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Paleontology and Geology of The Bridger Formation, Southern Green River Basin, Southwestern Wyoming. Part 3. Notes on *Hyopsodus*.

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Paleontology and Geology of The Bridger Formation, Southern Green River Basin, Southwestern Wyoming. Part 3 Notes on *Hyopsodus*.

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Abstract. The small condylarth *Hyopsodus* is among the more common mammals collected from the middle Eocene Bridger Formation in southwestern Wyoming. It has been exhaustively reviewed by Gazin (1968) and has more recently been included in several faunal papers. The present study is based upon the large collections at the American Museum of Natural History, New York, the United States National Museum of Natural History, Washington, and the Milwaukee Public Museum. Evidence is presented documenting the presence of 3 species of *Hyopsodus* in the Bridger Formation rather than the five accepted by Gazin.

Separation of sympatric species of Bridgerian *Hyopsodus* is largely a function of size, either absolute as tooth length or relative as a logarithmic transformation of occlusal surface area. In order to insure metric accuracy, only teeth of positive position in the jaws were measured. Three Bridgerian species of *Hyopsodus* are here considered valid: *H. paulus*, *H. minusculus* and *H. lepidus*. Some geographic variation seems apparent in the distribution pattern of *H. minusculus* and *H. lepidus*. The metric data presented here can be variously interpreted to show gradual phyletic evolution or the rather abrupt introduction of species from outside.

Several specimens retaining deciduous teeth are discussed and illustrated. Samples of deciduous teeth are now large enough to allow a modest statistical study.

INTRODUCTION

In a recent mongoraphic study, Gazin (1968) summarized the history of study of *Hyopsodus*, proposed some modifications of previous taxonomic practices, described the skull, skeleton and dentition in considerable detail, and speculated on the paleoecology of the genus. This note updates the

Bridgerian *Hyopsodus*, suggests some taxonomic changes, comments on the deciduous dentition, provides statistical data, and photographically illustrates specimens from the middle Eocene.

Since Gazin's review, *Hyopsodus* specimens have been considered in several faunal studies dealing with the early Eocene (Guthrie 1967, 1971; West 1973; Dorr 1969; Prichinello 1971; Delson 1971; Savage *et al.* 1972; McKenna 1972), the middle Eocene (West 1973; West and Dawson 1973, 1975; Turnbull 1972; McKenna 1972) and the late Eocene (McKenna 1972; Turnbull 1972). Most of these authors utilized Gazin's revised taxonomy and simply applied the appropriate specific name to the *Hyopsodus* specimens on hand. Unfortunately, *Hyopsodus* was not the major focus of any of these studies so data was not analysed in such fashion as to test the validity of Gazin's conclusions.

More recently, Gingerich (1974a, 1976) has used early Eocene *Hyopsodus* from the Big Horn Basin of northwestern Wyoming as a primary example in his model of phyletic gradualism as an evolutionary mode. Wasatchian *Hyopsodus* was used to develop the methodology known as stratophenetic analysis (Gingerich 1976) because large collections housed at Yale and at Michigan have detailed associated stratigraphic data. These assemblages, therefore, can be studied in a stratigraphic context.

The stratophenetic analysis employed by Gingerich differentiated numerous minor variations in stratigraphic size trends within Wasatchian *Hyopsodus*. He used all five Wasatchian *Hyopsodus* species names considered valid by Gazin (1968), resurrected five other species placed in synonymy by Gazin, and proposed a new but as yet undescribed species. All are based upon a combination of tooth dimensions and stratigraphic position. A similar study of Bridgerian *Hyopsodus* (West, in press) yields data which can be interpreted to suggest a reduction of the five Bridgerian species recognized by Gazin (1968) to three. Documentation for this consolidation is given below.

BRIDGERIAN *HYOPSODUS* COLLECTIONS

This study is based upon the three large collections of Bridgerian *Hyopsodus* which have at least minimally adequate stratigraphic and locality data. The Marsh collection at the Yale Peabody Museum is the oldest Bridgerian mammal collection of any size, but its field data is adequate only for crude stratigraphic placement of individual specimens. The American Museum of Natural History (AMNH) collection, made in 1893 by Wortman and between 1903 and 1906 by Granger, Matthew and associates, was the first to use the now generally accepted vertical alphabetical subdivisions of the Bridger Formation (Matthew 1909; West 1976), so the formation (and thus the collection) can be organized into a number of superpositional segments. The United States National Museum of Natural

History collection (USNM), accumulated by Gilmore in 1930 and by Gazin and associates between 1940 and 1969, also employs this alphabetical system,. but incorporates the stratigrpahy of W.H. Bradley of the United States Geological Survey. The Milwaukee Public Museum collection (MPM) is being made by West during annual field campaigns since 1970. This most recent collection has the advantage of being tied to new topographic maps and aerial photographs. In addition, many important localities have been measured (pace and Brunton Compass and/or Jacob's staff) from the nearest white layer, thereby insuring relatively precise correlations. Included under the MPM heading in the statistical charts are numerous specimens collected by West between 1970 and 1972 which ultimately will be deposited at the American Museum of Natural History.

In addition to the three major Bridger Formation collections, all made in the southern part of the Green River Basin, there are several smaller but geographically critical collections of Bridgerian *Hyopsodus* from localities outside the southern Green River Basin. These include Sand Wash Basin, Colorado (West and Dawson, 1975); Powder Wash, Utah (Gazin 1968); Tabernacle Butte, northern Green River Basin (McGrew *et al.* 1959); and the Big Bend area of western Texas (West, in preparation).

HYOPSODUS ABUNDANCE

Most of the specimens in the various Bridger Formation collections were found during the course of intensive surface collection. Only minor parts of the total sample were recovered during quarrying and/or screen-washing. Thus, most specimens are "float" occurrences, but generally were found within ten meters of their point of origin in the rock sequence. The only notable exception to this generalization is localities in coarse sandstones, resulting from stream action with considerable transport prior to deposition.

Because of their relatively large size, coupled with apparent abundance in the Bridger Formation biocenose, *Hyopsodus* specimens are the most commonly recovered taxon in surface collections. Gazin (1976, p. 6) indicates that *Hyopsodus* makes up 39% (1229 of 3151) of the identified Bridger Formation specimens in the National Museum of Natural History collections. The only other family to exceed 10% of the total identified specimens is the ischyromyid (paramyid) rodents — 12%.

This preponderance of *Hyopsodus* is greatly reduced in screen-washed collections where rodents, insectivores and marsupials are recovered in substantial numbers. West and Dawson (1975) found *Hyopsodus* to be only 16% of the identified specimens in a small screen-washed early Bridgerian collection, while West's (1973) washed collection of 470 specimens from Fault Locality, in presumed Bridger B rocks, was 10% *Hyopsodus*. In the incompletely studied southern Green River Basin Bridger Formation collection at the Milwaukee Public Museum, approximately 14% of the specimens (436 of 3183) from Sage Creek Locality, high in the Bridger B, and 10% of the specimens (79 of 777) from LSV Locality (high in bridger C) are referable to *Hyopsodus*. This contrasts with 53% *Hyopsodus* (130 of 246) in surface collections in the Leavitt Creek-Smiths Fork (Bridger B) area and 29% *Hyopsodus* (39 of 133) on the Twin Buttes White Layer (basal Bridger D). It is now apparent that *Hyopsodus* jaw fragments are near the lower size limit of objects readily seen in surface collecting. While the genus is certainly important in the faunal structure of the middle Eocene, it is over-represented in most surface collections.

HYOPSODUS SYSTEMATICS

Species differentiation.—Prior students of middle Eocene *Hyopsodus* have distinguished the various sympatric species largely on the basis of size. Both Matthew (1909; 1915) and Gazin (1968) noted certain long term trends in Eocene *Hyopsodus;* these include the development of the hypocone on the upper molars, the progressive loss of the paraconid on the lower molars, the increasing complexity of the premolars, variations in the number of roots on the anterior premolars, and increasing lophodonty. These trends are relatively easily perceived when specimens separated by large intervals of geologic time (e.g., early Wasatchian and Bridgerian) are compared, but intrapopulation variation is substantial enough to mask these trends through as little time (approximately two million years) as the Bridgerian. This was clearly recognized by Gazin (1968, p. 17): "the amount and nature of intraspecific variation renders a definition on morphologic grounds infeasible for practical application."

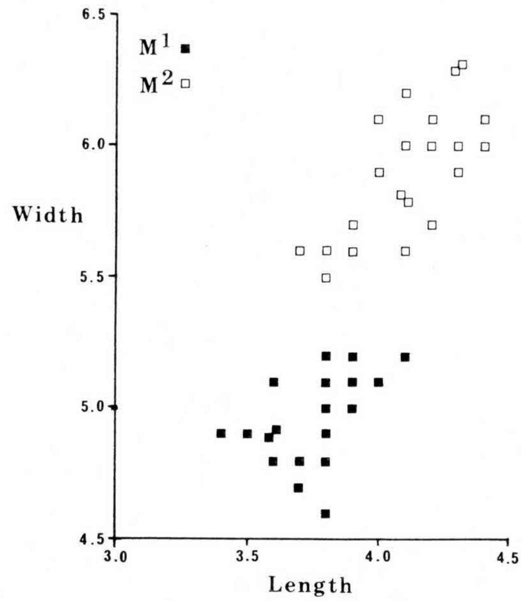
Three different approaches to tooth size have been employed. Matthew (1909, p. 517-522) measured the lengths of several combinations of cheek teeth and recognized five species plus two intermediate groupings; his averages suggest a size difference of no more than 15% in the primary *(H. paulus* to *H. despiciens)* line, while *H. lepidus* was only about 10% smaller. No measurements were given for *H. minusculus*. Gazin (1968, pp. 16-30) relied upon M_2 length as his primary parameter, for reasons that are not explained, but showed M_1 length and M^2 length in several histograms. His conclusions parallel those of Matthew, with a similar 10% to 15% difference in tooth length considered sufficient for species differentiation.

Gingerich (1974a; 1976), in his discussion of Wasatchian *Hyopsodus* as an example of a gradualistic evolutionary pattern, used the logarithm of the occlusal surface area (length multiplied by maximum width) of the lower first molar. Selection of this as the primary taxonomic parameter is based upon a study (Gingerich 1974b) of dentitions of living sympatric primate species, in which M_1 was the most relatively invariable tooth. A mathematical treatment of some of Gingerich's data (Bookstein *et al.* 1978) added the stratophenetic "trend" of size change as a means of differentiating species units.

The present study presents data graphically both as absolute tooth measurements and as logarithmic transformations. Thus direct comparison with the work of both Gazin and Gingerich is possible. More complete data on relatively large assemblages from particular productive localities are given in the Appendix.

I have used only those teeth of certain jaw position. The last premolar and the last molar, both upper and lower, are morphologically distinctive teeth, and are readily recognized when isolated. However, it is difficult to differentiate first and second molars, especially in the lower dentition. The second lower molar is slightly wider on the average than the first lower molar (fig. 1), but there is enough overlap in these measurements to render positive identification of every isolated lower molar impossible. Second upper molars are substantially wider and slightly longer than first upper molars, permitting many isolated upper molars to be identified with some certainty. Nonetheless, some specimens are difficult to assign. Incorrect assignment of those molars that do closely resemble each other would bias the statistical treatment. Consequently, isolated first and second molars have been omitted from the study; this reduces the size of the statistical samples, but insures the legitimacy of every measurement.

There is enough dental morphologic difference that Bridgerian *Hyopsodus* may be distinguished readily from early and middle Wasatchian taxa, and with some difficulty from later Wasatchian species. Characters that appear to be consistently different include the following. In the upper teeth, Bridgerian species have a large internal cone on P^3; a well-developed hypocone on M^1 and M^2, with variable development on M^3; a distinct crest uniting the hypocone and protocone on M^1 and M^2 (present in late Wasatchian species, as well); distinct molar conules; M^2 generally much larger than M^1; and a general increase in angularity and lophodonty over the Wasatchian forms, an attribute which is very hard to quantify. In the lower teeth, Bridgerian species show an incipient trignoid on P_3; more complete development of the trigonid of P_4; no paraconid on M_1 to M_3, thereby eliminating the trigonid basin and increasing the "angularity" of the trigonid; a distinct molar entoconid; a broad molar talonid basin which opens lingually; a well-developed median molar hypoconulid; a small variably developed molar metastylid; no molar entostylid; and increased lophodonty due to the presence of more pronounced crests between the conids, another highly subjective character. This character suite encompasses enough variability that within Bridgerian *Hyopsodus* species must be differentiated almost totally on the basis of size, with stratigraphic position also playing a role (see revised classification, below).



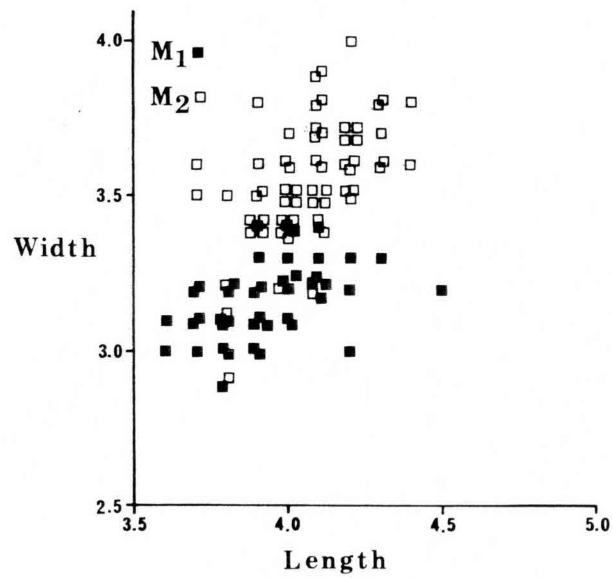


Figure 1. Bivariate plots of length and width measurements in millimeters of first and second molars of *Hyopsodus paulus* from selected lower Bridger Formation localities. The M_1-M_2 plot is based on MPM specimens from the Leavitt Creek drainage, middle Bridger B; the M^1-M^2 plot is based on USNM specimens from Grizzly Buttes, virtually the same area in Bridger B.

