More recently Dashzeveg (1982) reviewed the primitive Dinocerata (Prodinoceratinae, according to him) in a revision concerned mainly with central Asiatic taxa. Tong and Lucas (1982) suggested a number of synonymies of dinoceratan genera, and Schoch and Lucas (1985) formalized several of these.

Here we shall revise the systematics of early North American *Probathyopsis* to reflect our current understanding of the evolution of late Paleocene and early Eocene dinoceratans, describe the incisor morphology of *Probathyopsis*, and discuss the early evolution of dinoceratans on the basis of dental, mandibular, and astragalar evidence.

Maps showing the geographic distribution of localities that have yielded late Tiffanian and Clarkforkian *Probathyopsis* are shown in Figure 1. Species discussed here range from Plateau Valley in the Piceance Basin of western Colorado (39°N latitude) to Foster Gulch and Sand Coulee in northwestern Wyoming (45°N latitude). Sand Coulee in the Clark's Fork Basin and Foster Gulch in the northern Bighorn Basin are the only areas yielding *Probathyopsis* in stratified context, where direct superposition of strata in the field determines the polarity of observed morphological trends.

Measurements of upper cheek teeth are taken parallel (length) or perpendicular (width) to a line connecting the paracone and metacone cusps. In the lower dentition, the long axis of each tooth is used as a line of reference. Crown length in incisors and canines is measured as the distance between the mesiodistal extremities, height is the greatest distance from the tip of the crown to the most basal edge of enamel. Details of morphology of the cheek teeth are not discussed in this paper, as they seem to be relatively stable through time. Detailed descriptions and figures of primitive dinoceratan cheek teeth were published by Simpson (1929), Patterson (1939), Flerov (1957), Dorr (1958), Rose (1981), and Schoch and Lucas (1985).

INSTITUTIONAL ABBREVIATIONS

ACM—Amherst College Museum, Amherst, Massachusetts.

AMNH—American Museum of Natural History, New York, New York.

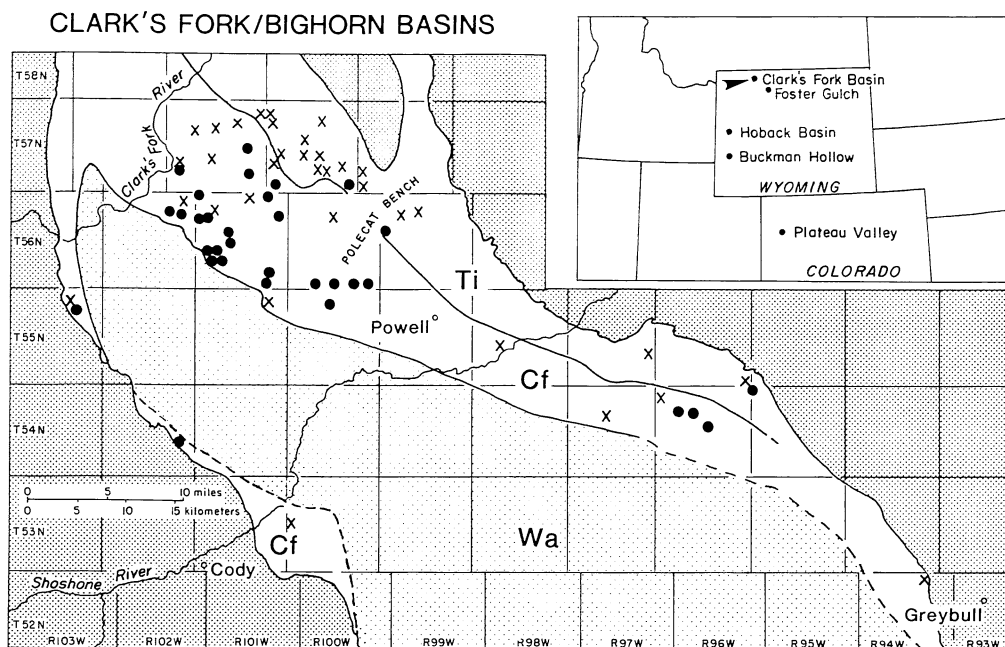


FIG. 1— Geographic distribution of *Probathyopsis harrisorum* and *P. praecursor* in western North America. Inset map shows location of late Paleocene and earliest Eocene localities (and depositional basins) yielding specimens discussed here. Most specimens come from Sand Coulee in the Clark's Fork Basin and Foster Gulch in the northern Bighorn Basin, where they are preserved in stratigraphic sequence in sediments ranging in age from late Tiffanian (*Ti*, late Paleocene) through Clarkforkian (*Cf*, transitional Paleocene-Eocene). Approximate contact of Tiffanian and Clarkforkian is shown with a solid line. Darker stippling shows outcrop distribution of Cretaceous and older sedimentary rocks. Lighter stippling shows outcrop distribution of Wasatchian (*Wa*, early Eocene) sediments. *Probathyopsis* has never been found in any early or middle Wasatchian locality. Localities yielding *Probathyopsis* are shown with *x* (Princeton University specimens) and or a closed circle (University of Michigan specimens). Holotypes of late Tiffanian or early Clarkforkian *Bathyopsoides harrisorum* Patterson and synonym *Probathyopsis newbilli* Patterson are from Plateau Valley (Piceance Basin) in western Colorado. Holotype of late Clarkforkian *Probathyopsis praecursor* Simpson and late Clarkforkian *Probathyopsis successor* Jepsen are from approximately the same location and level: Section 2, T55N, R101W, in the Clark's Fork Basin (Rose, 1981). Late Clarkforkian synonym *Prouintatherium hobackensis* Dorr is from locality UM-Sub-Wy 7 (Hoback Basin) in western Wyoming. Map showing distribution of faunal zones in the Clark's Fork and Bighorn Basins is abstracted from Gingerich (1983), with modifications based on subsequent field work.

FMNH—Field Museum of Natural History, Chicago, Illinois.

PU—Princeton University, Natural History Museum, Princeton, New Jersey.

UM—University of Michigan, Museum of Paleontology, Ann Arbor, Michigan.

UMMZ—University of Michigan, Museum of Zoology, Ann Arbor, Michigan.

USGS—U. S. Geological Survey, Denver, Colorado.

USNM—National Museum of Natural History, Washington, D. C.

YPM—Yale Peabody Museum of Natural History, New Haven, Connecticut.

SYSTEMATIC PALEONTOLOGY

Order DINOCERATA Marsh, 1872
Family PRODINOCERATIDAE Flerov, 1952

Bathyopsidae (in part), Osborn, 1898, p. 182.

Uintatheriidae (in part), Patterson, 1939, p. 373. Gazin, 1956, p. 16. Dorr, 1958, p. 507. Rose, 1981, p. 93.

Prodinoceratidae Flerov, 1952, p. 1029. Flerov, 1957, p. 11. Schoch and Lucas, 1985, p. 36.

Bathyopsinae (in part), Wheeler, 1961, p. 19.

Prodinoceratinae, Szalay and McKenna, 1971, p. 312. Dashzeveg, 1982, p. 91.

Type genus.—*Prodinoceras* Matthew, Granger, and Simpson, 1929.

Referred genus.—*Probathyopsis* Simpson, 1929.

Age and distribution.—Late Paleocene and early Eocene (Tiffanian through Clarkforkian, and possibly late Wasatchian land-mammal ages) in North America. Late Paleocene and early Eocene in Asia.

Differential diagnosis.—Prodinoceratidae differ from Uintatheriidae in retaining three upper incisors in each premaxilla. Lower incisors have a single cusp. Lower canine is projecting, not incisiform. Size smaller than Uintatheriidae. Horns are absent. Astragalus has a distinct neck and no expanded trochlear facet.

Discussion.—Wheeler (1961) considered *Probathyopsis* (and its synonym *Bathyopsoides*), *Prodinoceras* (and its synonym *Mongolotherium*), and *Bathyopsis* to constitute a subfamily Bathyopsinae of Uintatheriidae. Considering the morphological conservatism of the cheek teeth throughout the order, he recognized only a single family of Dinocerata. We agree with Flerov (1952) that the very different morphology of the anterior dentition (Wheeler's extrapolations from "*Mongolotherium*," a synonym of *Prodinoceras*, are confirmed by new American material), astragalus, and skull merit recognition of a separate family for generalized *Probathyopsis* and *Prodinoceras*. In contrast to Wheeler (1961), but in agreement with Flerov (1957), Dashzeveg (1982), and Schoch and Lucas (1985), we exclude *Bathyopsis* from Prodinoceratidae. The lower incisors of middle Eocene *Bathyopsis* have two cusps, prestaging the elongated complex incisors of large uintatheriids (cf. Osborn and Speir, 1879). *Bathyopsis* has small maxillary horns (Osborn, 1913), and its astragalus (illustrated here in Fig. 7) is decidedly more like a uintatheriid (Marsh, 1885) than like a prodinoceratid. *Bathyopsis* is intermediate in most features between Prodinoceratidae and Uintatheriidae, but has, incipiently at least, all of the specializations characteristic of the latter family. Bathyopsidae Osborn (1898, p. 182) cannot be used as a family name for the stem family of Dinocerata because the family, as now delineated, does not include the type genus.

Szalay and McKenna (1971) used Prodinoceratidae for "*Bathyopsoides*," *Prodinoceras*, and "*Mongolotherium*," and included *Probathyopsis*, *Bathyopsis*, and "*Prouintatherium*" in Uintatheriidae, assuming that the "*Prouintatherium*"-*Uintatherium* lineage and the *Bathyopsis*-*Tetheopsis*-*Eobasileus* lineage originated independently from *Probathyopsis*. Excluding *Probathyopsis* from Uintatheriidae would make the family diphyletic. As there appears to be little evidence favoring diphyly of Bridgerian and Uintan uintatheres, it seems best to include *Probathyopsis* and *Prodinoceras* with "*Prouintatherium*" and "*Bathyopsoides*" in a morphologically coherent Prodinoceratidae, the stem group of all Dinocerata.

Probathyopsis Simpson, 1929

Probathyopsis Simpson, 1929, p. 1. Jepsen, 1930, p. 128. Patterson, 1939, p. 378. Kelley and Wood, 1954, p. 356. Flerov, 1957, p. 12. Wheeler, 1961, p. 19. Rose, 1981, p. 93. Tong and Lucas, 1982, p. 552.

