THE PEARCE-SELLARDS *Series*

NUMBER 33

EARLY TERTIARY VERTEBRATE FAUNAS
TRANS-PECOS TEXAS:
AMYNODONTIDAE

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June 15, 1981

Texas Memorial Museum/2400 Trinity/Austin, Texas 78705
William G. Reeder, Director

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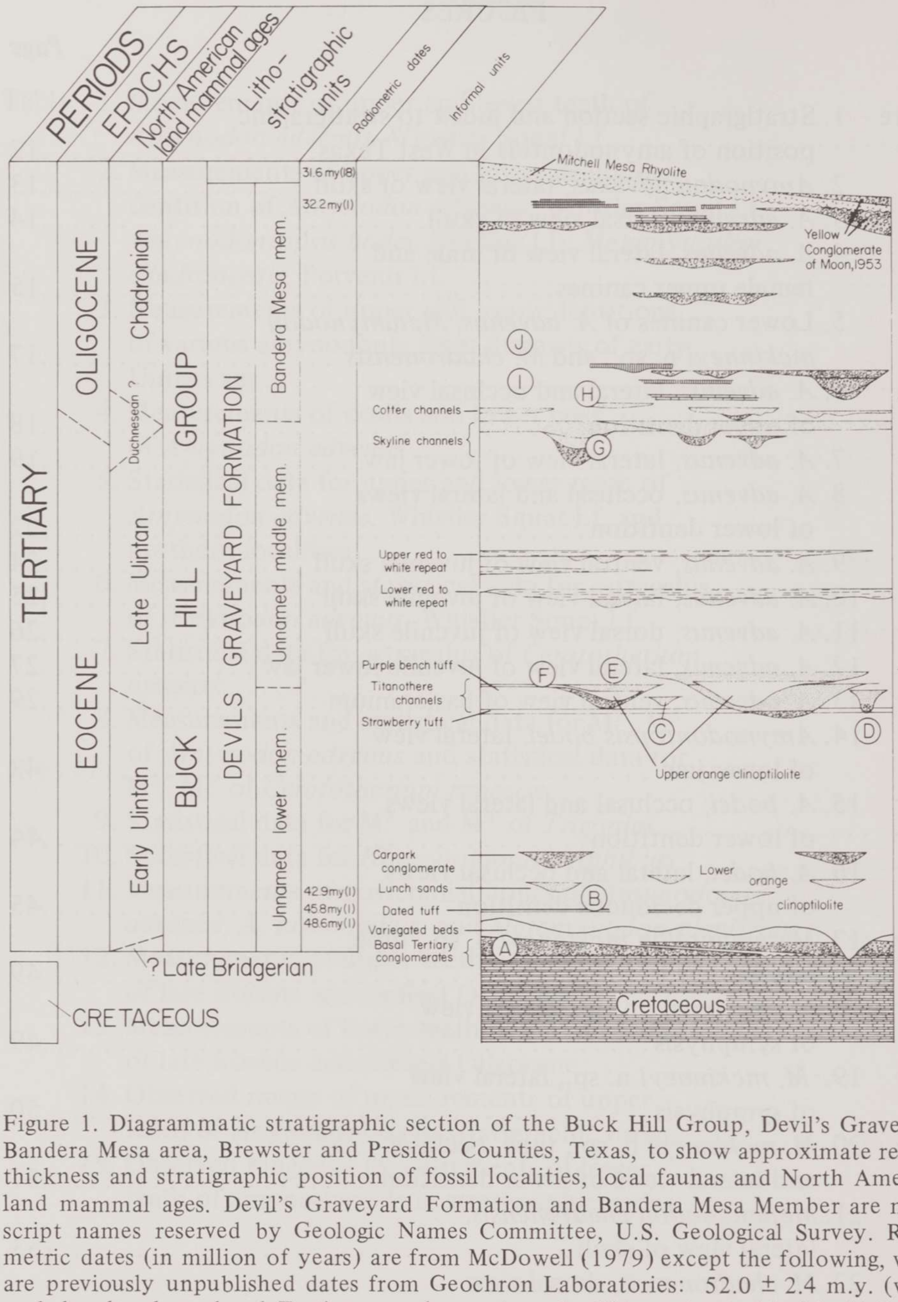

Figure 1. Diagrammatic stratigraphic section of the Buck Hill Group, Devil's Graveyard-Bandera Mesa area, Brewster and Presidio Counties, Texas, to show approximate relative thickness and stratigraphic position of fossil localities, local faunas and North American land mammal ages. Devil's Graveyard Formation and Bandera Mesa Member are manuscript names reserved by Geologic Names Committee, U.S. Geological Survey. Radiometric dates (in million of years) are from McDowell (1979) except the following, which are previously unpublished dates from Geochron Laboratories: 52.0 ± 2.4 m.y. (whole rock basalt, above basal Tertiary conglomerate and within variegated beds); 41.7 ± 1.6 m.y. (biotite-bearing ash, just below Skyline channel); 32.2 ± 1.5 m.y. (whole rock basalt, lowest basalt Bandera Mesa). The number in parentheses following the date signifies the number of samples. Letters refer to stratigraphic position of one or more fossil localities. Fossil localities referred to in this paper are: B. 41372, Whistler Squat quarry; 41576, southwest of wax camp; 41747, Boneanza; E. 41723, Titanothere hill; 41549, Margaret's bonebed. G. 41715, North Fork of the Alamo de Cesario; 41668, east side Devil's Backbone. H. 41853, Horseshoe stone coral, Cotter channels. Stratigraphic section compiled by James B. and Margaret S. Stevens, Lamar University, Beaumont Texas.