Species-level systematics.—In the absence of definitive morphologic characters, all available *Hyopsodus* cheek tooth size data has been plotted (figs. 2-9) in formats paralleling those used by Gazin and by Gingerich. However, in view of the greater variability of P^4_4 and M^3_3 (see Appendix), the taxonomy is based primarily upon the pattern shown by M^1_1 and M^2_2. Only selected plots are presented here; the remaining data is in my files.

The positions of each sample on the X-axis of the stratophenetic plots (figs. 4-9) were determined from stratigraphic rather than faunal infor-

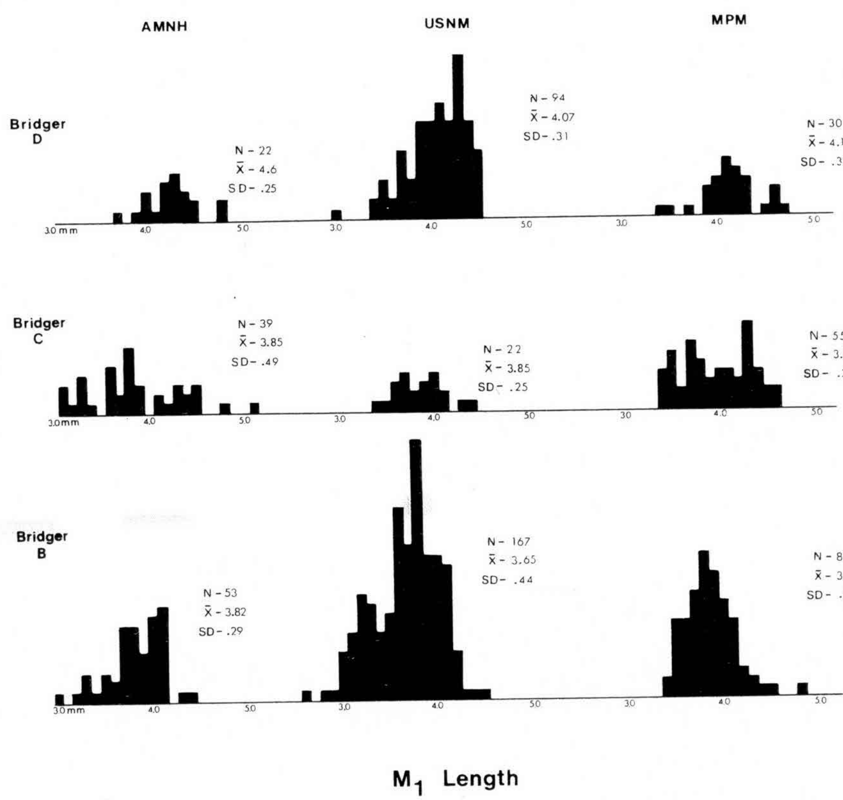


Figure 2. Histograms of lower first molar length in Bridger Formation *Hyopsodus*, grouped according to major lithostratigraphic level and institutional collection (AMNH — American Museum of Natural History; USNM — United States National Museum; MPM — Milwaukee Public Museum).

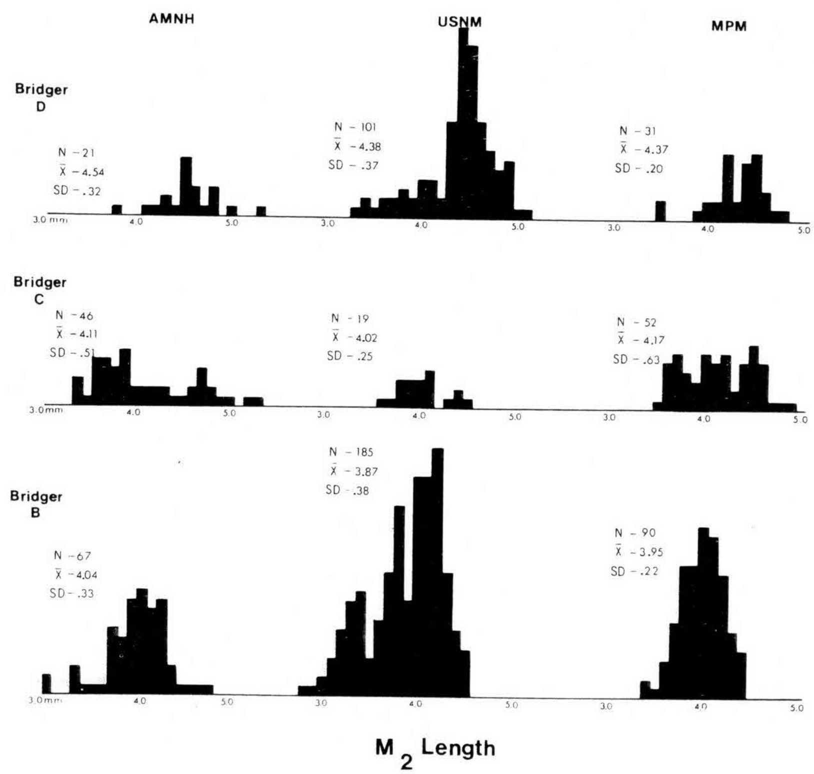


Figure 3. Histograms of lower second molar length in Bridger Formation *Hyopsodus*, grouped according to major lithostratigraphic level and institutional collection. Abbreviations are as in Figure 2.

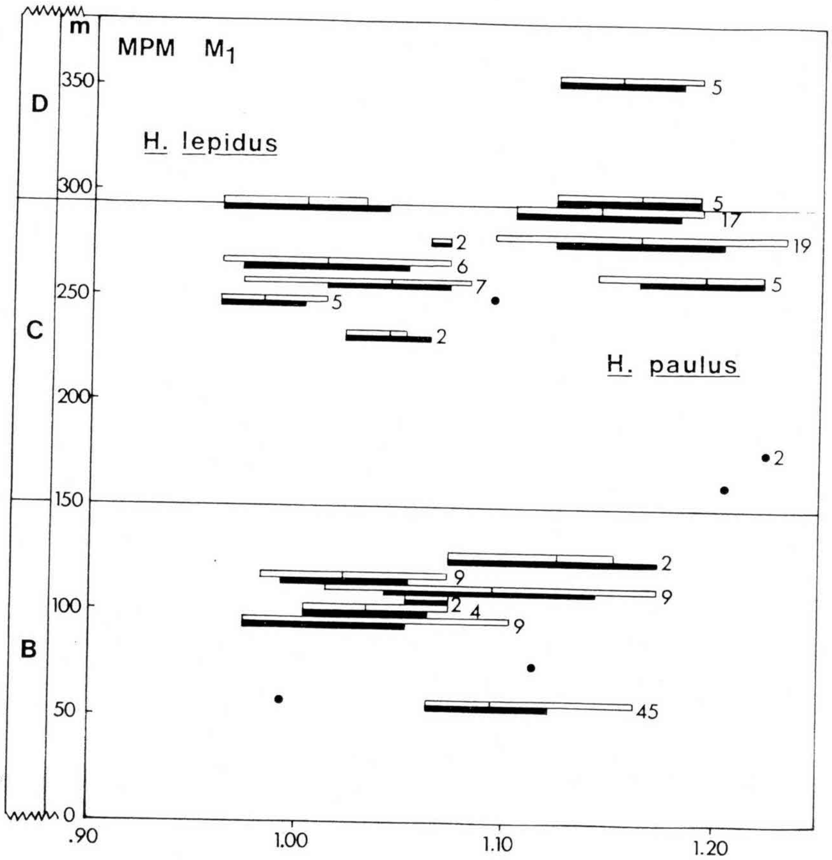


Figure 4. Stratigraphic occurrence and size of Bridger Formation *Hyopsodus* lower first molars in the Milwaukee Public Museum collection (abbreviations as in Fig. 2). The abcissa is the $\log_{10}$ of the length (in mm) times the width (in mm) of the lower first molar. The ordinate is the distance in meters above an arbitrary point in the lower part of the Bridger Formation (Bridger B), and includes middle and upper Bridger B, all of Bridger C, and much of Bridger D. The vertical line is the mean of each sample, the heavy bar is one standard deviation from the sample mean, the open bar is the observed range, numerals indicate sample size, and unnumbered dots denote single specimens.

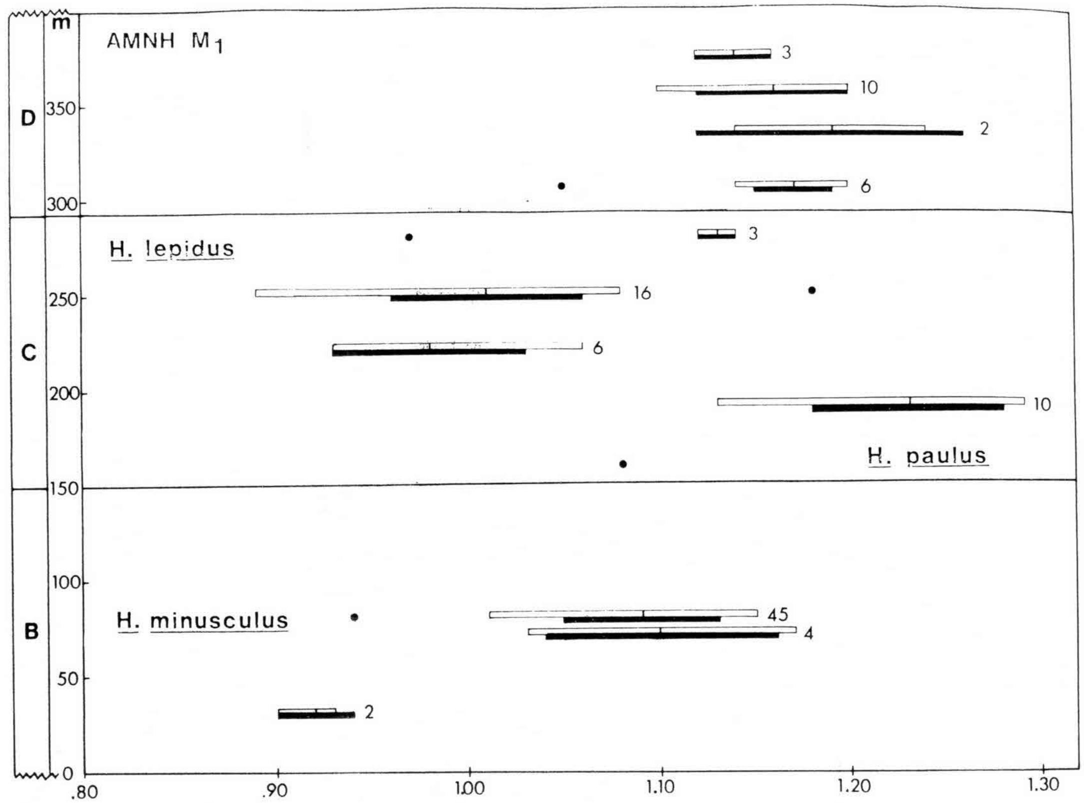


Figure 5. Stratigraphic occurrence and size of Bridger Formation *Hyopsodus* lower first molars in the American Museum of Natural History collection. Plot and symbols are as in Figure 4.

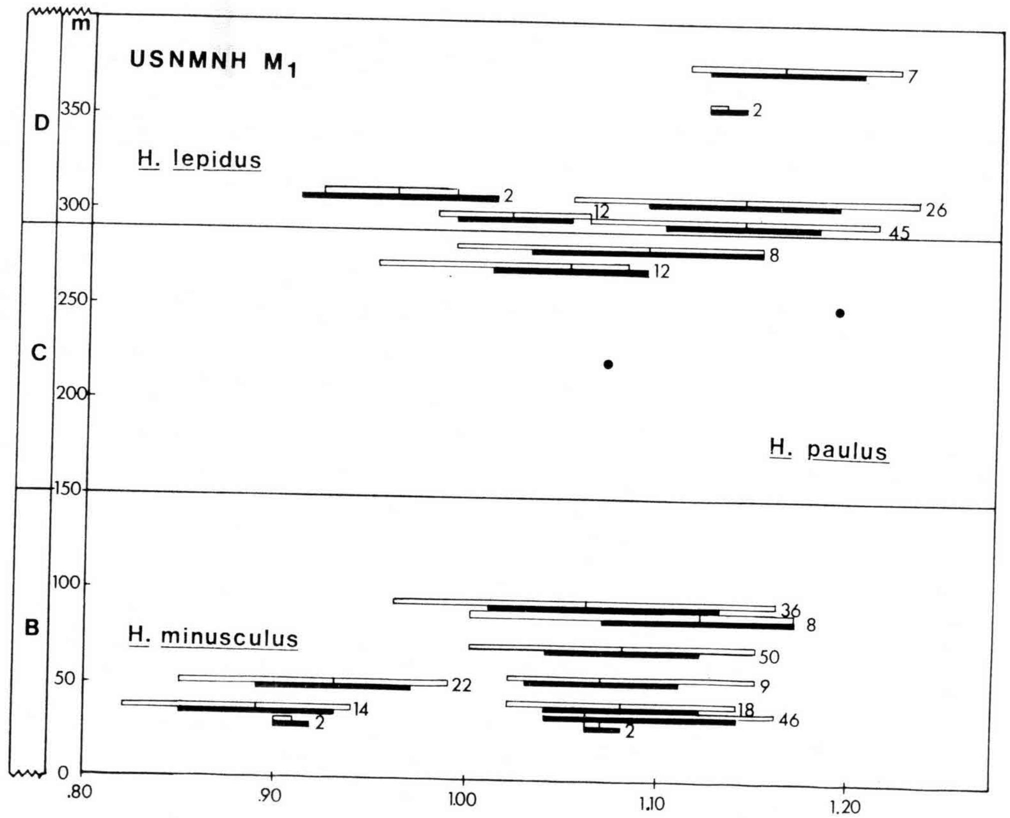


Figure 6. Stratigraphic occurrence and size of Bridger Formation *Hyopsodus* lower first molars in the United States National Museum collection. Plot and symbols are as in Figure 4.