Bathyopsoides Patterson, 1939, p. 373. Wheeler, 1961, p. 22.

Prodinoceras (in part), Dashzeveg, 1982, p. 82. Schoch and Lucas, 1985, p. 37.

Type species.—*P. praecursor* Simpson, 1929.

Referred species.—*P. harrisorum* (Patterson, 1939), and possibly *P? lysitensis* Kelley and Wood, 1954.

Diagnosis.—Differs from *Prodinoceras* in having M_1 much smaller than M_2 ; M^1 much smaller than M^2 ; narrow P^4 , M^1 , and M^2 ; and an astragalus with a longer astragalar neck (in *P. harrisorum*). Astragalar canal present (Fig. 3; contra Schoch and Lucas, 1985).

Age and distribution.—Late Tiffanian through late Clarkforkian (*Plesiadapis simonsi* through *Phenacodus-Ectocion* zones) of western North America. May also range through the late Wasatchian if *P? lysitensis* is correctly referred to *Probathyopsis*.

Discussion.—Differences in dental proportions and other features distinguishing these two genera are discussed in a section on relationships of *Probathyopsis* and *Prodinoceras* included at the end of this paper.

?*Probathyopsis sinyuensis* Chow and Tung, 1962, may not belong in *Probathyopsis* according to Tong and Lucas, 1982.

Probathyopsis harrisorum (Patterson, 1939)

Figs. 2, 3, 5A-B, and 6A-B

Bathyopsoides harrisorum Patterson, 1939, p. 374, fig. 109-110. Wheeler, 1961, p. 21.

Probathyopsis newbilli Patterson, 1939, p. 378, fig. 111. Wheeler, 1961, p. 21.

Holotype.—FMNH P15546, left and right mandible with right M_{2-3} , left P_{3-4} and M_{2-3} , fragments of I_1 , I_2 , C_1 and M_1 of both sides. Most of the incisors figured in the type description (Patterson, 1939) are plaster reconstructions.

Type locality.—"Plateau Valley, one mile north of the Douglas Harris ranch house," Colorado (Patterson, 1939).

Type of synonym.—FMNH P15549, holotype of *Probathyopsis newbilli*, is a mandible with P_4 and M_{1-3} in the left ramus, and P_{3-4} and M_{1-3} in the right ramus (P_4 , M_1 , and M_3 are represented by crown fragments only). The mandibular symphysis is fused. According to Patterson (1939, p. 378), this specimen comes from the same locality as the holotype of *Bathyopsoides harrisorum*, being found some 50 meters from it.

Age and distribution.—Late Tiffanian through early Clarkforkian (*Plesiadapis simonsi* through *P. gingerichi* zones). Bighorn and Clark's Fork basins, Wyoming, and Piceance Basin, Colorado.

Diagnosis.—*P. harrisorum* differs from *P. praecursor* in being larger (ca. 10% in dentary length), retaining P_1 (at least in young individuals), having a relatively long astragalar neck, and in having an ectal facet on the astragalus that is longer proximodistally than it is mediolaterally.

Description.—Upper incisors are preserved in place in a partial premaxilla of *Probathyopsis harrisorum* from the *Plesiadapis simonsi* zone (PU 18869). I^2 is a small pointed tooth, labially convex and lingually concave. Its anterior cutting edge is slightly convex and its posterior cutting

edge is flat. A thickened rib runs from the tip to the base just posterior to the axis on the lingual side, and the enamel is crenulated (Fig. 2A, B, and C). Maximum crown length at the base of the crown is 8.4 mm, and maximum crown height is 7.0 mm. I^3 is separated from I^2 by a diastema and it is smaller (Fig. 2, only the base is preserved). Maximum crown length at the base is 6.0 mm. An isolated incisor with the same specimen number (PU 18869) probably represents I^1 (Figs. 2F and G). Its lingual face is flat, and labially it is convex. The cutting edges are convex and end basally in a small cusp. A lingual rib is present as in I^2 . Maximum crown height (16.7 mm) is much greater than maximum crown length (13.1 mm). On the basis of size it appears that this incisor cannot fit into the premaxilla of the same number. Another incisor (PU 18844), also from the *Plesiadapis simonsi* zone, resembles I^2 in shape, but it too is much larger (Fig. 2D and E; crown length is 10.5 mm; crown height is 11.7 mm). The I^2 of Figure 2D and E may be from an animal of the same size as that of the figured I^1 (Figure 2F and G). The crown bases of I^2 and I^3 are more skewed than that of I^1 .

Lower incisors of *Probathyopsis harrisorum*, preserved in PU 18869, are strong, pointed teeth, closely spaced and lacking diastemata. They have a small heel and, as a result, the posterior edge of each tooth is concave (Fig. 2H and I), which distinguishes them from upper incisors. The anterior cutting edge is convex. I_2 is the largest of the lower incisors (crown length 13.9 mm; crown height measures 18.3 mm but the tip is worn). I_1 is next largest incisor (crown length is 13.9 mm; height is 14.2 mm with the tip worn). I_3 is the smallest of the lower incisors (crown length is 12.8 mm; height is 11.1 mm). No diastema separates I_3 from the lower canine. The lower canine is a simple pointed tooth. Its anterior and posterior cutting edges are somewhat thickened. The crown measures 17.2 mm in maximum length and 11.1 mm in height.

Two size classes of dentaries are apparent in the Tiffanian of the Clark's Fork Basin (Fig. 3). The larger form, presumably male, has an anteriorly deepening ramus with a very large mandibular flange (e.g., PU 14991), while the smaller form (PU 18869) has a much smaller flange that descends abruptly. Mandibular depth of the smaller form, presumably female, is less than that of the larger form (see Table 1). In life, the mandibular flanges fit between the upper canines when the mouth was closed, suggesting a correlation between flange size and canine size. FMNH P14950, an upper canine fragment from the Tiffanian Plateau Valley beds, is much larger (measuring 28.5 by 18.5 mm at the base of the crown) than the upper canine associated with PU 18869 (measuring 24.4 by 15.4 mm at the base of the crown). These two specimens probably represent males and females (compare Figs. 5A and B). PU 14861, which includes parts of another upper canine (measuring approximately 24 by 16 mm at the base of the crown), is probably also a female. Dorr (1958) reasoned similarly that *Probathyopsis* (= *Prouintatherium*) with large mandibles and canines are males, and *Probathyopsis* from the same stratigraphic intervals with small mandibles and canines represent females.

An alveolus for P_1 is present in PU 14991 just behind the canine. This tooth may have been present in all specimens of *Probathyopsis harrisorum*. Three additional dentaries of *P. harrisorum* are known: the holotype of *Probathyopsis newbilli* and possibly the holotype of *Bathyopsoides harrisorum* from Plateau Valley beds have an alveolus for P_1 . A small broadening in the diastema of PU 18869 just behind the canine shows that this specimen too may have had a P_1 early in life, the alveolus being filled with bone after the tooth itself was shed. Thus this tooth may have been present in all *Probathyopsis harrisorum*, in contrast to the statement by Schoch and Lucas (1985) that its presence varies intraspecifically.

PU 18869 has another peculiarity. The specimen consists of parts of both dentaries. The left dentary preserves M_3 , but the rest of its alveolar border is badly damaged: only the canine alveolus is clearly visible, and no parts anterior to that are preserved. The right dentary preserves the mandibular flange with the canine alveolus and following diastema (interrupted by the filled P_1 alveolus mentioned above). When the two dentaries are combined into one composite figure

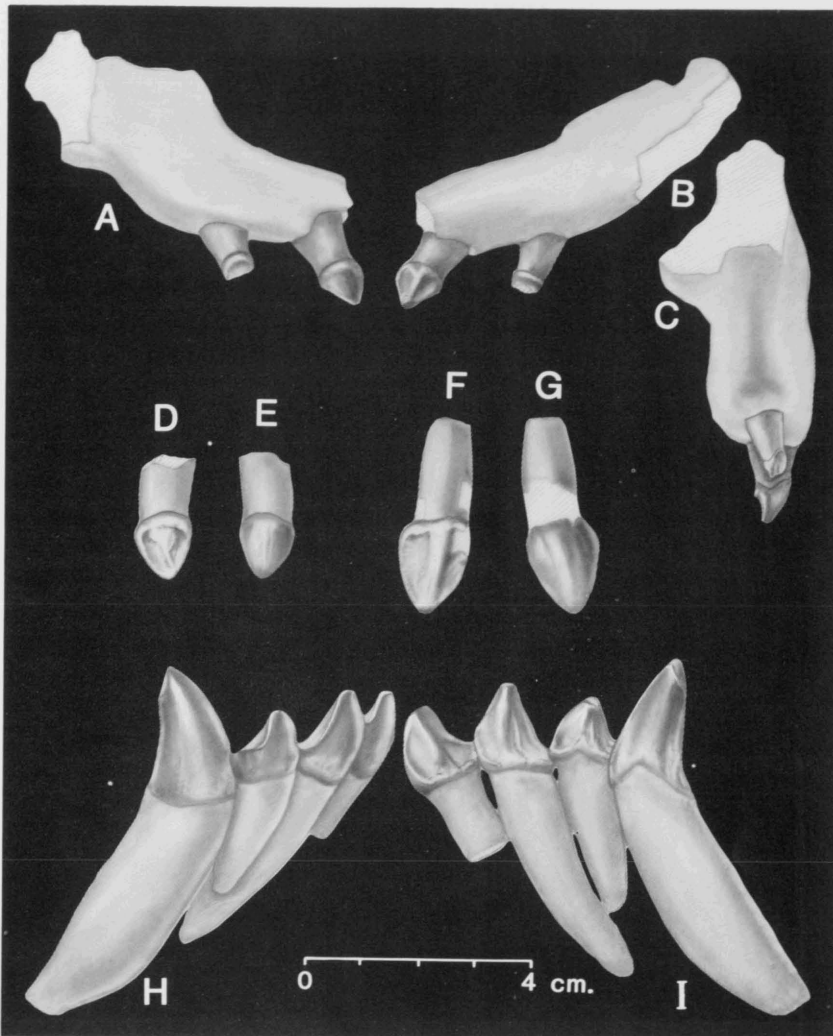


FIG. 2.— Anterior dentition of *Probathyopsis harrisorum*, based largely on specimen PU 18869 (approximate coordinates of locality: NE 1/4, Section 12, T57N, R101W). A-C, partial right premaxilla with I^2 and root and crown base of I^3 (PU 18869 in labial, lingual, and posterior views). D-E, isolated I^2 (PU 18844 in lingual and labial views). F-G, isolated I^1 (PU 18869 in lingual and labial views). H-I, I_1 -C (PU 18869 in lateral and lingual views). PU 18844 is morphologically similar to I^2 in PU 18869, but much larger. Both specimens are from the *Plesiadapis simonsi* zone and PU 18844 is probably from a (male?) individual much larger than that represented by PU 18869. All incisors of *Probathyopsis*, except I^1 , are in place in a premaxilla or reliably reassociated using interproximal contact facets. The tooth in illustrations F and G differs in form from incisors of known position, and we therefore assume that it is I^1 . It is, however, too large to fit into the premaxilla of the same number. Thus PU 18869 may include remains of two different individuals. Lower incisors of prodinoceratids are single-cusped, in contrast to those of uintatheriids, and the lower canines are not incisiform.