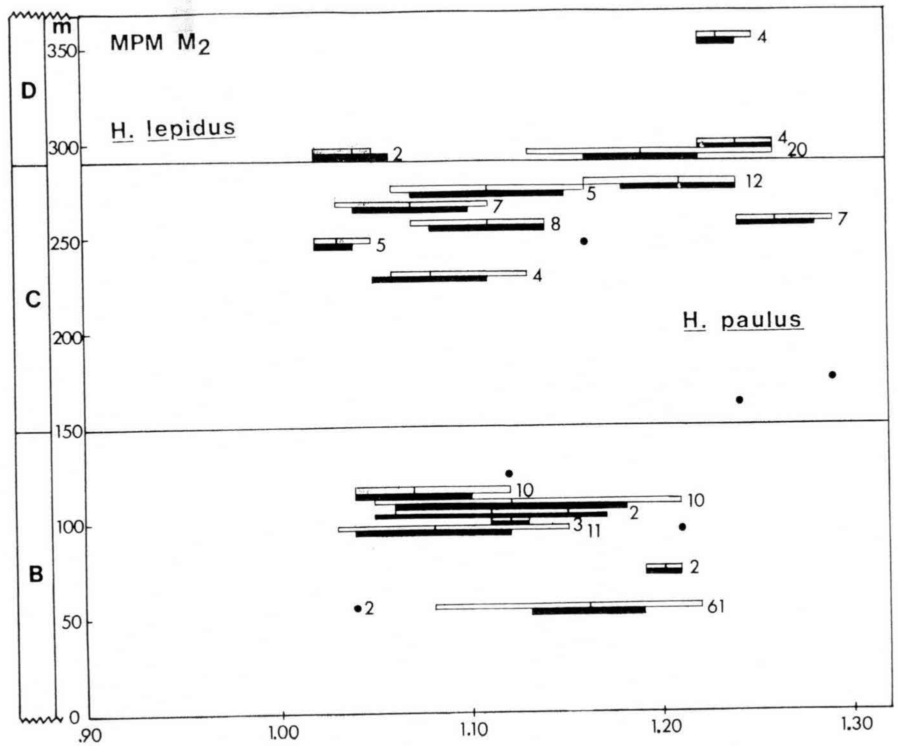


Figure 7. Stratigraphic occurrence and size of Bridger Formation *Hyopsodus* lower second molars in the Milwaukee Public Museum collection. Plot and symbols are as in Figure 4.

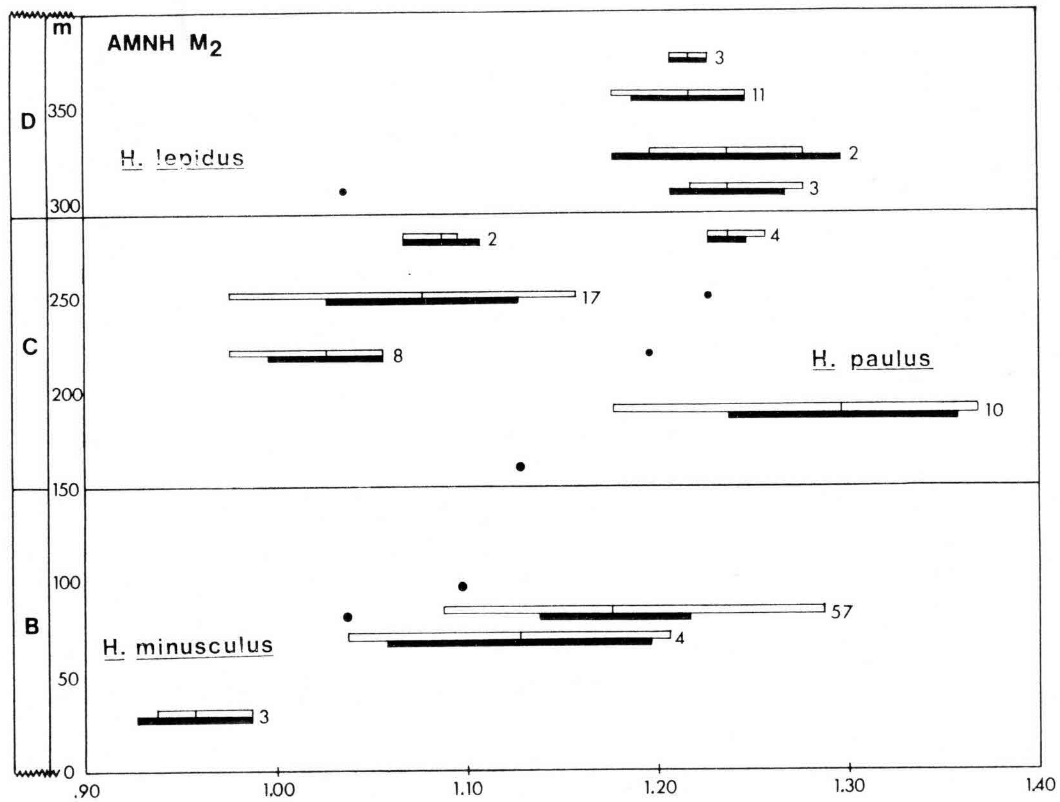


Figure 8. Stratigraphic occurrence and size of Bridger Formation *Hyopsodus* lower second molars in the American Museum of Natural History collection. Plot and symbols are as in Figure 4.

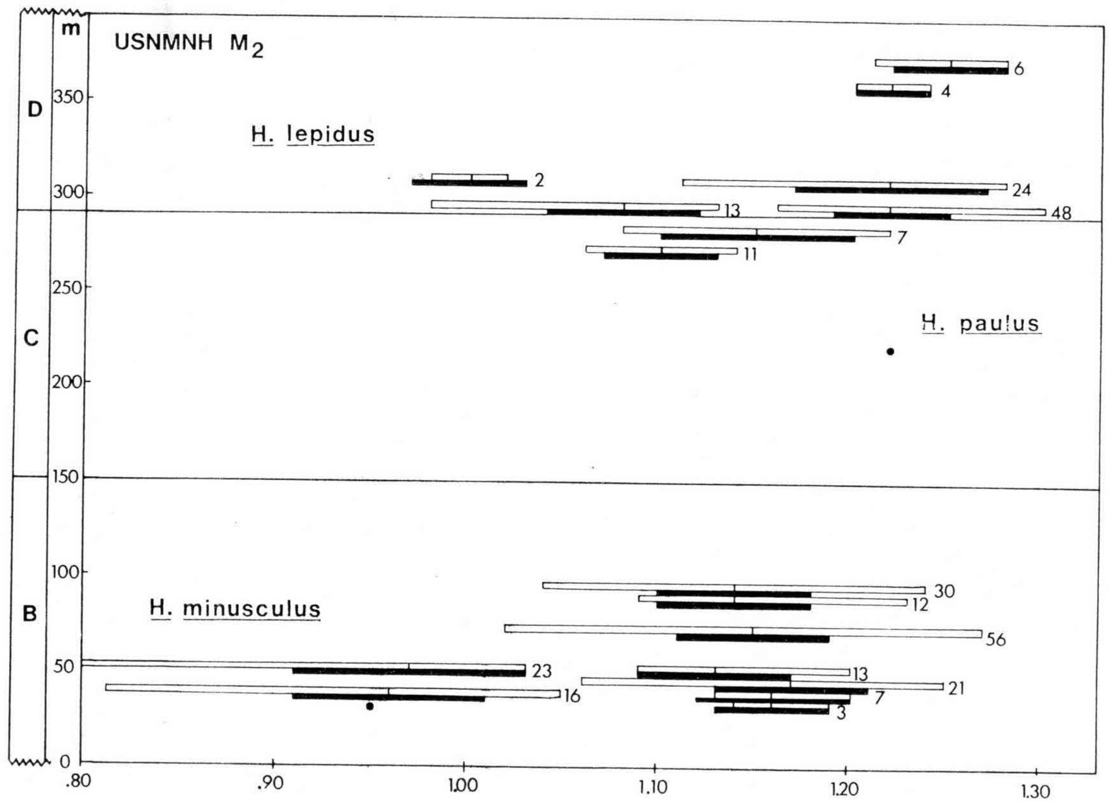


Figure 9. Stratigraphic occurrence and size of Bridger Formation *Hyopsodus* lower second molars in the United States National Museum collection. Plot and symbols are as in Figure 4.

mation. Several of the assemblages in the American Museum and U.S. National Museum collections had only approximate horizon data; these data indicate relative stratigraphic position within the major Bridger Formation zones (C_1, C_2, etc.), and were placed arbitrarily uniformly spaced through the appropriate stratigraphic interval on the plots. Other assemblages were from readily recognized regions and were assigned positions based upon field information accumulated during my field work in the Bridger Formation. As a result, the relative positions are certain, but the absolute distance between assemblages may be incorrect.

Gazin's unification of the entire USNM Bridger Formation sample into two (upper and lower) or three (B, C, D) assemblages appears to me to be unrealistic. It carries two implications: first, that a taxonomic boundary parallels the Sage Creek White Layer so a species cannot pass from the lower Bridger Formation into the upper Bridger Formation, and second, that no recognizable differences exist among the various localities within these major lithostratigraphic units. My analysis considers *Hyopsodus* on a locality-by-locality basis; this approach is surely one of the strengths of the stratophenetic analysis developed by Gingerich.

Since the metric data is drawn from collections in three museums, each of which has its own set of stratigraphic and locality data, specimens from each museum are plotted separately. This prevents erroneous correlations of locality data, especially in view of the varying accuracy of that data through the 20th Century. This is, then, a form of internal testing of the data. The marked similarity in the plots, despite different collectors and exploitation of different specific localities and collecting techniques, suggests the general validity of the approach.

Study of the plots shows that there is a prominent large-sized population present at all levels of the Bridger Formation. This population increases in physical size through the thickness of the sampled part of the formation. Fairly low in the Bridger B, in the rich Grizzly Buttes area (see fig. 1, West 1976)*, M_1 has an average length of 3.9mm and M_2 and average length of 4.1mm. By the middle of the Bridger C these have increased to 4.3mm and 4.6mm, respectively, and the stratigraphically highest available sample

*The map in West (1976) shows most of the major Bridger formation collecting areas. The Church Buttes delineated on that map is an operating gas field; the Church Buttes collecting data is approximately 16 kilometers (10 miles) to the north-northwest, just at the edge of the map in R112W. Grizzly Buttes, as shown on the map, is far too restricted. The locality actually extends eastward to the drainage of Leavitt Creek, and includes areas called "Upper Leavitt Creek" and "Little Dry Creek" in older collections.

(USNM specimens from high in Bridger D) shows an M_1 average length of 4.3mm and an M_2 average length of 4.8mm. This general increase of 10%-17% is reflected in the other tooth measurements as well as in the logarithmic derivations. The slow trend toward increase in size continues through the entire sampled part of the Bridger Formation, though it is not a continuous progression. As shown in figs. 4-9, certain local populations are rather larger than a straight line trend would project, and there is some indication of a slight reduction in size after the middle of Bridger C.

This larger population is here regarded to be the species *Hyopsodus paulus*, which persisted through the Bridgerian, from the deposition of middle Bridger B rocks onward. Krishtalka (pers. comm., December 1978) regards several specimens from the White River Pocket locality in the Uinta Formation (early Uintan) of northern Utah as also referable to *H. paulus*, so the temporal range of the species is now perhaps as long as four or five million years. *H. paulus* is the name selected because it has priority over *H. despiciens*, the name used by Gazin for the upper Bridger part of essentially the same assemblage. Both Matthew (1909) and Gazin (1968) recognized a still larger species, named *H. marshi* by Matthew (1909). My measurements and plots do not suggest the presence of such a larger species; Matthew's type material was only about 5% larger than typical *H. despiciens* (here *H. paulus*) from high in the Bridger Formation, so a size-separation seems to be unnecessary. Gazin retained *H. marshi* because of the progressive nature of the upper second premolar. In the absence of other distinctive characters, I prefer to regard *H. marshi* as a synonym of *H. paulus*.

Two zones within the Bridger Formation show the presence of two statistically different populations of smaller size. Low in the formation (figs. 4-9) the species *H. minusculus* is readily differentiable from *H. paulus*. The M_1 and M_2 average length of the USNM sample from Millersville (3.2mm and 3.3mm) are each 15% to 18% smaller than the presumably sympatric population of *H. paulus* from the same locality. Similar differences are seen in samples from the lower Bridger Formation near Church Buttes. *H. minusculus* apparently did not flourish, as localities stratigraphically higher in the Bridger B are composed almost exclusively of *H. paulus*. This pattern is complicated, however, by apparent geographic variation in the relative abundances of these two species. *H. minusculus* is the dominant early Bridgerian species in New Fork - Big Sandy area (West 1973; West and Dawson 1973) near the northern end of the Green River Basin. USNM collections from Millersville and Church Buttes, near the northern end of the major Bridger Formation exposure area, have about twice as many individuals of *H. minusculus* as of *H. paulus*. Still farther south, and slightly higher in the section, the Grizzly Buttes/Leavitt Creek collections in all three museums have less than 5% *H. minusculus*. The New Fork - Big Sandy area lower Bridger Formation localities cannot be precisely correlated with the sequence in the southern Bridger Formation, and all levels of the lower Bridger Formation are not exposed in all geographic areas. Therefore, it is not possible to completely separate geographic variation in the relationships of these two species from the possibility that *H. minusculus* had a very short temporal range and virtually disappeared well before the end of Bridger B time.