(as in Fig. 3A), the distance between the canine and M_3 is about 110 mm. Isolated P_3 , P_4 , and M_2 with the same specimen number, PU 18869, together add up to a total length of 46 mm. The diastema measures at least 45 mm. This leaves only 19 mm for the missing P_2 and M_1 , which is clearly not enough space to include these teeth. Thus the assumption on which the reconstruction is based, namely that the left and right dentaries are mirror images of each other, cannot be valid. We suspect that the diastema of the right dentary is secondarily enlarged by a pathological(?)

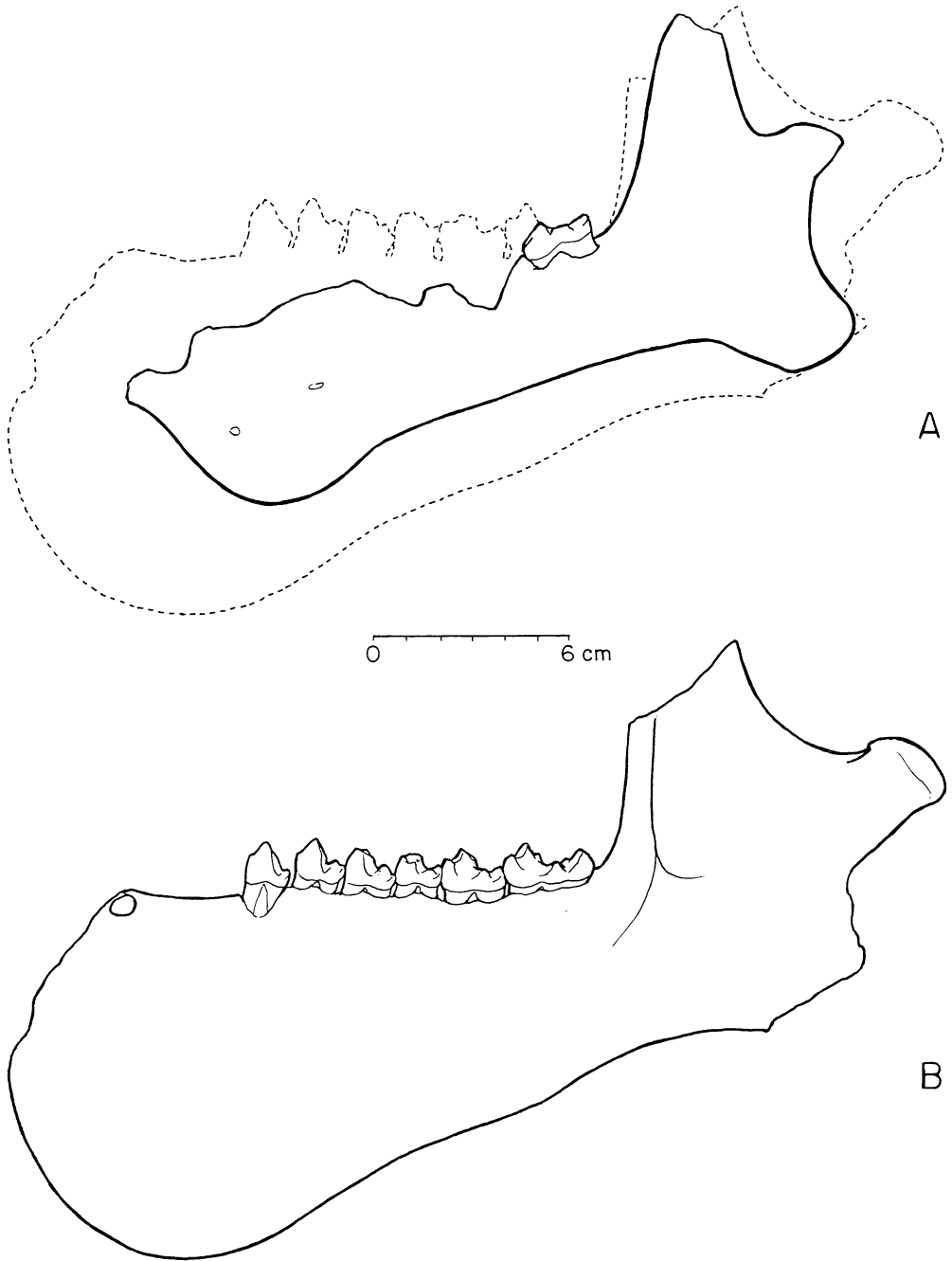


FIG. 3— Graphic comparison of dentaries of *Probathyopsis harrisorum*. A, PU 18869, presumed female, reconstructed from partial left and right dentaries of the same animal). B, PU 14991, presumed male. Outline of male superimposed on female in upper figure shows size and shape differences distinguishing the sexes. Note the alveolus for P_1 in PU 14991. Dentaries of *Probathyopsis harrisorum* are much larger than those of *P. praecursor* (compare Fig. 4, drawn to the same scale).

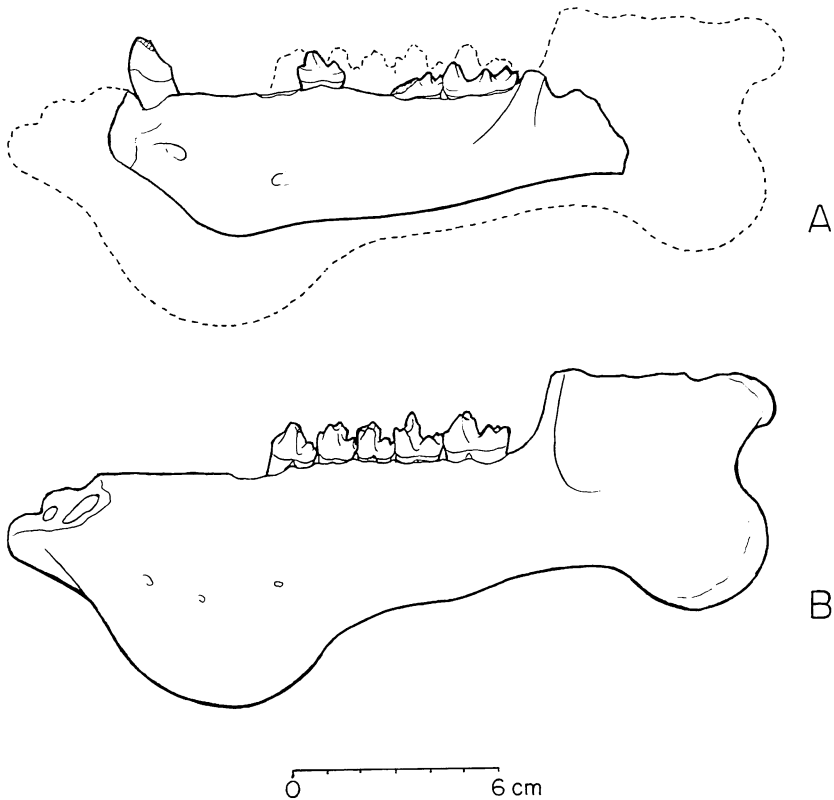


FIG. 4— Graphic comparison of dentaries of *Probathyopsis praecursor*. A, AMNH 16786, holotype and presumed female, redrawn from Simpson, 1929. B, UM 27249, holotype of synonym *Prouintatherium hobackensis* and presumed male. Outline of male superimposed on female in upper figure to show size and shape differences between the sexes. Dentaries of *Probathyopsis praecursor* are much smaller than those of *P. harrisorum* (compare Fig. 3, drawn to the same scale).

absence of teeth. Pathology is also suggested by the width of the left dentary near its alveolar border. At this point the left dentary is much broader than the right dentary, as it housed the roots of teeth missing on the right side. Asymmetry of wear in the lower incisors, P^4 and M^1 , is a further indication that this specimen was aberrant.

Measurements of the cheek teeth of *Probathyopsis harrisorum* are presented in Table 2 (Plateau Valley sample) and Table 3 (Bighorn Basin and Clark's Fork Basin sample).

One dinoceratan astragalus is known from Plateau Valley beds (FMNH P26063, Fig. 6A and B). It has a distinctive neck and an unextended trochlear facet (cf. *Bathyopsis* in Fig. 7). The ectal facet is longer proximodistally than it is wide mediolaterally. An astragal canal is present, and the fibular facet is well developed (as in all later Dinocerata, in contrast to a statement by Cifelli, 1983).

Discussion.—The holotype of *Bathyopsoides harrisorum* (FMNH P15546) is comparable in size and shape to PU 14991 from the northern Bighorn Basin. Additional material of this large form consists of parts of a skull (FMNH P15552). Based on a comparison of skull length (31 cm), we estimate the weight of larger specimens (presumed males) of *Probathyopsis harrisorum* to have been similar to that of *Tapirus bairdi*, that is, approximately 300 kg.