A second occurrence of smaller-sized *Hyopsodus* populations in in localities ranging from the middle of Bridger C into the lower part of Bridger D (figs. 4-9). Specimens from the stratigraphically lower localities are occasionally difficult to separate into two discrete populations, yet the coefficients of variation of the full samples are so large that subdivision is mandatory. This region, therefore, seems to conform to Gingerich's model of phyletic gradualism with a character displacement event slowly separating one population into two. Such a gradual separation, which is apparent on the stratigraphic plots, is lost when all of the upper Bridger Formation localities, or even all of the Bridger C localities are treated as a unit (figs. 2 and 3), as was done by Gazin. By the end of Bridger C time and the beginning of Bridger D time, this population is readily recognizable as *H. lepidus*, the smallest later Bridgerian species accepted by Gazin. Its relative abundance is quite variable, though *H. lepidus* was relatively more common at the top of Bridger C than it was on into Bridger D. Within the lowest 30 meters of Bridger D, *H. lepidus* apparently disappeared, and *H. paulus* was the only species to carry onward.

The nature of the outcrop pattern of the upper part of the Bridger Formation (West 1976) does not allow a serious consideration of the possible role of geographic variation in the occurrences of *H. lepidus* and *H. paulus* in the upper part of the Bridger Formation. The only other occurrence of presumed upper Bridger Formation rocks in the Green River Basin is at Tabernacle Butte in the northern part of the basin (McGrew *et al.* 1959). Like the rocks in the New Fork - Big Sandy area, precise correlations with the main exposures of the Bridger Formation are not possible. However, most of the *Hyopsodus* specimens from Tabernacle Butte fall within the range of *H. lepidus*, and only a single *H. paulus* seems to be present. (My measurements for M_1 closely approximate those published by McGrew [McGrew *et al.* 1959, p. 170], but my M_2 measurements suggest a considerably larger tooth than do McGrew's.) This duplicates the apparent pattern shown by *Hyopsodus* from lower Bridger Formation localities: smaller *Hyopsodus* predominates farther north in the Green River Basin. There is no obvious paleoecological explanation for this regional size variation.

In summary, the present statistical and stratigraphic study of Bridger Formation *Hyopsodus* indicates that all the available materials fall into three species, one of which *(H. paulus)* is of long duration and is apparently little changed from the lower to the upper part of the Bridger Formation. The other two species are physically smaller, of much shorter temporal duration, and appear to be relatively much more abundant toward the northern end of the Green River Basin.

The relationships among these three species can be interpreted in various ways. A stratophenetic interpretation suggests that *H. paulus* gave rise, by phyletic splitting, to two smaller species, *H. minusculus* and *H. lepidus*. Each of these was physically smaller than the "mainstream" species, and became rather quickly (a hundred thousand years at the most) quite distinct. The *H. paulus* lineage underwent a modest change in trend during the Bridger C (figs. 4 and 5); a determination such as made by Bookstein *et al.* (1978) might well indicate a speciation event there as well.

An alternative interpretation to the one presented above has a persistent smaller-sized lineage *(H. minusculus)* paralleling *H. paulus* through much of Bridgerian time. This smaller lineage is present in the available fossil record only sporadically either because of the geographic distribution of Bridgerian rocks or because it made only episodic incursions into the southern Green River Basin and did not survive there for extended periods. If this is the case, *H. lepidus* becomes a junior synonym of *H. minusculus*, and the roster of Bridgerian *Hyopsodus* species is reduced to two.

The apparent *in situ* origin of *H. lepidus* from *H. paulus* during the latter half of Bridger C time (figs. 4 and 5) argues against the alternative interpretation.

Examination of several populations of *Hyopsodus* from localities outside the Bridger Formation show that they fall well within the size range and morphologic boundaries established for the large Green River Basin collections. Specimens from the Sand Wash Basin of northwestern Colorado (Washakie Formation rocks presumed to be of late Bridgerian or early Uintan age) are clearly in the size range of *H. paulus*. Specimens from presumed early Bridgerian rocks in the Green River Formation at Powder Wash, Uinta Basin, Utah, are mostly referable to *H. minusculus*, though one individual falls into the size range of *H. paulus*. Unfortunately there is only a single Bridgerian (or early Uintan) locality that is significantly removed from the Green River Basin region. *Hyopsodus* specimens from the Pruett Formation of the Big Bend region of Texas fall, both in morphology and in size, into *H. paulus*, thus giving the species a substantial geographic as well as temporal range.

Following is a revised classification of Bridgerian *Hyopsodus*, after Gazin 1968, pp. 14-15.

H. paulus Leidy, 1870 (figs. 10-13, 16 and 18).

Synonym.—(?) *Stenacodon rarus* Marsh, 1872; *Lemuravus distans* Marsh, 1875; *Hyopsodus vicarius* (Cope), 1873; *Hyopsodus marshi* Osborn, 1902; *Hyopsodus despiciens* Matthew, 1909.

Type.—USNM 1176, right ramus with M_1-M_3.

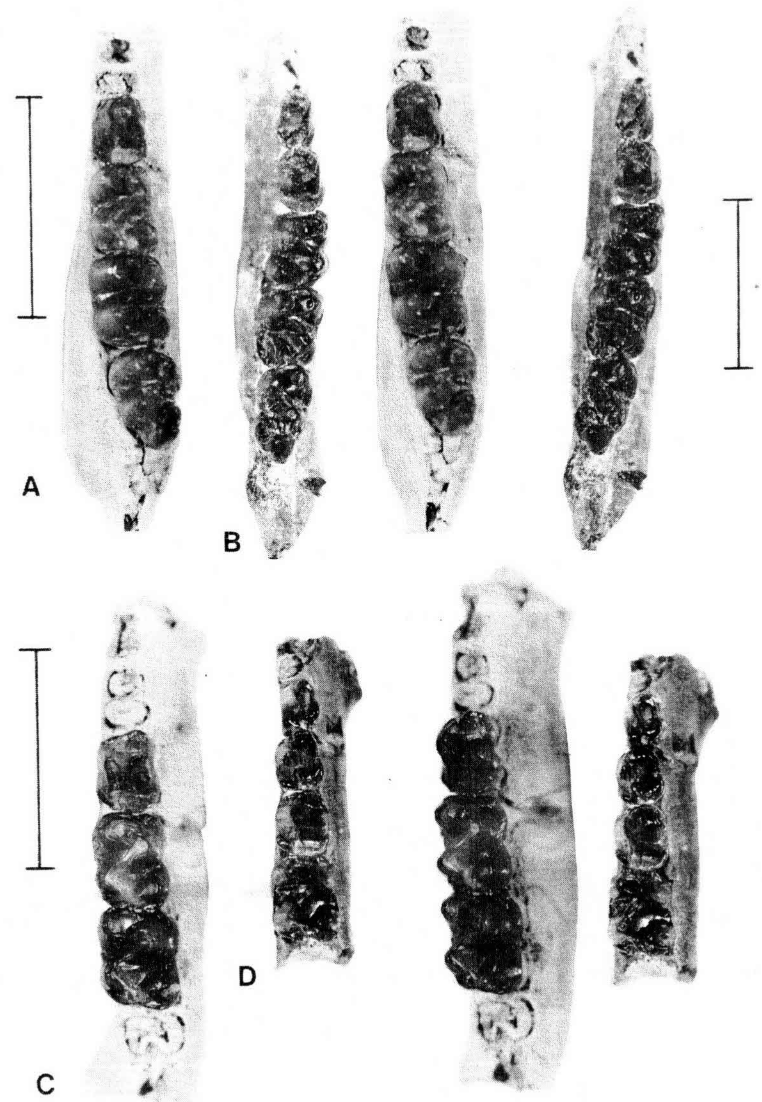


Figure 10. Stereophotographs of *Hyopsodus* lower dentitions. A. *H. paulus*, MPM 3975. left P_4-M_3. Locality 2143 (Bridger C). B. *H. paulus*, MPM 3966, right P_3-M_3. Locality 2239 (Bridger C). C. *H. paulus*, AMNH 91232, left P_4-M_2. Upper Leavitt Creek (Bridger B). D. *H. lepidus*, MPM 3973, left P_2-M_1. Locality 1126 (Bridger C). Scale units equal 1 cm.

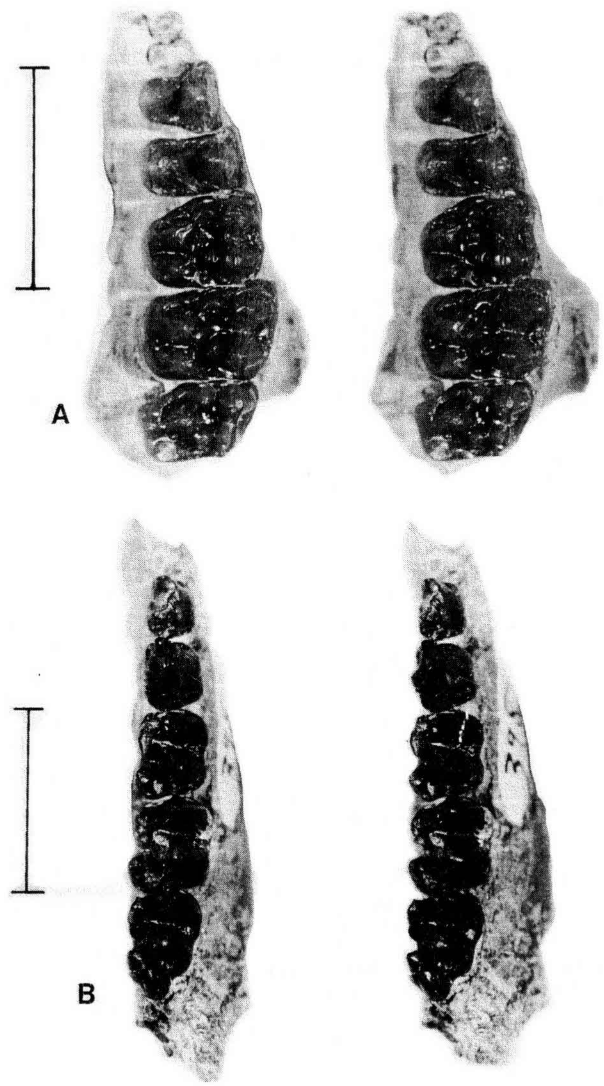


Figure 11. Stereophotographs of *Hyopsodus* dentitions. A. *H. paulus*, MPM 3984, left P^3-M^3. Locality 2786 (Bridger B) B. *H. paulus*, MPM 3982, right P_3-M_3. Locality 2187 (Bridger C). Scale units equal 1 cm.

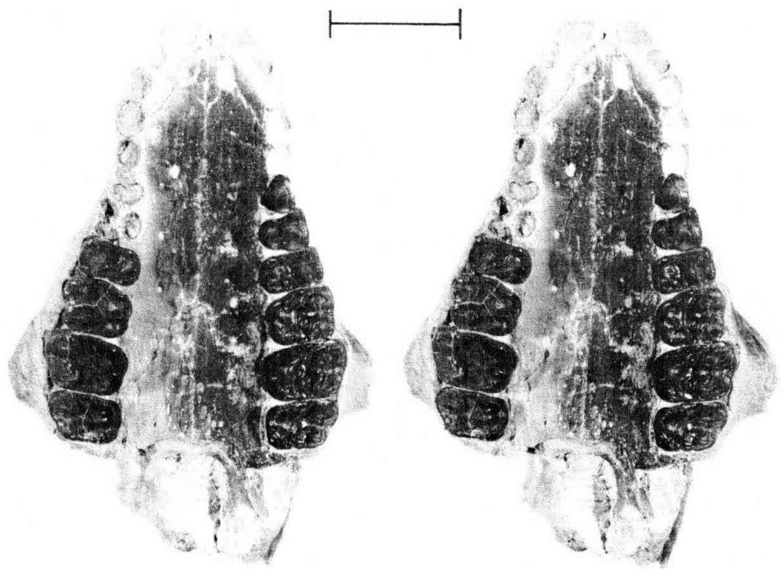


Figure 12. Stereophotographs of *Hyopsodus paulus* palate, MPM 3954. Locality 2836 (Bridger B). Scale equals 1 cm.

Horizon and locality.—Lower Bridger Formation, early middle Eocene, near Fort Bridger, southern Green River Basin, Wyoming.

Range.—Bridger Formation, lower Washakie Formation, lower Uinta Formation, upper Green River Formation, Pruett Formation; middle Eocene and early late Eocene, Wyoming, Utah, Colorado and Texas.

Comments.—This species is present throughout the Bridgerian, and is the most common *Hyopsodus* in most southern Green River Basin localities. It undergoes a size increase, from an average M_1 length of 3.9mm low in the formation to 4.3mm higher in the Bridger. When smaller species are present, *H. paulus* is usually clearly distinct (the middle part of Bridger C, when *H. lepidus* arises, is an exception).

H. minusculus Leidy, 1873 (fig. 17).

Type.—ANS (Academy of Natural Sciences, Philadelphia) 10259, left maxilla with partial P^4, M^1-M^3.

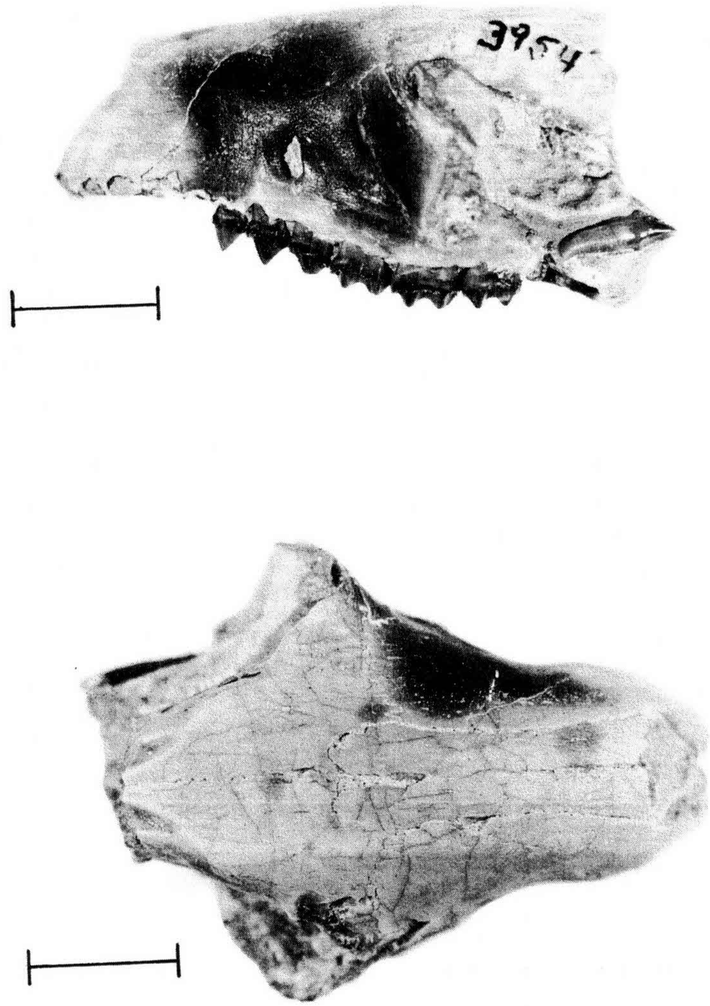


Figure 13. Partial skull of *Hyopsodus paulus*, MPM 3954. Locality 2836 (Bridger B). Scale equals 1 cm.

Horizon and locality.—Lower Bridger Formation, early middle Eocene, "Buttes of Dry Creek," southern Green River Basin, Wyoming.

Range.—Lower Bridger Formation, Green River Formation; early middle Eocene, Wyoming and Utah.

Comments.—This species is abundant in more northerly exposures of the lower part of the Bridger Formation. It is generally 15% to 20% smaller than sympatric *H. paulus*, and stratophenetic trends suggest approximate size stability until the species disappears from the fossil record in the middle of Bridger B.

H. lepidus Matthew, 1909 (figs. 10 and 15).

Type.—AMNH 11900, right maxilla with P^2–M^3 and left mandible with partial P_3, P_4-M_3.

Horizon and locality.—Upper Bridger Formation, late middle Eocene, Bridger C, Henry's Fork, southern Green River Basin, Wyoming.

Range.—Upper Bridger Formation, late middle Eocene, Wyoming.

Comments.—This small species differentiated from *H. paulus* in the middle of Bridger C and was clearly distinct and relatively abundant by the end of Bridger C time. Its absolute size overlaps with earlier *H. paulus*, so it is here effectively recognizable only if adequate stratigraphic data is available. By the end of Bridger C time, *H. lepidus* was about 15% smaller than sympatric *H. paulus*. It disappeared from the existing record early in Bridger D time.

DECIDUOUS DENTITION AND SKULL STRUCTURE

Gazin (1968, pp. 50-52) intimated, without providing any numerical data, that deciduous teeth of *Hyopsodus*, especially upper teeth, are rare. The Milwaukee Public Museum collection suggests otherwise: 57 of 1003 measured lower cheek teeth (P_4-M_3) are deciduous (6%), and 45 of 623 measured upper cheek teeth (P^4–M^3) are deciduous (7%). Virtually all of these deciduous teeth are found as isolates, probably shed by the maturing animals. They are identified as *Hyopsodus* teeth by reference to deciduous teeth remaining in jaws and thus associated with identifiable upper teeth, and by the special characteristics of deciduous teeth: low crowns; weak roots (if not resorbed prior to being shed); often very heavily worn; and often markedly lighter in color than other teeth from the same locality (West 1971). Practically all the deciduous specimens are of dP_4 or dP^4, so relatively little is known about the range of variation in the anterior deciduous teeth. Enough deciduous fourth premolars are available from several

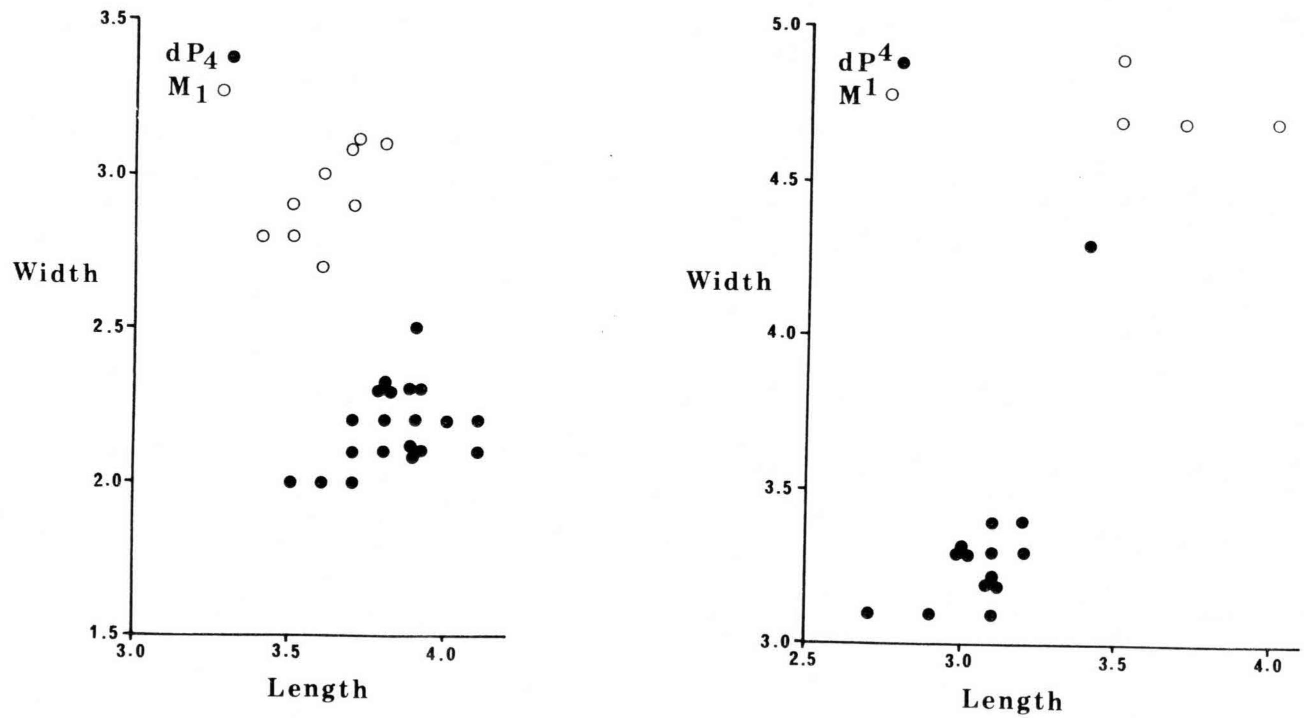


Figure 14. Bivariate size frequency plot of length and width measurements (in millimenters) of last deciduous premolars and first molars of *Hyopsodus paulus* in the MPM collection from several localities high in Bridger B. The proportional differences between deciduous and functionally homologous permanent teeth are quite apparent.

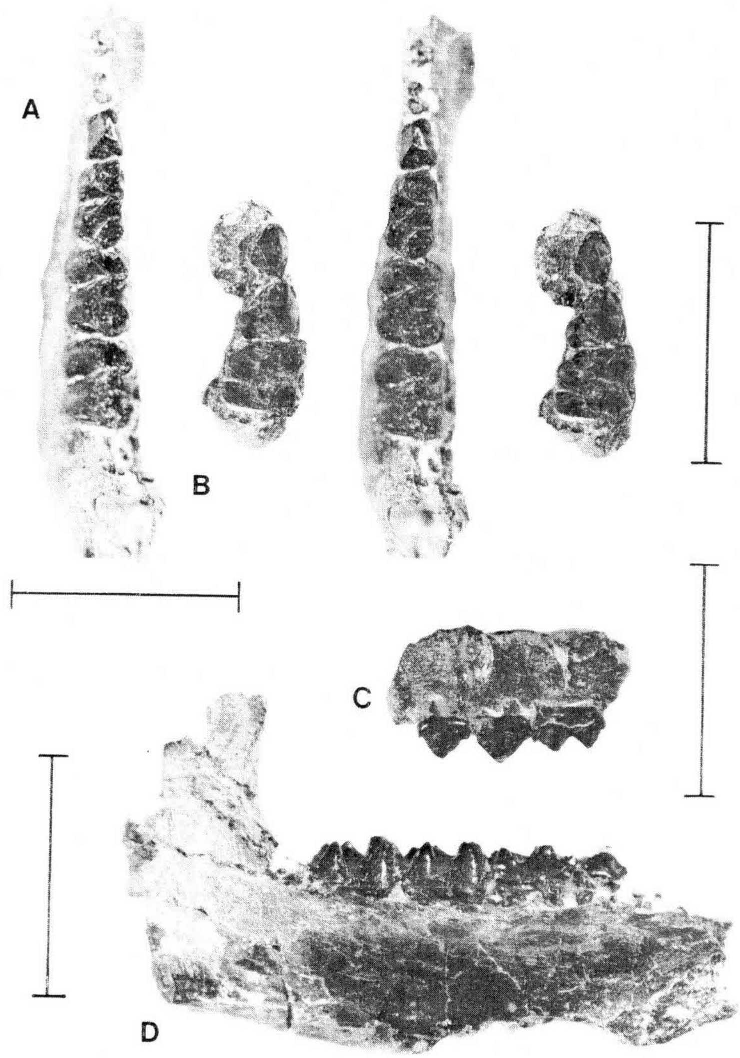


Figure 15. Deciduous dentition of *Hyopsodus lepidus*, AMNH 11959, Henry's Fork (Lonetree), Bridger C_4. A. Stereophotographs of left dentary, dP_3-M_2. B. Stereophotographs of left maxilla, dP^2–dP^4. C. Left maxilla, buccal view. D. Left dentary, lingual view. Note how low-crowned dP_3 and dP_4 are relative to the permanent teeth. This specimen was figured by Gazin (1968, plate 6). Scale equals 1 cm.

localities to permit size-frequency scatter diagrams (fig. 14) to be constructed.

AMNH 11959, *Hyopsodus lepidus* (fig. 15) from Bridger C_4 near Lonetree was described by Gazin. It remains the best example of anterior de-

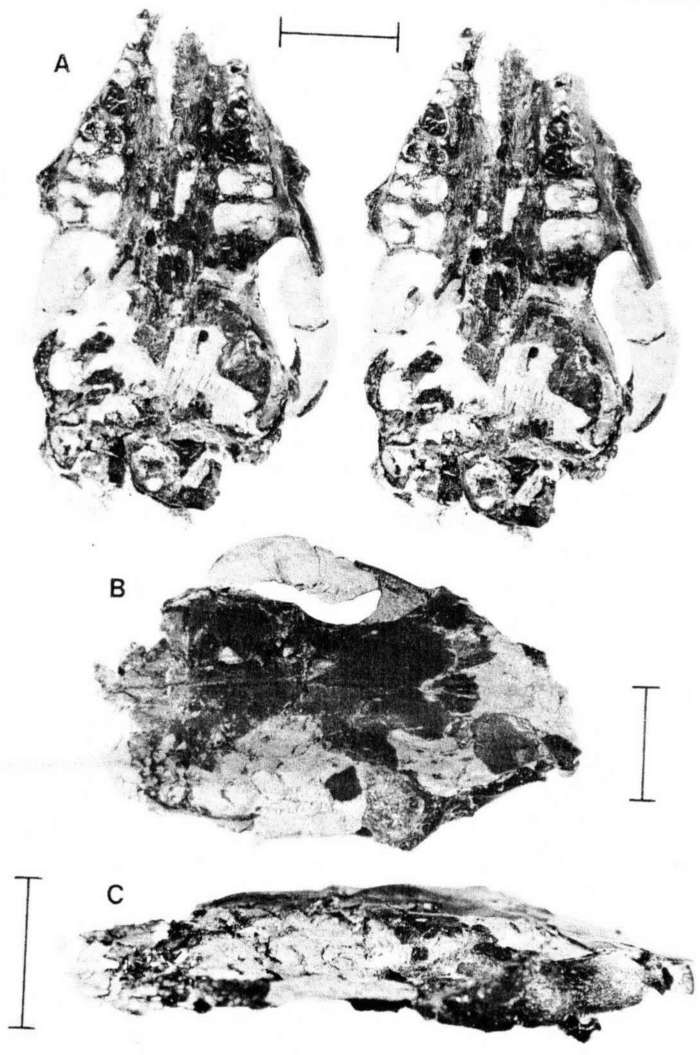


Figure 16. Juvenile skull of *Hyopsodus paulus*, MPM 3906. Locality 2401 (Bridger B). A. Stereophotographs of ventral side of skull. B. Dorsal view of skull. C. Lateral view, right side. Scale units equal 1 cm.

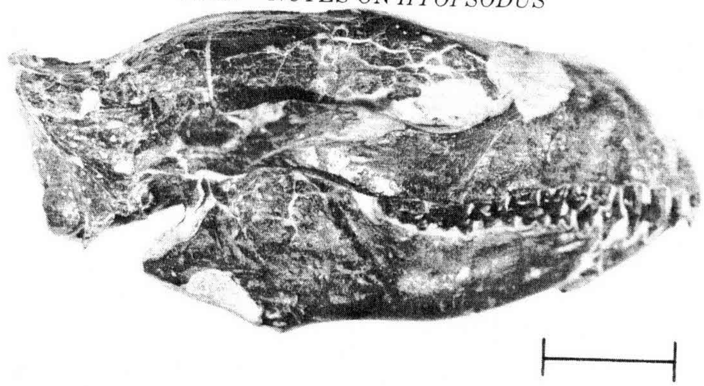


Figure 17. Skull of *Hyopsodus minusculus*, USNM 24891, lateral right view. Near Blacks Fork Bridge, south of Church Buttes. Bridger B. This specimen was figured by Gazin (1968, plate 11). Scale equals 1 cm.

ciduous teeth, as well as being the only known sample of associated upper and lower deciduous teeth. The descriptions given by Gazin are quite adequate. The differences in proportions between dP_4 and M_1 are clearly shown in figs. 16 and 17. DP_4 is much narrower than its permanent counterpart, M_1, and dP^4 is a more nearly square tooth than is M^1 which is substantially wider than it is long.