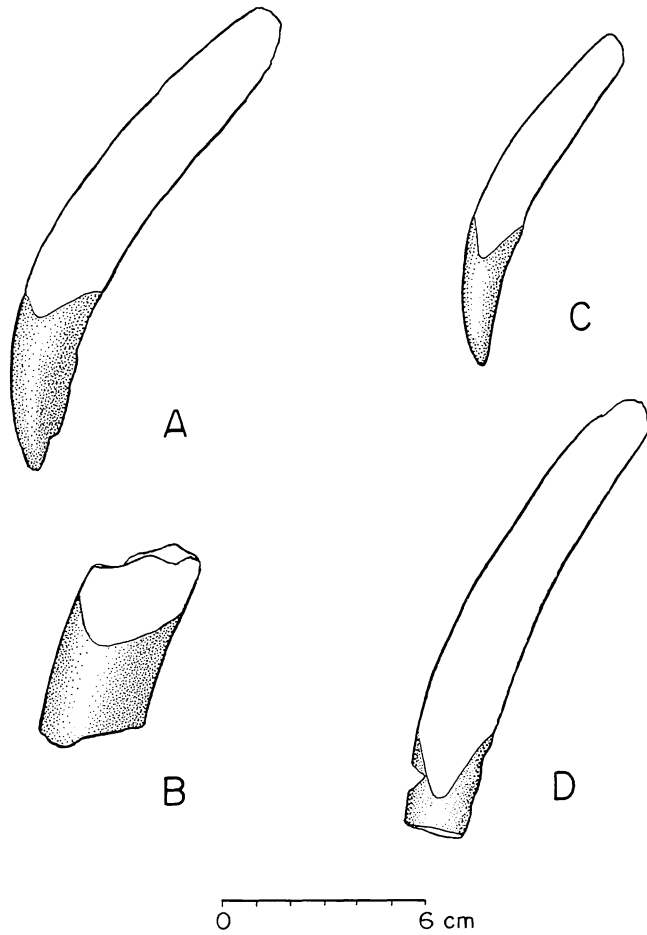


FIG. 5— Comparison of upper canines of *Probathyopsis*. A-B, at left, *P. harrisorum* (A, PU 18869, presumed female; B, PU 14950, presumed male). C-D, at right, *P. praecursor* (C, UM 13234, presumed female; D, UM 27250, presumed male). Note size differences between sexes and between species.

Synonymy of *Bathyopsoides harrisorum* and *Probathyopsis newbilli* was first suggested by Gazin (1956). The holotype of *Probathyopsis newbilli* (FMNH P15549), has a much smaller dentary than that of the holotype of *Bathyopsoides harrisorum*, although its teeth are only slightly smaller in size. The *P. newbilli* type dentary is clearly that of a juvenile: the deciduous premolars have been shed but M_3 has not yet erupted. Alveoli for C_1 , P_1 , and P_2 are well preserved and no diastemata are present between these teeth. This dentary has not yet reached adult size, but it compares well with small specimens of *Probathyopsis harrisorum* (e.g., PU 18869), presumed females, known from the Clark's Fork Basin.

As indicated above, it seems that the diastema of PU 18869 is larger than it would be in a normal individual, and a small diastema may not yet have developed in FMNH P15549. As for absolute size, we compared the juvenile (FMNH P15549) with an adult male (FMNH P15546, no well preserved adult female is available). In order to compare changes in mandible size during the ontogeny of mammals, the change in two descriptive indices was compared with that in a juvenile (UMMZ 81838, M_3 erupted, dC_1 not shed) and an adult (UMMZ 96180) of *Ursus americanus*. Relative diastema size (distance from C_1 to P_4 divided by the length of P_4 - M_3) differs between the

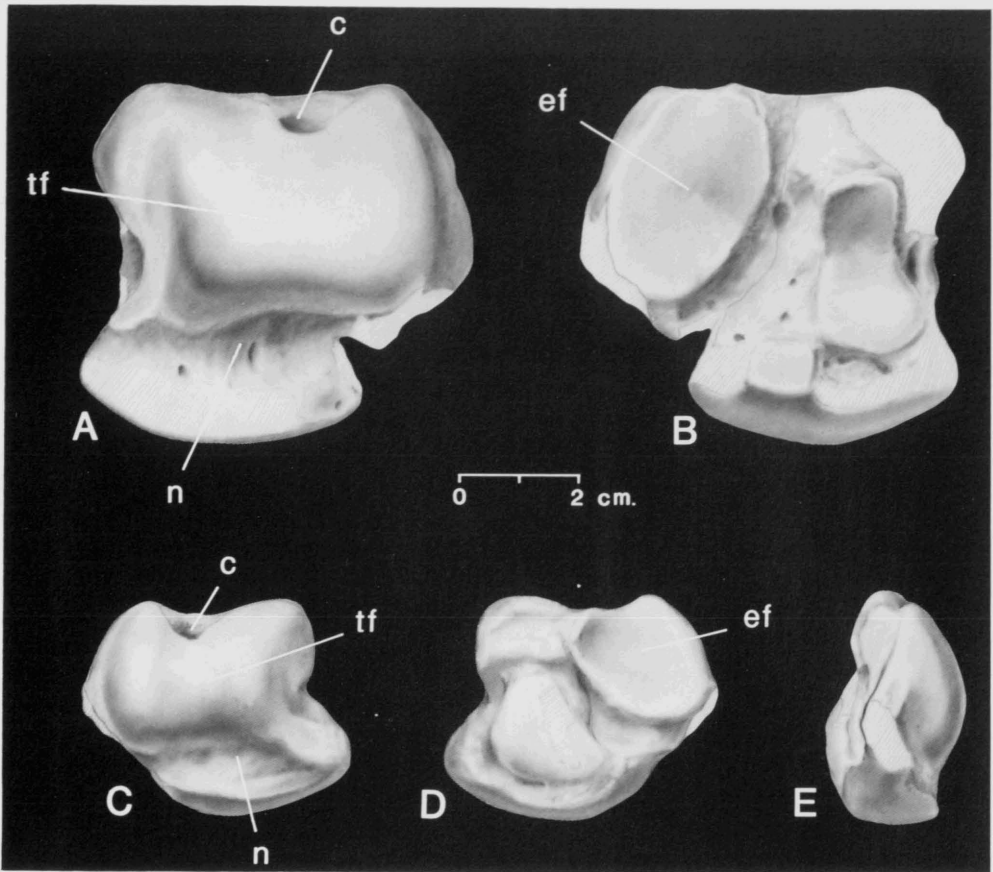


FIG. 6—Astragali of *Probathyopsis*. A-B, *P. harrisorum* (FMNH P26063 in dorsal and plantar view), C-E, *P. praecursor* (UM 77018 in dorsal, plantar, and lateral view). Note the smaller size and the medially expanded ectal facet (ef) of *P. praecursor*. Both prodinoceratid astragali shown here differ from those of uintatheriids (e.g., *Bathyopsis*, Fig. 7) in retaining an astragalar canal (c), a distinct astragalar neck (n), and an unexpanded trochlear facet (tf).

juvenile and adult dinoceratans by a factor 2.1, and in *Ursus* by a factor 1.9. Although the difference in dinoceratans is somewhat larger than that in *Ursus*, we assume that this could easily be compensated by the fact that the juvenile is a female rather than a male. Relative depth of the dentary (depth below the trigonid of M_2 divided by the length of P_4-M_3) increases ontogenetically by a factor of 1.6 in dinoceratans and 1.7 in *Ursus*. Dashzeveg (1982) describes a similar change in the ontogeny of diastema size when synonymizing *Prodinoceras* and "*Mongolotherium*." Thus the holotype of *Probathyopsis newbilli* is likely to be a juvenile specimen of the species of the holotype of *Bathyopsoides harrisorum*.

The presence of alveoli for upper incisors in "*Mongolotherium*" led Wheeler (1961) to suppose that these teeth were present in all Paleocene taxa. The upper incisors in Flerov's figure 35 (1957) are entirely hypothetical, as stated in his figure caption. Tong (1979) briefly described upper incisors of *Prodinoceras*. Upper incisors of *Probathyopsis* were not known previously.

Patterson (1939) reviewed the sample of dinoceratans known from the Plateau Valley beds of Colorado, source of the holotype of *Probathyopsis harrisorum*. Following Patterson (1939), the type locality of *P. harrisorum* is usually regarded as being late Tiffanian in age, but Gingerich

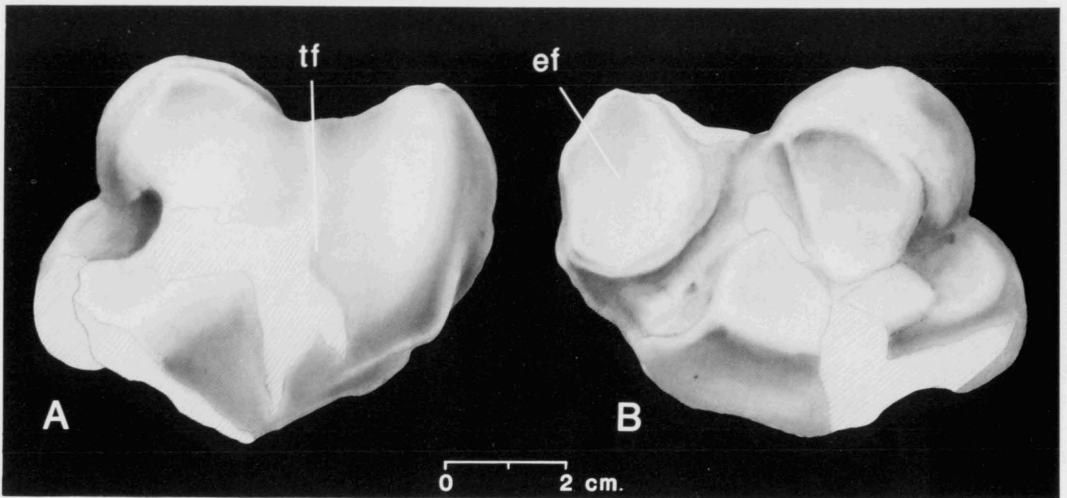


FIG. 7.— Astragalus of *Bathyopsis* sp. cf. *B. fissidens* (AMNH 17444, from Locality I, early Bridgerian of the Huerfano Basin; identified by Robinson, 1966, p. 60). A, dorsal view. B, plantar view. This astragalus resembles astragali of uintatheriids rather than prodinoceratids in lacking an astragal canal, lacking a neck, and in having an extended trochlear facet (*tf*). Note rounded ectal facet (*ef*).

(1976) and Kihm (1984, unpubl.) have suggested that it may be Clarkforkian. The presence of *P. harrisorum* in beds of both latest Tiffanian and early Clarkforkian age in the Bighorn and Clark's Fork basins corroborates correlation of the Plateau Valley beds with the Tiffanian-Clarkforkian transition elsewhere, but it is still not possible to determine with certainty whether the Plateau Valley beds are latest Tiffanian or early Clarkforkian in age.

The dentary is the most informative element of prodinoceratids yet identified: it indicates sex (Figs. 3 and 4), and usually also species (Figs. 3 and 4, and Table 1). Males of *P. harrisorum* are distinguished from either sex of *P. praecursor* by their deep mandibular flange (maximum mandibular depth in Table 1). Females of *P. harrisorum* have a longer dentary with a more anteriorly positioned flange than that seen in either sex of *P. praecursor* (anterior position of flange in Table 1). Unfortunately, the total number of known specimens is still small and reasonable samples are known only from the late Tiffanian to early Clarkforkian of Plateau Valley and the middle to late Clarkforkian of the Hoback Basin. Only one relatively complete dentary is known from the *Plesiadapis cookei* zone of the middle Clarkforkian.

Measurements of cheek teeth show some overlap in size between *Probathyopsis harrisorum* (Tables 2 and 3) and *P. praecursor* (Tables 4 and 5, see also Fig. 9). Since so few dentaries are known, the boundary between the species is conveniently placed at the early to middle Clarkforkian transition (transition from *Plesiadapis gingerichi* to *P. cookei* zones) where intermediates are rare. Schoch and Lucas (1985) claim that the presence of P_1 is intraspecifically variable. With the small amount of material available, it seems just as likely that P_1 was present in *P. harrisorum* but not in *P. praecursor*. We have therefore included this feature in diagnosing these species.

Hypodigm.—Clark's Fork Basin, Wyoming. *Plesiadapis simonsi* zone of late Tiffanian: PU 18320 (not seen), 18342, 18350, 18837, 18839, 18840, 18842 (includes 18845), 18843, 18844, 18849, 18866, 18869, 18920, 19106, 19118 (not seen), 19344 (not seen), 19345 (not seen), 19451 (not seen); UM 66213 and 68257. *Plesiadapis gingerichi* zone of early Clarkforkian: PU 13378, 18720, 18838, 19005 (not seen), 21524 (not seen), and 21676 (not seen); UM 68030, 68419, 68439, 71796, and 73333.

TABLE 1 — Selected measurements of dinoceratan mandibles from the late Tiffanian and Clarkforkian land-mammal ages of the northern Bighorn and Clark's Fork basins. All measurements are in millimeters. Tiffanian specimens are larger than those from the Clarkforkian. Male specimens have larger mandibles with relatively deeper mandibular rami and mandibular flanges than females. Anterior position of flange is distance from front of M₂ to point on top of dentary directly above deepest part of mandibular flange.

Specimen	Length of P ₃ -M ₃	Mandibular depth beneath M ₂	Maximum mandibular depth	Anterior position of flange	Sex
<i>Late Tiffanian</i> [Ti-5]					
FMNH P15546	92	63	94	80	Male
PU 14491	93	72	109	94	Male
PU 18869	—	42	70	91	Female
<i>Middle Clarkforkian</i> [Cf-2]					
UM 69668	—	52	—	87	Male
<i>Late Clarkforkian</i> [Cf-3]					
UM 27249	72	42	68	60	Male
UM 27250	—	38	—	—	Female
UM 77018	72	38	—	—	Female

TABLE 2 — Measurements of crown length (L) and width (W) of the cheek teeth of late Tiffanian or early Clarkforkian *Probathyopsis harrisorum* from Plateau Valley beds, Colorado. FMNH P15546 is holotype of *Bathyopsoides harrisorum* Patterson, and FMNH P15549 is holotype of junior synonym *Probathyopsis newbilli* Patterson.

Specimen	P3		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W
<i>Upper dentition</i>										
FMNH P15526							18.7	19.2		
<i>Lower dentition</i>										
FMNH PM239			15.8	10.9			20.7	15.3		
FMNH PM15584							19.4	18.8		
FMNH P15106							20.7	15.3		
FMNH P15546							20.1	14.8	25.0	15.9
FMNH P15549			15.4	11.1			18.4	12.7		
FMNH P15574			16.2	11.9	16.0	11.1	20.7	15.0		

Central Bighorn Basin, Wyoming. *Plesiadapis simonsi* zone: PU 14861. *Plesiadapis simonsi* zone?: PU 14991 (dentary mentioned by Wheeler, 1961, but not described). *Plesiadapis gingerichi* zone: UM 85250. *P. simonsi* or *P. gingerichi* zone: UM 77286.

Piceance Basin, Colorado (late Tiffanian in age according to Patterson, 1939, and Rose, 1981, but possibly Clarkforkian according to Gingerich, 1976, and Kihm, 1984, unpubl.): FMNH PM239; FMNH P14950, P15106, P15526, P15546, P15549, P15552, P15574, P15584, P26063, and P26117.

Specific determination questionable. From the Clark's Fork Basin, Wyoming—Tiffanian or Clarkforkian, *P. simonsi*, *P. gingerichi*, or *P. cookei* zone: UM 77286. Clarkforkian, zone unknown: PU 16444, UM 86622. *Plesiadapis gingerichi* or *P. cookei* zone: PU 20513 (not seen). From the northern Bighorn Basin, Wyoming—Clarkforkian, zone unknown: UM 85297, 85420,

TABLE 3 — Measurements of crown length (L) and width (W) of the cheek teeth of late Tiffanian and early Clarkforkian *Probathyopsis harrisorum* from the Bighorn and Clark's Fork basins, Wyoming.

Specimen	P3		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W
<i>Upper dentition</i>										
PU 18720			12.0	13.1			16.5	13.7	18.3	14.8
PU 18837			15.6	16.8						
PU 18869			12.3	15.3			20.1	18.0	22.9	21.4
<i>Lower dentition</i>										
PU 13378			12.9	8.6						
PU 14861									26.1	15.2
PU 14991	15.3	10.0	15.0	12.2	14.0	10.4	20.0	14.5	25.8	15.3
PU 18849			15.3	11.4						
PU 18869	14.5	9.4			14.0	10.5	17.9	13.5		
PU 19344					13.9	11.1				
UM 85250			12.6	8.4			15.7	10.9		

86618-86620. From Buckman Hollow, Green River Basin, Wyoming—*Plesiadapis gingerichi* or *P. cookei* zone: UM 71331, and 79846.

Probathyopsis praecursor Simpson, 1929
Fig. 4, 5C-D, and 6C-E

Probathyopsis praecursor Simpson, 1929, p. 2, fig. 1-3. Wheeler, 1961, p. 19, Pl. 13, fig. 3. Rose, 1981, p. 93, Pl. 4, fig. 1-2.
Probathyopsis successor Jepsen, 1930, p. 128, fig. 8-11. Wheeler, 1961, p. 19.
Probathyopsis? sp., Gazin, 1956, p. 16, Pl. 1, fig. 2-3. Wheeler, 1961, p. 21.
Probathyopsis sp., Jepsen, 1930, p. 129. Wheeler, 1961, p. 20.
Prouintatherium hobackensis Dorr, 1958, p. 508, Plate 75-77 (in part, see discussion).
Prodinoceras (in part), Dashzeveg, 1982, p. 92.

Holotype.—AMNH 16786, left and right dentary with left C, M₂ and M₃, right P₄, M₂, and M₃.

Type locality.—"Head of Big Sand Coulee" (Simpson, 1929), Clark's Fork Basin, Wyoming. According to Rose (1981) the specimen comes from the *Phenacodus-Ectocion* zone.

Types of synonyms.—PU 13234, holotype of *Probathyopsis successor*, consists of numerous associated teeth (left I₁₋₂, C₁; right M₃; left I², C¹, P³⁻⁴, M¹⁻³; and right P², M²⁻³) from Section 2, T55N, R101W, Clark's Fork Basin, Park County, Wyoming (Jepsen, 1930). UM 27249, holotype of *Prouintatherium hobackensis*, is a left dentary with P₃-M₃ from UM locality Sub-Wy-7 in the NE¼, Section 6, T38N, R113W, Hoback Basin, Sublette County, Wyoming.

Age and distribution.—Middle and late Clarkforkian (*Plesiadapis cookei* and *Phenacodus-Ectocion* zones) of the Clark's Fork Basin, and late Clarkforkian of the Hoback Basin.

Diagnosis.—P₁ absent, mandibles of both male and female are about 10% smaller than in *P. harrisorum*. This difference is more pronounced in length than in depth. The neck of the astragalus is shorter than in *P. harrisorum* and the ectal facet is more rounded.

Description.—The presence of upper incisors in *P. praecursor* is attested by association of I² with the holotype of synonym *P. successor* and by isolated incisors recovered at middle and late Clarkforkian localities (UM 65660, 77286 and 85991).

Lower incisors of *P. praecursor* were described by Jepsen (1930) for the holotype of synonym *Probathyopsis successor*. These compare well with *P. harrisorum* incisors, but specimens collected since 1930 indicate that Jepsen's "I₁" is really I², his "I₂" is I₁ and his "I₃" is I₂. Lower incisors of *P. praecursor* (UM 27254, 65478, 65556, 71440, and 83761) resemble those of *P. harrisorum*.

Size dimorphism like that of *P. harrisorum* was described by Dorr (1958) for the type material of *Prouintatherium hobackensis* from the Hoback Basin. Large canines are present in the large form (measuring 23.5 by 18.2 mm in diameter at the base of the crown in UM 27249) and small canines are present in the small form (these measure 15.1 by 11.6 mm at the base of the crown in UM 27250, and 15.3 by 11.1 in UM 27251). We agree with Dorr (1958) and later authors that this is due to sexual dimorphism. The mean size of these mandibles is smaller than that of specimens from the *Plesiadapis simonsi* zone (see Figures 3, 4, and Table 1). P₁ is absent in the only ramus that preserves the diastema (UM 27249). Size decrease of the cheek teeth in the evolution of the genus is suggested by Figure 9, but samples are too small to substantiate this fully.

Dentary and canine dimorphism is also evident in Prodinoceratidae from the *Phenacodus-Ectocion* zone of the Clark's Fork Basin. UM 77018 represents a dentary of the smaller sex, and so does AMNH 16786, the holotype of *Probathyopsis praecursor*. PU 13234, holotype of *P. successor*, has a small upper canine (measuring 15.2 by 11.0 mm in diameter at the base of the crown), as does PU 16163 (measuring 18.8 by 11.5 mm at the base of the crown). UM 71677, from the same area of the Clark's Fork Basin, has a much larger upper canine (measuring 26.6 by 14.6 mm in diameter at the base of the crown).