A crushed juvenile skull (MPM 3906) (fig. 16) preserves dP^3 and dP^4 in place, erupting C and M^3 and the alveoli for $P^2P^3M^1$ and M^2. The teeth that are in place are more heavily worn than the dP^3dP^4 in AMNH 11959, so the occlusal surface is less definitive. The lingual cusps, in particular, are badly worn, and the posterointernal slope of the paracone on dP^3 is worn flatter than the comparable area in AMNH 11959. The entire skull of MPM 3906 is completely flattened and the brain case region severely shattered, so little can be seen of the basicranium (fig. 16). The rostrum and palate are in somewhat better condition, although the premaxillary region is missing. The snout seems to be more rounded than in the several adult skulls illustrated by Gazin, and refigured here in figs. 17 and 18.

The cheek teeth of MPM 3906 are in a broad V configuration, less nearly parallel than in the adults. Apparently allometric growth in maturing *Hyopsodus* produced elongation of the snout.

The material on hand makes specific allocation of the isolated deciduous teeth very difficult. They appear to be more variable than are permanent teeth, making species assemblages less definitive. However, statistics calculated on the deciduous teeth do not contradict taxonomic decidions made on the basis of the permanent teeth alone.

The paucity of juvenile jaws retaining both deciduous and permanent teeth in various stages of eruption makes the actual sequence of eruption difficult to reconstruct. We have no idea of the eruption sequence of the deciduous battery, and there is no evidence pertaining to the permanent incisors. The two specimens mentioned above, AMNH 11959 and MPM 3906, indicate that the dP^4_4 persists until all the molar teeth are in place and functioning. The molars erupt in an anterior to posterior sequence; presumably the permanent premolars did also, but there is enough known variation among modern mammals (West 1971, p. 30), to render this pure speculation.

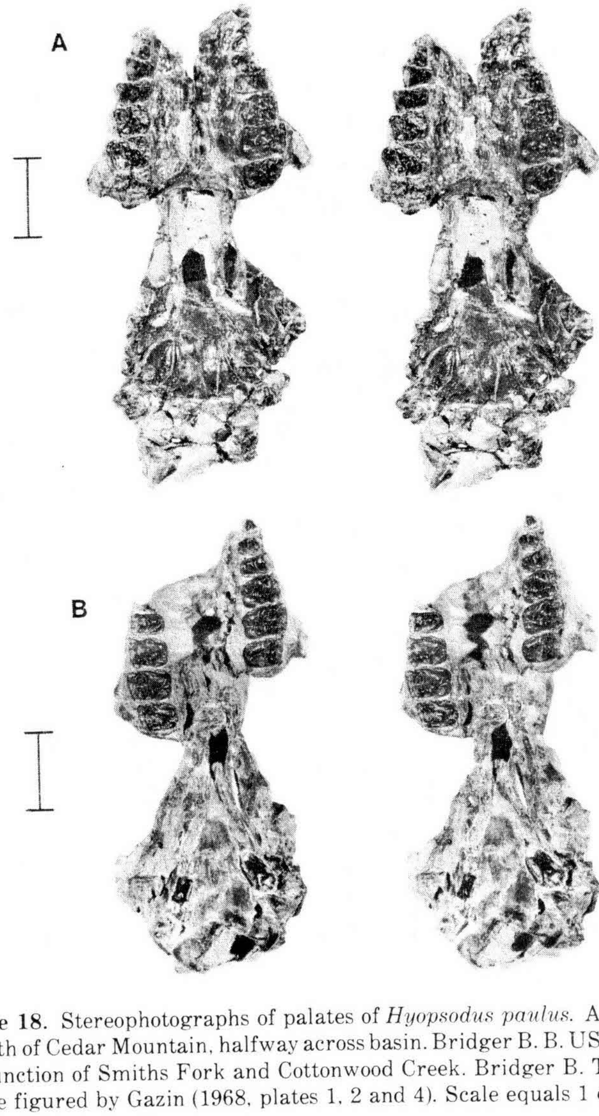


Figure 18. Stereophotographs of palates of *Hyopsodus paulus*. A. USNM 23740. North of Cedar Mountain, halfway across basin. Bridger B. B. USNM 17980. East of junction of Smiths Fork and Cottonwood Creek. Bridger B. These specimens were figured by Gazin (1968, plates 1, 2 and 4). Scale equals 1 cm.

BIOSTRATIGRAPHIC UTILITY OF BRIDGERIAN *HYOPSODUS*

The interplay of size plus stratigraphic position within the Bridger Formation used here to differentiate species of *Hyopsodus* severely limits the value of the species for biostratigraphic purposes. The Bridgerian grade of *Hyopsodus* persist through several million years and, as noted by Matthew in 1909 (pp. 516-517), shows very little diversity in comparison with Wasatchian *Hyopsodus*. *H. paulus* shows a modest increase in size through the Bridgerian, and its absolute measurements, coupled with the periodic presence of a smaller species (either *H. minusculus* or *H. lepidus)* provides some indication of vertical position within the Bridger Formation. The presence of *H. paulus* at White River Pocket in Utah further reduces its biostratigraphic significance. Thus, for practical purposes, Bridgerian *Hyopsodus* is essentially useless for other than land mammal age - level correlations.

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APPENDIX

Statistical Data on Bridgerian *Hyopsodus*

The following 30 tables give primary statistical parameters on the larger and better-documented local assemblage of *Hyopsodus*. Tables 1 through 14 present data for all teeth; Tables 15 through 30, specimens from localities that are less well documented or of less geographic importance than those of tables 1-14, show only M_1 and M_2 since these teeth are the basis for the visual presentations in Figures 2-9. Museum collection abbreviations: MPM — Milwaukee Public Museum; USNM — United States National Museum of Natural History, Washington; AMNH — American Museum of Natural History, New York; CM — Carnegie Museum of Natural History, Pittsburgh; UCM — University of Colorado Museum, Boulder. Statistical abbreviations: N = number of specimens; X = mean; CV = coefficient of variation; OR = observed range; LxW = average of product of length times width; X Log_{10} = mean of the Log_{10} of the LxW measurement.

TABLE 1

Taxon: *Hyopsodus minusculus*
Locality: Church Butte (low B)
Collection: USNM

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR (mm)	LxW	$\overline{X}$ Log_{10}
P_4	L	9	2.42	.20	8.21	2.1-2.7		
	Want	9	1.89	.21	11.11	1.5-2.2	4.75	.67
	Wpost	9	1.92	.15	7.22	1.7-2.2		
M_1	L	14	3.13	.18	5.75	2.8-3.5		
	Want	14	2.45	.14	5.71	2.3-2.7	7.78	.89
	Wpost	14	2.44	.20	8.20	2.1-2.8		
M_2	L	16	3.28	.21	6.40	2.8-3.6		
	Want	16	2.70	.22	8.15	2.4-3.1	9.08	.96
	Wpost	16	2.72	.22	8.09	2.3-3.0		
M_3	L	15	3.81	.36	9.56	3.1-4.3		
	Want	15	2.51	.24	9.36	2.1-2.8	9.64	.98
	Wpost	15	2.22	.25	11.06	1.7-2.7		
P^4	L	2	.95	.07	3.63	1.9-2.0		
	W	1	3.50			- - -	7.00	.85
M^1	L	4	3.80	.22	5.68	3.5-4.0		
	Want	4	5.08	.10	1.88	5.0-5.2	20.03	1.30
	Wpost	3	5.27	.21	3.95	5.1-5.5		
M^2	L	1	3.20					
	Want	1	4.40				14.08	1.15
	Wpost	1	3.90					
M^3	L	1	2.40					
	W	1	3.50				8.40	.92

TABLE 2

Taxon: *Hyopsodus paulus*
Locality: Church Butte (low B)
Collection: USNM

Tooth	Dimension	N	$\overline{X}$ (mm)	s	CV	OR (mm)	LxW	$\overline{X}$ Log_{10}
M_1	L	4	3.85	.17	4.42	3.7-4.1	12.25	1.09
	Want	4	3.05	.17	5.57	2.9-3.3		
	Wpost	4	3.18	.22	6.92	3.0-3.5		
M_2	L	7	4.09	.25	6.11	3.7-4.5	14.38	1.16
	Want	7	3.47	.15	4.32	2.9-3.6		
	Wpost	7	3.40	.18	5.29	3.0-3.7		
M_3	L	8	4.71	.30	6.36	4.3-5.1	15.26	1.18
	Want	8	3.24	.09	2.83	3.1-4.3		
	Wpost	8	2.64	.13	4.93	2.5-2.8		
P^4	L	4	2.93	.05	1.71	2.9-3.0	12.95	1.12
	W	4	4.43	.15	3.39	4.2-4.5		
M^1	L	5	3.18	.08	2.63	3.1-3.3	13.22	1.12
	Want	5	4.16	.30	7.13	3.9-4.6		
	Wpost	5	4.08	.40	9.71	3.6-4.6		
M^2	L	4	4.05	.26	6.53	3.7-4.3	24.40	1.39
	Want	4	6.00	.49	8.16	5.4-6.4		
	Wpost	4	5.50	.42	7.71	4.9-5.8		
M^3	L	5	3.32	.22	6.53	3.0-3.5	17.00	1.23
	W	5	5.12	.18	3.49	4.9-5.3		

TABLE 3

Taxon: *Hyopsodus paulus*

Locality: 1129, 2409, 2413 (high B) **Collection: MPM**

Tooth	Dimension	N	$\overline{X}$ (mm)	s	CV	OR (mm)	LxW	$\overline{X}$ Log_{10}
P_4	L	40	3.06	.17	5.67	2.6-3.4		
	Want	40	2.25	.19	8.50	1.8-2.8	7.22	.86
	Wpost	40	2.34	.18	7.60	1.9-2.8		
M_1	L	9	3.61	.13	3.60	3.4-3.8		
	Want	9	2.80	.07	2.50	2.7-2.9	10.60	1.02
	Wpost	9	2.90	.19	6.55	2.6-3.1		
M_2	L	10	3.75	.18	4.80	3.4-4.0		
	Want	10	3.16	.12	3.80	3.0-3.3	11.86	1.07
	Wpost	10	3.08	.17	5.52	2.8-3.3		
M_3	L	44	4.28	.20	4.66	3.7-4.7		
	Want	43	2.89	.15	5.26	2.5-3.2	12.38	1.09
	Wpost	43	2.46	.16	6.59	2.0-2.8		
dP_4	L	21	3.85	.16	4.08	3.5-4.1		
	Want	20	1.92	.14	7.29	1.6-2.1	8.37	.92
	Wpost	20	2.18	.13	6.67	2.0-2.5		
P^4	L	31	2.52	21	8.18	2.1-3.0		
	W	31	3.70	.30	8.06	3.0-4.1	9.33	.97
M^1	L	4	3.68	.24	6.42	3.5-4.0		
	Want	4	4.75	.10	2.11	4.7-4.9	17.45	1.24
	Wpost	4	4.60	.08	1.77	4.5-4.7		
M^2	L	7	3.84	.15	3.94	3.6-4.0		
	Want	7	5.20	.27	5.21	4.7-5.5	19.96	1.30
	Wpost	7	4.81	.27	5.56	4.5-5.2		
M^3	L	48	3.12	.28	8.84	2.3-3.7		
	W	47	4.43	.43	9.63	2.8-4.8	13.90	1.14
dp^4	L	14	3.07	.16	5.18	2.7-3.4		
	Want	14	3.31	.31	9.29	3.0-4.3	10.26	1.01
	Wpost	14	3.26	.27	8.30	3.1-4.1		

TABLE 4

Taxon: *Hyopsodus paulus*

Locality: 1094, 2400, 2401, 2766 (high B) **Collection: MPM**

Tooth	Dimension	N	$\overline{X}$ (mm)	s	CV	OR (mm)	LxW	$\overline{X}$ Log_{10}
P_4	L	15	3.07	.19	6.11	2.8-3.4	7.08	.85
	Want	15	2.22	.13	5.70	2.0-2.4		
	Wpost	15	2.29	.14	6.06	2.1-2.5		
M_1	L	9	3.63	.21	5.79	3.4-4.1	10.39	1.02
	Want	9	2.78	.10	3.60	2.6-2.9		
	Wpost	9	2.86	.14	4.90	2.7-3.1		
M_2	L	11	3.81	.17	4.46	3.5-4.1	11.99	1.08
	Want	11	3.10	.20	6.45	2.7-3.5		
	Wpost	11	3.08	.19	6.17	2.8-3.3		
M_3	L	22	4.30	.21	4.81	4.0-4.7	12.41	1.09
	Want	22	2.88	.19	6.66	2.7-3.4		
	Wpost	22	2.46	.17	7.05	2.3-2.9		
dP_4	L	7	3.90	.32	8.11	3.2-4.1	8.82	.94
	Want	7	2.00	.15	7.64	1.8-2.2		
	Wpost	7	2.26	.10	4.32	2.1-2.4		
P^4	L	16	2.55	.14	5.36	2.3-2.9	10.05	1.00
	W	16	3.93	.27	6.87	3.4-4.4		
M^1	L	5	3.60	.25	7.08	3.2-3.9	17.15	1.23
	Want	5	4.76	.09	1.88	4.7-4.9		
	Wpost	5	4.64	.15	3.27	4.4-4.8		
M^2	L	10	3.91	.20	5.04	3.6-4.2	21.23	1.33
	Want	10	5.42	.30	5.49	5.0-5.8		
	Wpost	10	4.92	.21	4.37	4.5-5.3		
M^3	L	17	3.24	.24	7.48	2.9-3.6	14.66	1.16
	W	17	4.52	.28	6.17	4.2-5.2		
dP^4	L	6	3.20	.20	6.25	3.0-3.5	11.14	1.05
	Want	6	3.45	.34	9.83	3.2-4.1		
	Wpost	6	3.28	.38	11.48	3.0-4.0		