A dinoceratan astragalus from the *Phenacodus-Ectocion* zone (UM 77018, Fig. 6C-E) is about half the size of the astragalus described for *Probathyopsis harrisorum*, and its neck is somewhat shorter. As in *P. harrisorum*, there is an astragalar foramen and the trochlear facet is unextended. The ectal facet, however, is larger transversely than proximodistally.

Discussion.—Synonymy of *P. successor* with *P. praecursor* was suggested by Rose (1981). Synonymy of *Prouintatherium hobackensis* with *Probathyopsis praecursor* was also proposed by Rose (1981). Tong and Lucas (1982) synonymized *Prouintatherium* and *Probathyopsis*. As mentioned before, the canine figured by Dorr (1958, his Plate 77, fig. 14) for "*Prouintatherium hobackensis*" is probably a deciduous canine of *Coryphodon*. The astragalus figured by Dorr (his Plate 76, figs. 18 and 19) is undoubtedly also *Coryphodon*. We doubt Schoch and Lucas' (1985) claim that all postcrania referred to *Prouintatherium hobackensis* by Dorr (1958) are *Coryphodon*. Known Clarkforkian *Coryphodon* are all approximately twice as large as *Probathyopsis praecursor*, and most adult limb bones from Dorr's *Prouintatherium* quarry are closer in size to *Probathyopsis* than to *Coryphodon*.

Hypodigm.—Clark's Fork Basin, Wyoming. *Plesiadapis cookei* zone: PU 17933, 18141, 18717, 19346, 19540 (not seen), and 20826 (not seen); UM 63279, 65042, 65478, 65556, 65660, 66134, 66334, 66539, 66544, 66763, 66769, 67023, 68244, 69668, 69670, 69696, 69937, 71184, 71440, 75456, 83761, 85971, 86152, 86159, and 86275. *Phenacodus-Ectocion* zone: AMNH 16786, PU 13234, 16163, and 18145 (not seen); UM 65071, 66146, 67457, 67460, 68206, and 71677.

Hoback Basin, Wyoming. *Phenacodus-Ectocion* zone according to Rose, 1981: UM 27249, 27250, 27251, 27252, and 27254.

TABLE 4 — Measurements of crown length (L) and width (W) of the cheek teeth of middle and late Clarkforkian *Probathyopsis praecursor* from the Bighorn and Clark's Fork basins, Wyoming. AMNH 16786 is holotype of *Probathyopsis praecursor* Simpson, and PU 13234 is holotype of junior synonym *Probathyopsis successor* Jepsen.

Specimen	P3		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W
<i>Upper dentition</i>										
PU 13234			12.7	13.7	13.3	12.0	18.0	16.0	20.5	18.3
PU 16163	11.2	12.7	11.5	13.3	13.1	13.6	18.3	16.8	19.4	19.4
PU 18141									21.0	21.5
PU 18717			13.3	14.7					22.2	18.6
UM 63279			12.3	14.1						
UM 65042	11.8	12.2							20.0	20.2
UM 65071	11.3	12.7	12.0	14.1	12.7	11.1				
UM 65660							18.9	16.8	22.2	20.2
UM 66769							18.9	17.0		
UM 69696	10.8	12.4	11.9	13.7	11.9	11.2	15.8	14.4	17.9	17.0
UM 86159			13.7	13.6						
<i>Lower dentition</i>										
AMNH 16786			13.4	9.4					21.0	12.5
PU 18717							18.3	12.4	24.6	14.7
PU 19540					12.6	9.2				
UM 65042									21.6	12.5
UM 65071			12.5	9.3			16.3	10.5		
UM 65660									23.9	15.0
UM 67460							15.9	12.7		
UM 68206	14.4	8.8	14.5	10.4						
UM 68244			13.2	9.3	13.6	10.9			20.9	13.3
UM 71440	21.2	11.4	13.7	8.9	14.5	11.2				
UM 77018			12.1	11.3					20.6	13.5
UM 86152									23.7	14.3

TABLE 5 — Measurements of crown length (L) and width (W) of the cheek teeth of late Clarkforkian *Probathyopsis praecursor* from the Hoback Basin, Wyoming. UM 27249 is holotype of *Prouintatherium hobackensis* Dorr.

Specimen	P3		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W
<i>Upper dentition</i>										
UM 27249	12.6	13.1	13.2	13.2	10.8	12.7	18.1	17.8	21.2	18.8
UM 27250	10.2	12.3	11.0	12.7	10.0	10.0	15.3	14.8	18.7	16.7
UM 27251					11.7	10.5	16.0	15.6	19.4	17.0
UM 27252									18.5	18.5
<i>Lower dentition</i>										
UM 27249	12.1	8.3	11.9	9.4	11.5	8.4	16.8	12.0	21.9	13.9
UM 27250					11.7	8.8	15.8	10.9	18.8	12.3
UM 27251			13.9	8.7			15.8	11.6	20.9	12.7

Probathyopsis? lysitensis Kelley and Wood, 1954

Fig. 8

?*Bathyopsis fissidens* (in part), Cope, 1882, p. 176; 1885, p. 600, Pl. 58a, fig. 7.

Probathyopsis lysitensis Kelley and Wood, 1954, p. 356, fig. 10 a-b. Wheeler, 1961, p. 20. Guthrie, 1967, p. 41.

Prodinoceras lysitensis, Dashzeveg, 1982, p. 93.

Holotype.—ACM 11167, associated left P_{3-4} , fragments of M_1 and M_2 , and intact M_3 ; right P_{3-4} , M_1 , fragment of M_2 , and intact M_3 .

Type locality.—"Type locality of the Lysite member of the Wind River Formation," Wyoming (Kelley and Wood, 1954).

Age and distribution.—Late Wasatchian (Lysitean subage of the late Wasatchian land-mammal age) of the Wind River Basin and Bighorn Basin (Schankler, 1980), Wyoming.

Discussion.—Cope (1882, 1885) described a dinoceratan collected by J. Wortman during his 1881 collecting expedition to the Bighorn Basin. This specimen, said to include a considerable part of the mandibular dentition, was never adequately figured. It is now evidently lost. Wortman's 1881 collection included species characteristic of the middle and late Graybullian and the Lysitean subages of the Wasatchian land-mammal age (Gingerich, 1980). Dinoceratans have never been found in Graybullian strata. Consequently, it appears likely that Cope's specimen, if indeed a dinoceratan, was the first record of *Probathyopsis? lysitensis*.

Few differences in morphology distinguish the type sample of *Probathyopsis? lysitensis* from other Wasatchian and Clarkforkian dinocerates. Most of the differences described by Kelley and Wood (1954) and by Guthrie (1967) are variable within single populations. For example, the lack of a swelling on the labial base of P_4 in *P.? lysitensis* does constitute a difference from the type specimen of *P. praecursor* (Kelley and Wood, 1954; Schoch and Lucas, 1985), but not from the Hoback Basin sample of *P. praecursor*. *P.? lysitensis* has a strong hypoconulid crest on M_3 (Kelley and Wood, 1954; Schoch and Lucas, 1985), a feature not observed in *Probathyopsis praecursor*, but present in *Bathyopsis* and some specimens of *Probathyopsis harrisorum* (e.g., PU 14991).

We refer three new specimens from the late Wasatchian (Lysitean) of the central Bighorn Basin to *P.? lysitensis* (Fig. 8). UM 86621 includes a worn M^1 , broken I_2 , and trigonid of M_3 . USGS 12765 is an unworn M^1 . YPM 22954 is an isolated M^3 . These agree well in general morphology with Tiffanian and Clarkforkian *Probathyopsis*, but some differences do exist. In both M^1 and M^3 (the only upper teeth known) the labial cusps are sharper and more acutely angled than in the Tiffanian and Clarkforkian species, a resemblance to later *Bathyopsis*. *Probathyopsis? lysitensis* is larger than *P. praecursor*, while the trend for the Tiffanian and Clarkforkian is clearly one of size decrease (Fig. 9). *P.? lysitensis* is stratigraphically separated from other *Probathyopsis* by a gap in the early and middle Wasatchian record, while it is not separated from late Wasatchian and early Bridgerian *Bathyopsis* (see below). For all these reasons we query the generic allocation of "*Probathyopsis? lysitensis*"—it may well prove to fit more comfortably in *Bathyopsis* rather than *Probathyopsis*.

Hypodigm.—Wind River Basin, Wyoming: holotype, and ACM 3870 (left M_1 , identified as dP_3 by Guthrie, 1967, with associated tooth fragments). Bighorn Basin, Wyoming: UM 86621 (left M^1 , right I_2 , left M_3 trigonid), USGS 12765 (left M^1), and YPM 22954 (right M^3).

TABLE 6 — Principal morphological characteristics of *Probathyopsis harrisorum* and *P. praecursor* compared to those of other Prodinoceratidae and Uintatheriidae. Column for *Prodinoceras martyr* includes information based on junior synonyms. Column for *Bathyopsis* includes information from both *B. fissidens* and *B. middelswarti*. *Uintatherium anceps* is assumed to represent all species of advanced North American uintatheriids *Uintatherium*, *Tetheopsis*, and *Eobasileus*. Queries denote missing information.

Morphological characteristics	Prodinoceratidae			Uintatheriidae	
	North American <i>Probathyopsis harrisorum</i> Late Paleocene	North American <i>Probathyopsis praecursor</i> Early Eocene	Asian <i>Prodinoceras martyr</i> Early Eocene	North American <i>Bathyopsis</i> spp. E./M. Eocene	North American <i>Uintatherium anceps</i> Middle Eocene
<i>Cranium</i>					
Cranial horns	Absent	?	Absent	Small	Large
<i>Upper dentition</i>					
I ¹	Present	Present	Present	Present	Absent
I ²⁻³ relative to I ¹	Small	Small	Similar	Small	Absent
M ¹ relative to M ²	Much smaller	Much smaller	Smaller	Smaller	Smaller
Outline of P ⁴ and M ¹	Circular	Circular	Broad transversely	Circular	Circular
<i>Lower dentition</i>					
Incisors	Single-cusped	Single-cusped	Single-cusped	Double-cusped	Double-cusped
Canine	Caniniform	Caniniform	Caniniform	Caniniform	Incisiform
First premolar (P ₁)	Present	Absent	Absent	Present	Absent
M ₁ relative to M ₂	Much smaller	Much smaller	Smaller	?	Smaller
<i>Astragalus</i>					
Astragalar canal	Present	Present	Possibly absent	Absent	Absent
Astragalar neck	Long	Short	Short	Absent	Absent
Trochlear facet	Small	Small	Small	Expanded	Expanded
Ectal facet	Elongated	Rounded	?	Rounded	Rounded

SYNOPSIS OF THE EVOLUTION OF *PROBATHYOPSIS*

All Tiffanian and Clarkforkian Dinocerata from North America are referable to one genus, *Probathyopsis*, representing a single evolutionary lineage. The principal morphological characteristics of each of the two species of *Probathyopsis* are listed in Table 6 for comparison with other dinoceratans. This table summarizes discussion and comparisons presented in the preceding text.