TABLE 5

Taxon: *Hyopsodus paulus*

Locality: 2145, 2215 (high B) **Collection: MPM**

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
P_4	L	15	3.23	.15	4.78	3.0-3.5		
	Want	15	2.42	.15	6.09	2.2-2.6	8.25	.91
	Wpost	15	2.55	.18	7.24	2.3-3.0		
M_1	L	9	3.97	.38	9.57	3.5-4.8		
	Want	9	2.99	.09	3.01	2.8-3.1	12.27	1.09
	Wpost	9	3.09	.12	3.88	2.9-3.3		
M_2	L	10	3.94	.25	6.35	3.6-4.4		
	Want	10	3.33	.28	8.41	2.9-3.7	13.16	1.12
	Wpost	10	3.17	.23	7.26	2.9-3.5		
M_3	L	20	4.40	.26	5.92	4.0-4.9		
	Want	20	3.11	.24	7.59	2.9-3.9	13.69	1.13
	Wpost	20	2.57	.22	8.59	2.3-2.9		
dP_4	L	5	3.92	.11	2.79	3.8-4.0		
	Want	5	2.02	.15	7.34	1.8-2.2	8.78	.94
	Wpost	5	2.24	.09	3.99	2.2-2.4		
P^4	L	18	2.73	.16	5.87	2.3-3.0		
	W	18	4.05	.40	9.96	3.1-4.5	11.07	1.04
M^1	L	6	3.87	.12	3.13	3.7-4.0		
	Want	6	4.77	.31	6.59	4.4-5.3	18.64	1.27
	Wpost	6	4.72	.34	7.14	4.4-5.2		
M^2	L	9	3.93	.21	5.40	3.7-4.3		
	Want	9	5.60	.39	7.03	4.9-6.3	22.07	1.34
	Wpost	9	5.16	.30	5.90	4.7-5.7		
M^3	L	27	3.26	.37	11.29	2.5-4.2		
	W	27	4.81	.38	7.84	4.4-5.8	15.80	1.19
dP^4	L	3	3.13	.15	4.88	3.0-3.3		
	Want	3	3.43	.23	6.73	3.3-3.7	11.22	1.05
	Wpost	3	3.53	.49	13.97	3.2-4.1		

TABLE 6

Taxon: *Hyopsodus paulus*

Locality: 2407, 2408, 2412, 2415, 2417 (high B) Collection: MPM

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
P_4	L	23	3.29	.12	3.54	3.1-3.5		
	Want	23	2.44	.16	6.51	2.2-2.9	8.22	.91
	Wpost	23	2.47	.15	5.88	2.2-2.9		
M_1	L	46	3.93	.19	4.83	3.6-4.4		
	Want	46	3.07	.12	3.91	2.9-3.9	12.47	1.09
	Wpost	45	3.14	.14	4.46	2.9-4.0		
M_2	L	61	4.07	.17	4.18	3.7-4.4		
	Want	61	3.54	.18	5.08	3.1-3.9	14.47	1.16
	Wpost	61	3.46	.20	5.78	3.1-4.0		
M_3	L	54	4.69	.29	6.22	4.1-5.3		
	Want	54	3.31	.21	6.37	2.9-3.6	15.45	1.19
	Wpost	54	2.77	.20	7.30	2.4-3.1		
dP_4	L	3	4.03	.21	5.17	3.8-4.2		
	Want	3	2.10	.10	4.76	2.0-2.2	9.54	.98
	Wpost	3	2.37	.06	2.44	2.3-2.4		
P^4	L	8	2.79	.19	6.76	2.5-3.1		
	W	8	4.25	.17	3.98	4.0-4.6	11.86	1.07
M^1	L	8	3.79	.12	3.29	3.6-3.9		
	Want	8	4.90	.15	3.09	4.7-5.1	18.56	1.27
	Wpost	8	4.79	.12	2.60	4.6-4.9		
M^2	L	12	4.11	.31	7.66	3.7-4.7		
	Want	12	5.84	.36	6.09	5.4-6.6	24.08	1.38
	Wpost	12	5.31	.33	6.30	4.8-6.0		
M^3	L	16	3.40	.25	7.44	3.0-4.0		
	W	16	4.96	.33	6.58	4.4-5.7	16.90	1.23
dP^4	L	6	3.23	.14	4.23	3.1-3.4		
	Want	6	3.65	.10	2.87	3.5-3.8	11.92	1.08
	Wpost	6	3.65	.16	4.50	3.4-3.8		

TABLE 7

Taxon: *Hyopsodus lepidus*
Locality: 2924 (high C)
Collection: MPM

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
P_4	L	4	3.05	.13	4.26	2.9-3.2		
	Want	4	2.43	.10	4.12	2.3-2.5	7.55	.88
	Wpost	4	2.48	.05	2.02	2.4-2.5		
M_1	L	7	3.71	.16	4.31	3.5-4.0		
	Want	7	2.77	.11	3.97	2.6-2.9	11.04	1.04
	Wpost	7	2.97	.16	5.39	2.7-3.2		
M_2	L	8	4.04	.17	4.21	3.8-4.2		
	Want	8	3.23	.07	2.17	3.1-3.3	13.03	1.11
	Wpost	8	3.15	.12	3.81	2.9-3.3		
M_3	L	5	4.44	.09	2.03	4.4-4.6		
	Want	5	2.92	.13	4.45	2.8-3.1	12.97	1.11
	Wpost	5	2.38	.08	3.36	2.3-2.5		
M^2	L	6	3.98	.16	4.03	3.8-4.2		
	Want	6	5.38	.22	4.14	5.1-5.7	21.55	1.33
	Wpost	5	5.10	.14	2.77	5.0-5.3		
M^3	L	8	3.19	.10	3.11	3.0-3.3		
	Want	8	4.49	.24	5.25	4.1-4.7	14.24	1.15
	Wpost	7	4.04	.34	8.32	3.6-4.6		

TABLE 8

Taxon: *Hyopsodus paulus*
Locality: 2924 (high C)
Collection: MPM

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
P_4	L	3	3.57	.15	4.20	3.4-3.7		
	Want	3	2.87	.21	7.32	2.7-3.1	10.22	1.01
	Wpost	3	2.87	.21	7.32	2.7-3.1		
M_1	L	5	4.40	.19	4.32	4.2-4.6		
	Want	5	3.44	.30	8.72	2.9-3.6	15.49	1.19
	Wpost	5	3.56	.21	5.90	3.2-3.7		
M_2	L	7	4.64	.16	3.45	4.5-4.9		
	Want	7	3.97	.13	3.27	3.8-4.2	18.43	1.26
	Wpost	7	3.76	.08	2.13	3.7-3.9		
M_3	L	6	5.07	.12	2.37	4.9-5.2		
	Want	6	3.43	.10	2.92	3.3-3.6	17.40	1.24
	Wpost	6	2.87	.12	4.18	2.7-3.0		
M^1	L	4	4.25	.19	4.47	4.0-4.4		
	Want	4	5.53	.39	7.05	5.0-5.9	23.53	1.37
	Wpost	4	5.30	.39	7.36	4.8-5.7		
M^2	L	4	4.58	.10	2.18	4.5-4.7		
	Want	4	6.68	.22	3.29	6.5-7.0	30.55	1.49
	Wpost	4	6.23	.26	4.17	6.0-6.5		
M^3	L	5	3.84	.18	4.69	3.6-4.1		
	W	5	5.60	.25	4.55	5.2-5.9	21.53	1.33

TABLE 9

Taxon: *Hyopsodus lepidus*
Locality: 2236 (high C)
Collection: MPM

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
P_4	L	6	2.88	.12	4.17	2.7-3.0		
	Want	6	2.12	.13	6.13	1.9-2.3	6.60	.82
	Wpost	6	2.28	.15	6.58	2.1-2.5		
M_1	L	6	3.63	.16	4.41	3.4-3.8		
	Want	6	2.68	.15	5.60	2.5-2.9	10.37	1.01
	Wpost	6	2.85	.16	5.61	2.6-3.1		
M_2	L	7	3.81	.21	5.51	3.6-4.2		
	Want	7	3.10	.08	2.58	3.0-3.2	11.83	1.07
	Wpost	7	2.97	.13	4.38	2.8-3.1		
M_3	L	5	4.26	.15	3.52	4.1-4.5		
	Want	5	2.74	.11	4.01	2.6-2.9	11.67	1.07
	Wpost	5	2.34	.17	7.26	2.2-2.6		
P^4	L	6	2.50	.09	3.60	2.4-2.6		
	W	6	3.93	.15	3.82	3.7-4.1	9.84	.99
M^1	L	5	3.62	.11	3.04	3.5-3.8		
	Want	5	4.48	.16	3.57	4.2-4.6	16.22	1.21
	Wpost	5	4.38	.13	2.97	4.2-4.5		
M^2	L	6	3.65	.21	5.75	3.4-3.9		
	Want	6	5.23	.19	3.63	4.9-5.4	19.11	1.28
	Wpost	6	4.75	.14	2.95	4.6-4.9		
M^3	L	8	2.89	.16	5.54	2.6-3.1		
	W	8	4.34	.34	7.83	4.0-4.8	12.34	1.09

TABLE 10

Taxon: *Hyopsodus paulus*
Locality: 2239 (high C)
Collection: MPM

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
P_4	L	21	3.61	.15	4.14	3.3-3.8	10.01	1.00
	Want	21	3.54	.30	8.55	2.5-2.8		
	Wpost	21	2.76	.14	4.92	2.5-2.9		
M_1	L	19	4.21	.15	3.56	3.9-4.4	14.51	1.16
	Want	19	3.30	.21	6.36	3.0-3.9		
	Wpost	19	3.43	.20	5.83	3.2-3.9		
M_2	L	12	4.38	.14	3.20	4.1-4.6	16.48	1.21
	Want	12	3.76	.17	4.52	3.4-4.0		
	Wpost	12	3.56	.16	4.49	3.4-3.8		
M_3	L	15	4.88	.31	6.25	4.5-5.5	16.71	1.22
	Want	15	3.41	.15	4.36	3.2-3.7		
	Wpost	15	2.94	.15	5.11	2.7-3.2		
dP_4	L	2	4.45	.07	1.59	4.4-4.5	10.47	1.02
	Want	2	2.05	.07	3.45	2.0-2.1		
	Wpost	2	2.35	.21	9.03	2.2-2.5		
P^4	L	7	3.04	.13	4.28	2.9-3.3	14.43	1.16
	W	7	4.74	.11	2.32	4.6-4.9		
M^1	L	9	4.07	.21	5.16	3.8-4.4	21.96	1.34
	Want	8	5.31	.25	4.71	4.8-5.6		
	Wpost	8	5.21	.20	3.84	5.0-5.5		
M^2	L	16	4.34	.17	3.92	3.9-4.7	27.75	1.44
	Want	12	6.38	.22	3.45	6.1-6.7		
	Wpost	13	5.88	.32	5.44	5.4-6.4		
M^3	L	15	3.71	.21	5.66	3.4-4.0	20.49	1.31
	W	14	5.51	.16	2.90	5.2-5.7		

TABLE 11

Taxon: *Hyopsodus paulus*
Locality: 1096, 1128, 2149, 2385, 2402 (low D)
Collection: MPM

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
P_4	L	14	3.41	.26	7.76	3.0-3.9	9.16	.96
	Want	14	2.56	.15	5.88	2.2-2.7		
	Wpost	14	2.67	.17	6.48	2.4-3.0		
M_1	L	17	4.16	.23	5.53	3.9-4.7	13.82	1.14
	Want	17	3.17	.15	4.73	2.9-3.3		
	Wpost	17	3.31	.18	5.44	2.9-3.6		
M_2	L	20	4.28	.20	4.67	3.9-4.6	15.59	1.19
	Want	20	3.61	.20	5.54	3.2-4.1		
	Wpost	20	3.58	.21	5.87	3.2-4.0		
M_3	L	26	4.88	.23	4.64	4.6-5.4	16.63	1.22
	Want	26	3.38	.19	5.53	3.1-3.8		
	Wpost	26	2.87	.26	9.12	2.4-3.6		
dP_4	L	1	4.30				11.18	1.05
	Want	1	2.20					
	Wpost	1	2.60					
P^4	L	9	3.00	.12	4.08	2.8-3.2	13.72	1.14
	W	9	4.58	.24	5.32	4.1-5.0		
M^1	L	8	4.18	.18	4.38	3.9-4.4	22.07	1.34
	Want	8	5.29	.15	2.76	5.1-5.5		
	Wpost	8	5.13	.18	3.42	4.8-5.3		
M^2	L	11	4.37	.16	3.70	4.2-4.6	27.34	1.44
	Want	11	6.25	.30	4.87	5.8-6.9		
	Wpost	11	5.90	.26	4.48	5.6-6.5		
M^3	L	12	3.56	.21	5.92	3.2-4.0	18.56	1.27
	W	12	5.21	.23	4.44	4.9-5.7		