The *Probathyopsis harrisorum* - *P. praecursor* lineage is interesting as an example of a lineage becoming smaller over time (Fig. 9, compare Tables 2 and 3 with Tables 4 and 5). Late Tiffanian and early Clarkforkian *P. harrisorum* is about 10% larger in lower jaw length than middle and late Clarkforkian *P. praecursor*, although this difference is masked in small samples by sexual dimorphism. In the eleven dentaries available for study, smaller forms within *P. harrisorum*, interpreted as females, are nearly the same size as larger forms within *P. praecursor*, interpreted as males.

Decreasing body size is reflected in a trend toward decreasing size of the premolars and molars, teeth usually little affected by sexual dimorphism. As shown in Figure 9, diminution in crown

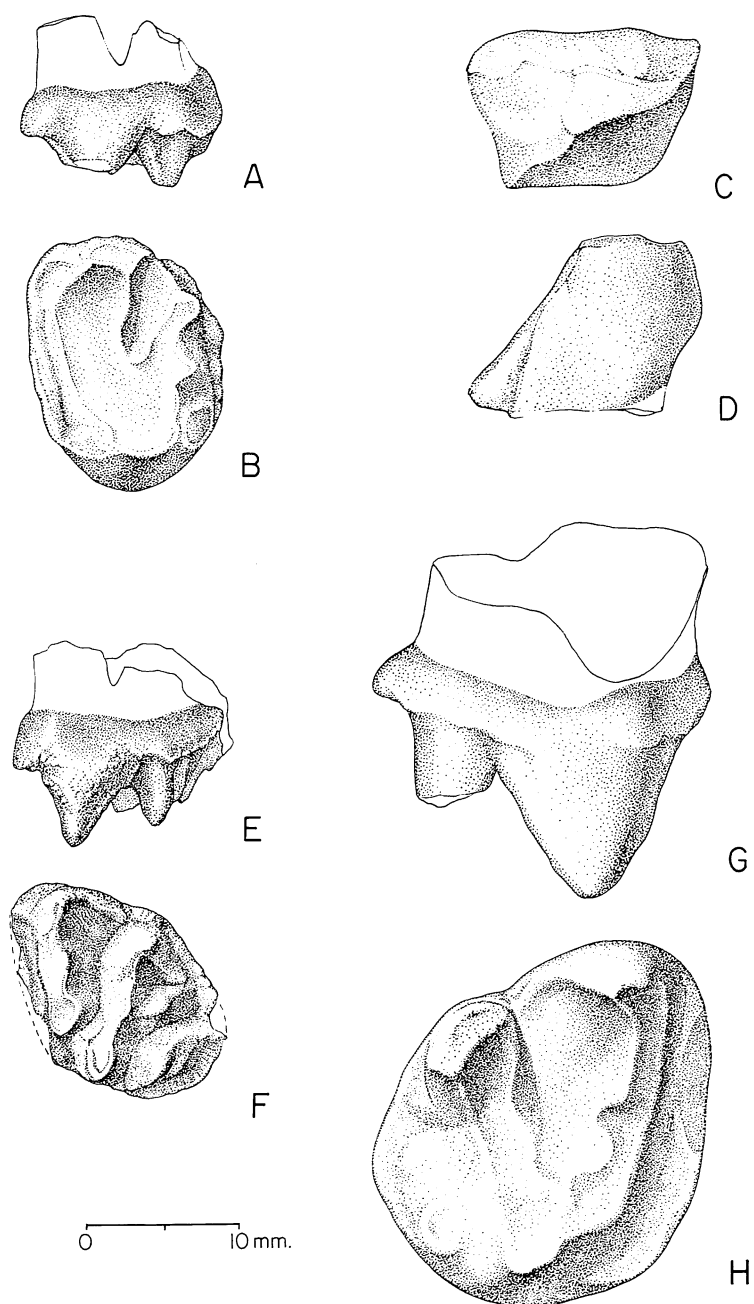


FIG. 8— *Probathyopsis? lysitensis* from the late Wasatchian (Lysitean) land-mammal age of the Bighorn Basin, Wyoming. A-B, worn left M¹ (UM 86621), labial and occlusal view. C-D, right I₂ (UM 86621, occlusal and labial view, apex and posterior margin are broken). E-F, isolated left M¹, unworn (USGS 12765, labial and occlusal view). G-H, isolated right M³ (YPM 22954, labial and occlusal view). Note acute labial cusps on unworn M¹ and little worn M³.

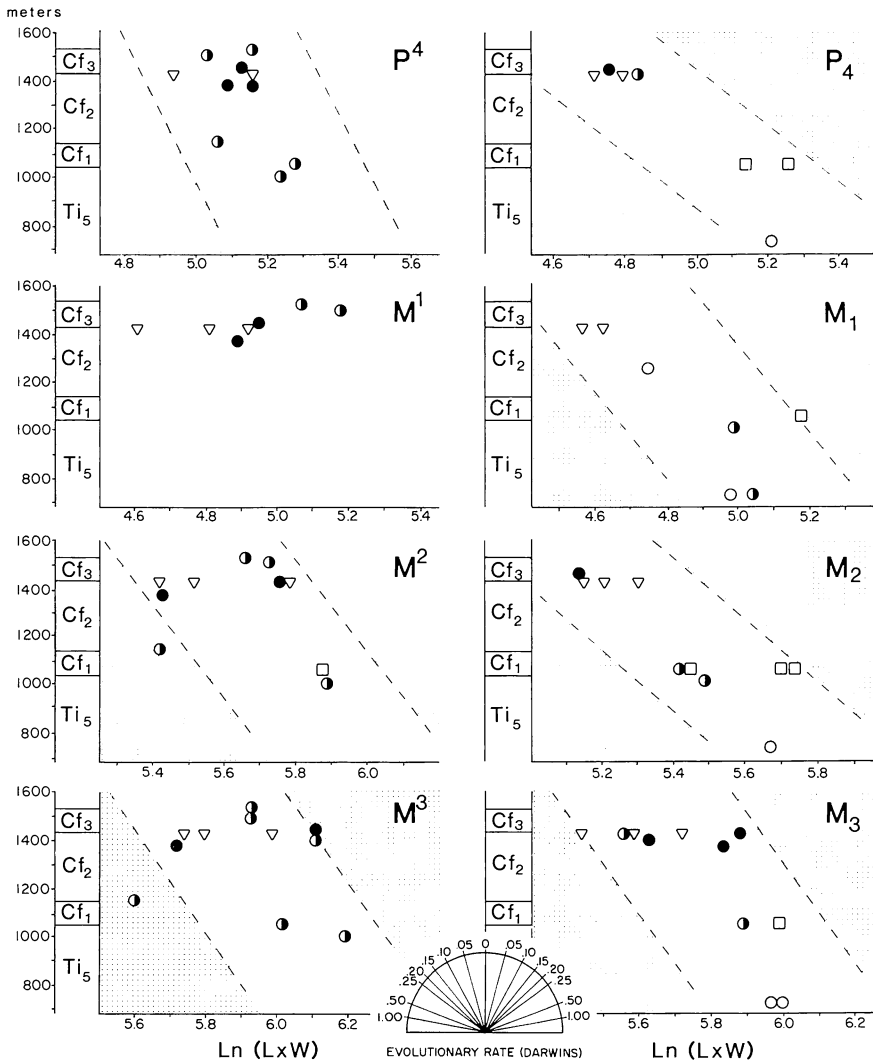


FIG. 9— Stratophenetic diagram showing size change over time in *Probathyopsis harrisorum* and *P. praecursor*. Abscissa is natural logarithm of crown length multiplied by crown width. Ordinate is stratigraphic level of specimens in measured sections in the Clark's Fork Basin. *Probathyopsis* appears in the *Plesiadapis simonsi* zone (approximately 700 m level) and disappears at the end of the *Phenacodus-Ectocion* zone (approximately 1515 m level). Circles represent specimens from the northern Bighorn and Clark's Fork basins. Triangles represent Hoback Basin specimens correlated faunally. Squares represent Piceance Basin specimens correlated faunally. Solid symbols indicate that specimen comes from a measured stratigraphic section, half-open symbol indicates that stratigraphic level is approximately known; open symbol indicates that a given specimen is constrained only to zone. Darwinometer is based on assumed constant sedimentation rate of 280 m/my, following Gingerich (1983). Dashed lines parallel regression of tooth size on stratigraphic level. These span 0.5 natural logarithm units, an approximation of the range of variation in these sexually dimorphic species. Note that all teeth known from the stratigraphic interval sampled here show a similar trend towards decreasing size.

area of the cheek teeth took place at rates varying from about 0.10 to 0.30 darwins, rates typical of those documented elsewhere for change over million-year time intervals.

In addition, the morphology of the astragalus changed significantly during the evolutionary history of *Probathyopsis*, judging from the two known specimens: the length of the neck decreased and the ectal facet became wider. Interestingly, reduction in the length of the astragalus neck exceeds reduction in the size of the astragalus itself, which is associated in turn with decreasing overall body size in *Probathyopsis*. Thus reduction in the length of the astragalus neck cannot be explained as a graviportal adaptation.

The stratigraphic boundary between lineage segments *Probathyopsis harrisorum* and *P. praecursor* is an arbitrary one, here drawn to correspond to the boundary between the early and middle Clarkforkian (between the *Plesiadapis gingerichi* and *P. cookei* zones), an interval where few *Probathyopsis* specimens are known. There is considerable overlap in measurements of *P. harrisorum* and *P. praecursor*. *Probathyopsis harrisorum* dentaries appear to differ from those of *P. praecursor* in being more elongated (compare anterior position of flange documented in Table 1). A single dentary (UM 69668) represents the transition from one species to the other and this specimen, from the base of the *Plesiadapis cookei* zone, has a large mandibular flange. It is intermediate in length between *Probathyopsis harrisorum* and *P. praecursor* (anterior position of flange in Table 1) and thus appears transitional.