TABLE 12

Taxon: *Hyopsodus minusculus*

Locality: Powder Wash (B) **Collection: CM**

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
P_4	L	6	2.80	.19	6.78	2.6-3.0	6.21	.79
	Want	6	2.18	.18	8.42	2.0-2.5		
	Wpost	6	2.20	.20	9.09	2.0-2.5		
M_1	L	5	3.28	.20	6.25	3.1-3.5	8.74	.94
	Want	5	2.58	.19	7.46	2.3-2.9		
	Wpost	5	2.64	.26	9.88	2.3-2.9		
M_2	L	7	3.50	.24	7.00	3.2-3.8	10.74	1.03
	Want	7	3.00	.18	6.09	2.7-3.2		
	Wpost	7	3.01	.29	9.67	2.6-3.5		
M_3	L	7	3.81	.18	4.65	3.5-4.0	10.36	1.01
	Want	7	2.71	.09	3.32	2.6-2.9		
	Wpost	7	2.27	.11	4.90	2.2-2.4		
dP_4	L	1	3.50				7.70	.89
	W	1	2.20					
P^4	L	4	2.35	.24	10.13	2.0-2.5	8.07	.91
	W	4	3.43	.21	6.01	3.2-3.6		
M^1	L	2	3.25	.21	6.53	3.1-3.4	13.82	1.14
	Want	2	4.25	.07	1.66	4.2-4.3		
	Wpost	2	4.25	.07	1.66	4.2-4.3		
M^2	L	2	3.30	.14	4.29	3.2-3.4	15.84	1.20
	Want	2	4.80	—	—	4.8		
	Wpost	2	4.50	—	—	4.5		
M^3	L	5	2.70	—	—	2.7	10.75	1.03
	W	5	3.98	.18	4.49	3.8-4.2		
dP^4	L	1	3.00				9.00	.95
	Want	1	3.00					
	Wpost	1	3.00					

TABLE 13

Taxon: *Hyopsodus lepidus*
Locality: Tabernacle Butte, Loc. 5 (C-D)
Collection: AMNH

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
P_4	L	15	3.08	.17	5.38	2.7-3.3	7.67	.88
	Want	15	2.32	.21	9.10	2.0-2.7		
	Wpost	15	2.49	.30	12.13	1.8-2.7		
M_1	L	10	3.69	.30	8.13	3.1-4.2	12.09	1.08
	Want	10	3.02	.19	6.29	2.8-3.4		
	Wpost	10	3.28	.17	5.18	3.0-3.6		
M_2	L	5	4.24	.22	5.19	3.4-4.5	15.18	1.18
	Want	5	3.46	.22	6.36	3.2-3.8		
	Wpost	5	3.52	.15	4.26	3.3-3.7		
M_3	L	8	4.75	.32	6.66	4.2-5.0	14.34	1.16
	Want	8	3.01	.18	6.01	2.6-3.2		
	Wpost	8	2.50	.15	6.05	2.3-2.7		
dP_4	L	2	3.95	.07	1.79	3.9-4.0	8.30	.92
	Want	2	1.95	.07	3.63	1.9-2.0		
	Wpost	2	2.10	—	—	2.1		
P^4	L	9	2.70	.17	6.14	2.3-2.9	11.49	1.06
	W	9	4.24	.24	5.67	3.8-4.5		
M^1	L	10	3.74	.36	9.62	3.1-4.1	18.07	1.25
	Want	8	4.88	.24	4.99	4.5-5.3		
	Wpost	8	4.75	.18	3.73	4.5-5.0		
M^2	L	15	4.01	.38	9.56	3.5-4.7	23.20	1.36
	Want	14	5.67	.44	7.78	5.0-6.4		
	Wpost	14	5.34	.39	7.26	4.7-5.8		
M^3	L	11	3.05	.22	7.09	2.8-3.4	13.91	1.14
	W	11	4.54	.42	9.36	4.0-5.2		

TABLE 14

Taxon: *Hyopsodus paulus*
Locality: Sand Wash (C-D)
Collection: CM-UCM

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log$_{10}$
P_4	L	5	3.44	.22	6.37	3.2-3.6	9.61	.98
	Want	4	2.75	.19	6.96	2.5-2.9		
	Wpost	5	2.78	.08	3.01	2.7-2.9		
M_1	L	12	4.17	.18	4.32	3.9-4.6	14.13	1.15
	Want	12	3.19	.20	6.27	3.0-3.7		
	Wpost	12	3.39	.15	4.42	3.2-3.7		
M_2	L	16	4.36	.16	3.67	4.2-4.8	16.25	1.21
	Want	16	3.70	.19	5.14	3.4-4.0		
	Wpost	16	3.66	.21	5.74	3.3-4.1		
M_3	L	7	5.14	.26	5.13	4.8-5.5	17.95	1.25
	Want	9	3.43	.15	4.37	3.2-3.7		
	Wpost	9	2.81	.19	6.76	2.5-3.1		
dP_4	L	1	4.00				10.00	1.00
	Want	1	2.20					
	Wpost	1	2.50					
M^1	L	2	4.05	.07	1.75	4.0-4.1		
	W	1	5.20					
M^2	L	1	4.50				29.25	1.47
	Want	1	6.50					
	Wpost	1	6.00					
M^3	L	2	3.55	.07	1.99	3.5-3.6	17.91	1.26
	Want	2	5.05	.49	9.80	4.7-5.4		

TABLE 15
Taxon: *Hyopsodus minusculus*
Locality: Millersville (low B)
Collection: USNM

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
M_1	L	23	3.22	.20	6.21	2.6-3.4		
	Want	23	2.50	.18	7.20	2.1-2.8	8.49	.93
	Wpost	23	2.62	.17	6.49	2.3-2.9		
M_2	L	23	3.32	.23	6.93	2.9-3.7		
	Want	23	2.77	.21	7.58	2.4-3.0	9.33	.97
	Wpost	23	2.75	.20	7.27	2.2-3.0		

TABLE 16
Taxon: *Hyopsodus paulus*
Locality: Millersville (low B)
Collection: USNM

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
M_1	L	8	3.90	.28	7.18	3.5-4.4		
	Want	8	3.01	.21	6.98	2.9-3.5	11.90	1.07
	Wpost	8	2.96	.26	8.78	2.4-3.3		
M_2	L	13	3.92	.25	6.38	3.5-4.3		
	Want	13	3.45	.21	6.09	3.1-3.8	13.55	1.13
	Wpost	13	3.33	.23	6.91	3.0-3.7		

TABLE 17
Taxon: *Hyopsodus paulus*
Locality: Grizzly Buttes West (middle B)
Collection: AMNH

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
M_1	L	45	3.86	.25	6.48	3.3-4.3		
	Want	45	3.12	.17	5.45	2.8-3.4	12.37	1.09
	Wpost	45	3.17	.16	5.05	2.9-3.5		
M_2	L	57	4.11	.26	6.33	3.4-4.7		
	Want	57	3.64	.18	4.95	3.4-4.2	15.07	1.18
	Wpost	57	3.54	.20	5.65	3.1-4.1		

TABLE 18
Taxon: *Hyopsodus paulus*
Locality: Grizzly Buttes (middle B)
Collection: USNM

Tooth	Dimension	N	$\bar{X}$(mm)	s	CV	OR(mm)	LxW	$\bar{X}$ Log_{10}
M_1	L	50	3.83	.19	4.96	3.3-4.2	12.09	1.08
	Want	50	3.06	.15	4.90	2.4-3.3		
	Wpost	50	3.13	.17	5.43	2.7-3.5		
M_2	L	56	3.99	.25	6.27	3.3-4.5	14.32	1.15
	Want	56	3.56	.17	4.78	3.2-4.0		
	Wpost	56	3.49	.20	5.73	3.1-4.1		

TABLE 19
Taxon: *Hyopsodus paulus*
Locality: 1941 #2 (high B)
Collection: USNM

Tooth	Dimension	N	$\bar{X}$(mm)	s	CV	OR(mm)	LxW	$\bar{X}$ Log_{10}
M_1	L	8	3.98	.28	7.04	3.6-4.5	13.07	1.12
	Want	8	3.10	.20	6.45	2.9-3.4		
	Wpost	8	3.15	.24	7.62	2.8-3.5		
M_2	L	12	4.12	.26	6.31	3.7-4.5	14.06	1.14
	Want	12	3.41	.22	6.45	3.2-3.9		
	Wpost	12	3.32	.28	8.43	3.1-3.9		

TABLE 20
Taxon: *Hyopsodus paulus*
Locality: C_2
Collection: AMNH

Tooth	Dimension	N	$\bar{X}$(mm)	s	CV	OR(mm)	LxW	$\bar{X}$ Log_{10}
M_1	L	10	4.46	.30	6.73	4.1-5.1	16.88	1.23
	Want	10	3.69	.25	6.78	3.6-4.0		
	Wpost	10	3.77	.25	6.63	3.6-4.1		
M_2	L	10	4.80	.32	6.67	4.3-5.3	20.17	1.30
	Want	10	4.19	.28	6.68	3.5-4.5		
	Wpost	10	4.04	.30	7.43	3.5-4.4		

TABLE 21

Taxon: *Hyopsodus lepidus*
Locality: C_3
Collection: AMNH

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
M_1	L	6	3.47	.31	8.93	3.1-3.8	9.53	.98
	Want	6	2.62	.15	5.73	2.4-2.8		
	Wpost	6	2.75	.18	6.55	2.5-3.0		
M_2	L	8	3.64	.18	4.95	3.4-3.9	10.73	1.03
	Want	8	2.89	.20	6.92	2.6-3.2		
	Wpost	8	2.85	.12	4.21	2.7-3.0		

TABLE 22

Taxon: *Hyopsodus lepidus*
Locality: C_4
Collection: AMNH

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
M_1	L	16	3.58	.26	7.26	3.1-3.9	10.27	1.01
	Want	16	2.69	.20	7.43	2.3-3.0		
	Wpost	16	2.85	.18	6.32	2.5-3.1		
M_2	L	17	3.80	.22	5.79	3.4-4.2	12.13	1.08
	Want	17	3.17	.23	7.26	2.7-3.6		
	Wpost	17	3.08	.23	7.47	2.7-3.5		

TABLE 23

Taxon: *Hyopsodus paulus*
Locality: Dead low Buttes (high C)
Collection: USNM

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
M_1	L	12	3.77	.18	4.77	3.4-4.0		
	Want	12	2.78	.13	4.32	2.5-3.0	11.12	1.05
	Wpost	12	2.95	.13	4.41	2.6-3.1		
M_2	L	11	3.94	.17	4.31	3.6-4.1		
	Want	11	3.21	.14	4.35	3.0-3.4	12.67	1.10
	Wpost	11	3.11	.15	4.82	2.9-3.3		

TABLE 24

Taxon: *Hyopsodus paulus*
Locality: C_5
Collection: USNM

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
M_1	L	8	3.93	.27	6.87	3.5-4.3		
	Want	8	2.95	.17	5.76	2.7-3.2	12.31	1.09
	Wpost	8	3.13	.21	6.71	2.8-3.4		
M_2	L	7	4.10	.29	7.07	3.8-4.5		
	Want	7	3.40	.31	9.12	2.8-3.7	14.09	1.15
	Wpost	7	3.33	.19	5.71	3.0-3.5		

TABLE 25

Taxon: *Hyopsodus paulus*
Locality: NE Twin Buttes (low D)
Collection: USNM

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
M_1	L	18	3.84	.22	5.73	3.5-4.3		
	Want	18	3.08	.15	4.87	2.9-3.4	12.18	1.08
	Wpost	18	3.16	.15	4.75	2.9-3.4		
M_2	L	21	4.12	.28	6.80	3.4-4.5		
	Want	21	3.50	.21	6.00	3.2-3.9	14.62	1.17
	Wpost	21	3.41	.23	6.74	2.9-4.0		

TABLE 26

Taxon: *Hyopsodus paulus*
Locality: D_1
Collection: USNM

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
M_1	L	45	4.14	.21	5.07	3.7-4.5		
	Want	45	3.19	.17	5.33	2.8-3.6	13.77	1.14
	Wpost	45	3.32	.19	5.72	3.0-4.0		
M_2	L	48	4.47	.19	4.25	4.0-5.0		
	Want	48	3.73	.20	5.36	3.4-4.2	16.79	1.22
	Wpost	48	3.65	.19	5.21	3.2-4.2		

TABLE 27

Taxon: *Hyopsodus lepidus*
Locality: D_1
Collection: USNM

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
M_1	L	12	3.60	.13	3.52	3.4-3.7		
	Want	12	2.78	.16	5.76	2.5-3.0	10.56	1.02
	Wpost	12	2.97	.16	5.39	2.7-3.1		
M_2	L	13	3.76	.21	5.59	3.4-4.1		
	Want	13	3.17	.18	5.68	2.7-3.3	11.99	1.08
	Wpost	12	3.04	.17	5.59	2.8-3.4		

TABLE 28

Taxon: *Hyopsodus paulus*
Locality: D_2
Collection: USNM

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
M_1	L	26	4.17	.24	5.76	3.6-4.5		
	Want	26	3.16	.22	6.96	2.7-3.6	13.83	1.14
	Wpost	26	3.30	.23	6.97	2.9-3.7		
M_2	L	24	4.49	.28	6.24	3.9-5.1		
	Want	24	3.65	.23	6.30	3.2-4.1	16.58	1.22
	Wpost	24	3.55	.20	5.63	3.2-4.0		

TABLE 29

Taxon: *Hyopsodus paulus*
Locality: D_4
Collection: AMNH

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
M_1	L	10	4.21	.20	4.75	3.9-4.5		
	Want	10	3.27	.13	3.98	3.0-3.4	14.41	1.16
	Wpost	10	3.41	.22	6.45	3.1-3.7		
M_2	L	11	4.51	.26	5.76	4.1-5.0		
	Want	11	3.69	.16	4.34	3.4-4.0	16.81	1.22
	Wpost	11	3.65	.18	4.93	3.4-3.8		

TABLE 30

Taxon: *Hyopsodus paulus*
Locality: D_5
Collection: USNM

Tooth	Dimension	N	$\overline{X}$(mm)	s	CV	OR(mm)	LxW	$\overline{X}$ Log_{10}
M_1	L	7	4.34	.19	4.38	4.0-4.6		
	Want	7	3.21	.11	3.43	3.1-3.3	14.47	1.16
	Wpost	7	3.36	.14	4.17	3.2-3.6		
M_2	L	6	4.78	.15	3.14	4.6-4.9		
	Want	6	3.75	.22	5.87	3.5-4.0	17.95	1.25
	Wpost	6	3.53	.22	6.23	3.2-3.8		