These observations on evolution within *Probathyopsis* suggest that careful study of all North American dinoceratans in stratigraphic and biostratigraphic context would amply repay the effort in providing important documentation of evolutionary patterns and rates. Further study would also clarify generic transitions within this group. *Bathyopsis* is particularly interesting as a genus intermediate between the two dinoceratan families Prodinoceratidae and Uintatheriidae.

SEXUAL DIMORPHISM IN *PROBATHYOPSIS*

Sexual dimorphism has long been recognized in uintatheriids (cf. Osborn, 1881; Marsh, 1885), but Dorr's study of *Prouintatherium* (Dorr, 1958) was the first to document dimorphism in prodinoceratids. In *Probathyopsis* (= *Prouintatherium*), the cheek teeth are similar in size in both sexes, but strong dimorphism is present in dentary size and shape.

The dentary of a male *Probathyopsis harrisorum* is approximately 10% longer and 40% deeper than that of a female, and the shape of its ventral margin is different. The dorsal and ventral margins of the dentary diverge gradually in male *Probathyopsis*, while the dorsal and ventral margins of the dentary are more or less parallel and the mandibular flange develops more abruptly in females (Fig. 3).

Upper canines of *Probathyopsis* are also dimorphic. No complete upper canines are known for male *Probathyopsis*, but a comparison of measurements of canine diameter at the base of the crown indicates that male canines were significantly larger than those of females (see also Figs. 5B and D). In *P. harrisorum* upper canines of males (FMNH P-14950) appear to be about 18% larger in diameter than those of females (PU 14861 and 18869). In *P. praecursor* the difference is much greater. Upper canines of males (UM 27249 and 71677) are 40-50% larger in diameter than those of females (PU 13234, 16163, and UM 27250). In *P. harrisorum*, dimorphism in canine diameter (18%) exceeds dimorphism in overall body size dimorphism (10%, based on dentary length). In *P. praecursor*, canine dimorphism may have exceeded body size dimorphism by an even greater margin.

PALEOENVIRONMENT OF NORTH AMERICAN DINOCERATA

Probathyopsis exhibits an interesting stratigraphic distribution in the Clark's Fork and Bighorn basins. It first appeared in the late Tiffanian and remained an important if rare faunal element through the Clarkforkian. Paleobotanical evidence indicates that the dominant vegetation during this interval was broad-leafed evergreen forest (Hickey, 1980). The early Wasatchian, when *Probathyopsis* disappeared, coincides with development of more seasonally dry and open forests than were present during the Paleocene. Forests remained, but these were separated by areas of park woodland and park savanna. Heliothermic iguanid lizards flourished (Gautier, 1982). By the middle and late Wasatchian (Graybullian and Lysitean), wind pollinated plants indicative of open habitats were common (Wing, 1980, pers. comm.). Three, possibly four, specimens of *Probathyopsis? lysitensis* are known among tens of thousands of identified mammalian specimens known from this interval in the central Bighorn Basin. The latest Wasatchian (Lostcabinian) records an increase in floral diversity with introduction of warmer subtropical and tropical trees (Wing, 1980). Dinoceratans have not been found in latest Wasatchian faunas of the Bighorn Basin, but *Bathyopsis* is moderately common in Wind River Basin faunas of this age (Stuckey, 1984).

The distribution and relative abundance of latest Paleocene and early through middle Eocene dinoceratans appear to mirror inversely the distribution and relative abundance of equid perissodactyls (Gingerich, 1981). Dinoceratans appear to have been most common in forest environments of the Tiffanian and Clarkforkian, virtually absent in open environments characteristic of most of the Wasatchian, and again more common in forest environments of the Bridgerian. Equid perissodactyls were absent during the Tiffanian and Clarkforkian (not yet having dispersed to North America), abundant in open environments of the Wasatchian (*Hyracotherium*), and rare in forest environments of the Bridgerian (*Orohippus*). This is not to suggest that dinoceratans and equids were in any sense linked ecologically, but rather to emphasize that both exhibit a common (if reversed) pattern of environmental association, an association suggesting that dinoceratans probably lived in forested environments.

RELATIONSHIPS OF *PROBATHYOPSIS* AND *PRODINOCERAS*

Close relatives of North American Dinocerata include a number of taxa described from the Paleocene and Eocene of Asia (e.g., Matthew *et al.*, 1929; Flerov, 1952; Flerov, 1957; Chow, 1960; Chow and Tung, 1962; Tong, 1978; Zhai, 1978; Tong, 1979; Tong and Lucas, 1982; Schoch and Lucas, 1985). We do not have representative samples of these forms available, so we can only speculate about the closeness of phylogenetic ties between the groups. Dashzeveg (1982) documented the synonymy of *Prodinoceras* and "*Mongolotherium*." The enlarged hypodigm for this combined taxon permits a better understanding of its range of variation. Dashzeveg (1982) was also the first to appreciate that the holotype of *Prodinoceras* represents a juvenile individual.

Probathyopsis is sometimes regarded as a possible synonym of *Prodinoceras* (e.g., Rose, 1981; Dashzeveg, 1982; Schoch and Lucas, 1985). On the basis of measurements given by Tong (1978) for Chinese Paleocene taxa and the sample of North American Prodinoceratidae studied here, we compared proportions of tooth size in Asian and North American Prodinoceratidae (Fig. 10). P^4 , M^1 , and M^2 are considerably broader in Asiatic than in North American species. Furthermore, M^1 is, in comparison with P^4 and M^2 , larger in the Asiatic species, and M_1 is larger in comparison with M_2 . These comparisons seem to hold also in the figures of "*Mongolo-*

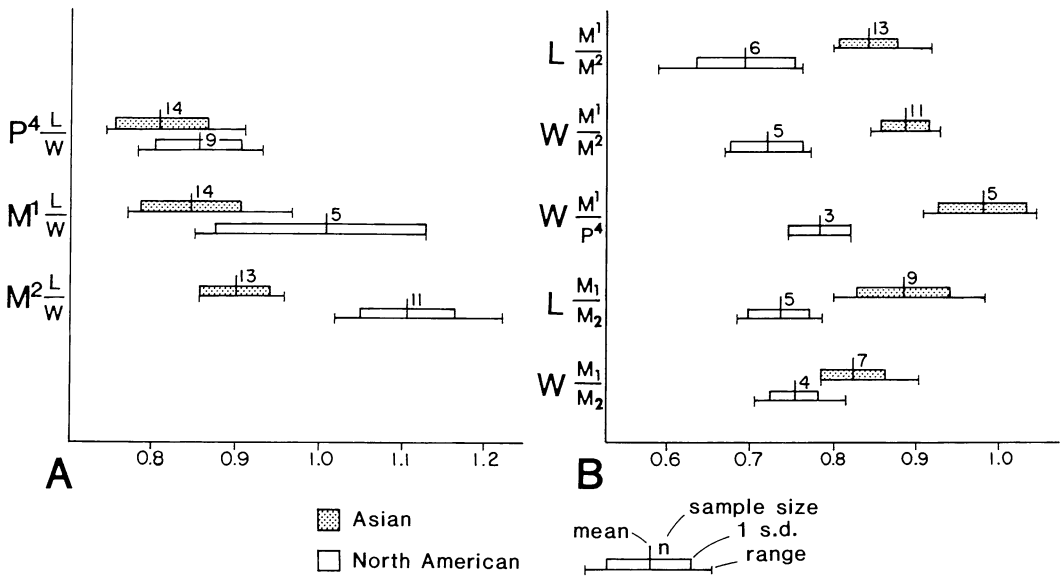


FIG. 10—Comparison of indices of tooth crown length (L) and width (W) of premolars and molars distinguishing Asiatic and North American Paleocene and earliest Eocene Prodinoceratidae. A, comparison of individual tooth shape, using ratios of length and width of P^4 , M^1 , and M^2 . Note that *Probathyopsis* has relatively longer, narrower upper molars. B, relative proportions of adjacent teeth, using ratios of the length or width of M^1 or M_1 compared to the length or width of M^2 , P^4 , or M_2 . North American *Probathyopsis* has relatively smaller first molars (smaller in both length and width) than Asian *Prodinoceras*. One standard deviation unit (s.d.) is drawn on either side of the mean. Measurements of the Asian sample are taken from Tong (1978). The American sample is that studied here, including both *Probathyopsis harrisorum* and *P. praecursor*.

therium” in Flerov (1952 and 1957) and the few casts of Asiatic specimens available to us, indicating the distinctiveness of Asiatic taxa from North American *Probathyopsis*.

Alveoli for the upper incisors of *Prodinoceras*, as figured by Flerov (1957), appear to be much larger than the alveoli in *Probathyopsis praecursor*. If so, then the upper incisors of *Probathyopsis* were more reduced than in the Asiatic taxon. Tong (1979) described upper and lower incisors of *Prodinoceras*. According to Tong, I^1 is small, I^2 is larger than I^3 , and I_1 is larger than I_2 . Neither the first nor the last of these size relationships characterize *Probathyopsis*.

In descriptions of the astragalus of *Prodinoceras* (Flerov, 1957; Tong, 1978) no mention is made of an astragalus canal. Schoch and Lucas (1985) use the absence of an astragalus canal, which they may have inferred from a *Prodinoceras* astragalus, as a diagnostic feature for their Uintatheriamorpha (however Schoch and Lucas’ Plate 3, figures 2 and 5, appears to show an astragalus canal in “*Jiaoluotherium turfanense*”). If there is indeed no astragalus foramen in *Prodinoceras*, then this important characteristic serves also to distinguish *Probathyopsis* and *Prodinoceras*.

Probathyopsis and Asiatic *Prodinoceras* are considered to represent a separate family, Prodinoceratidae, which differs from Uintatheriidae in retaining three upper incisors, retaining simple lower incisors, retaining a caniniform lower C, lacking horns, and retaining an astragalus neck and unexpanded trochlear facet. These are all primitive features, and Prodinoceratidae are a likely stem group for *Bathyopsis* and later Uintatheriidae.

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