EARLY TERTIARY VERTEBRATE FAUNAS, TRANS-PECOS TEXAS: Amynodontidae

John Andrew Wilson[1] and Judith A. Schiebout[2]

ABSTRACT

Skulls, lower jaws and limb bones, identified as *Amynodon advenus*, were recovered from a quarry and from other localities at the same stratigraphic level in deposits of early Uintan age that contain the Whistler Squat local fauna in West Texas. Forms with large canines and long post-canine diastemas are identified as males, whereas forms with smaller canines and shorter diastemas are identified as females. A new species of *Metamynodon* from the Myton Uintan is based on a massive lower jaw. *Amynodontopsis bodei* is found in the Skyline and Cotter channels of latest Eocene and earliest Oligocene. *Metamynodon chadronensis* from the Porvenir local fauna of the Vieja area is described.

INTRODUCTION

Amynodont remains have been found in the upper Eocene deposits of the Agua Fria area and in the lower Oligocene deposits of the Vieja area. A generalized stratigraphic section of the Agua Fria area is given in figure 1. The largest number of specimens was recovered from the lower part of the Pruett Fm. in the Agua Fria area. This sample, although not as large as desired, makes it possible to assess the amount of variation in an amynodont population at a small area over a short interval of time. Most of the material came from a single quarry located approximately 600 feet (183 m) east of Whistler Squat on the Agua Fria Quadrangle, Brewster County, Texas (Moon, 1953). Smaller, but important, samples occurred higher in the Pruett Fm. and in the lower part of the section in the Porvenir area. The location of the Vieja area and the stratigraphic occurrence of the metamynodonts are given in Wilson (1977b, tables 1, 2, 3, 4, 6).

PREVIOUS WORK

This is one of several papers that deal primarily with the early Tertiary stratigraphy and the fossil vertebrate faunas of Trans-Pecos, Texas. They are: Wilson (1966), Harris (1967), Hoffer and Wilson (1967), Wilson et al. (1968), Harris and Wood (1969), Wilson (1971a, 1971b), Wood (1973, 1974), Schiebout (1974), Wilson (1974), Szalay and Wilson (1976), Wilson and Szalay (1976), Schiebout (1977b), Wilson (1977a, 1977b).

The Whistler Squat locality was first mentioned by Wilson (1972), and the fauna is not yet completely described. Wood (1973) described the rodents and referred to the assemblage as the Whistler Squat local fauna.

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He believed on the basis of the rodents that the local fauna was of Bridgerian age. Wilson (1974), on the basis of the presence of *Leptoreodon* and the amynodont, herein identified as *Amynodon advenus,* believes the age to be early Uintan.

A succession of faunas in superposition is now known in the Agua Fria-Green Valley area as a result of further field work, particularly that of Dr. James B. Stevens and Margaret S. Stevens. The stratigraphy of the area and the position of the more important localities are in manuscript (J.A. Wilson, J.B. Stevens, & M.S. Stevens). The superpositional order and age of the local faunas are given here, for convenience, in figure 1.

The manuscript names, Devil's Graveyard Formation and Bandera Mesa Member (fig. 1), will be proposed by J.B. and M.S. Stevens and J.A. Wilson and have been reserved by the Committee on Geologic Names of the United States Geological Survey. The name Pruett Formation, however, will be used in the text of this paper. It will be abandoned in the later manuscript because the top of the Pruett Fm. was defined as the base of the Crossen Trachyte by Goldich and Elms (1949) and the Crossen Trachyte does not extend as far south as the Agua Fria or Tascotal Mesa Quadrangles.

The Whistler Squat quarry rested on a calcareous tuff (fig. 1, B) that was dated by Fred W. McDowell of the Department of Geological Sciences at The University of Texas at Austin as 45.8 ± 1.1 and 48.6 ± 1.3 (McDowell, 1979). Another date of 42.9 ± 0.9 is from a micaceous tuff associated with the first clinoptilolite channel above the stratigraphic level of the quarry. This would place the quarry in rocks of early Uintan or Wagonhound age. The latest occurrence of amynodontids in Texas is in the Vieja area where *Metamynodon chadronensis* occurs in the Chambers Tuff which is bracketed by dates of 38.6 and 36.8 (Wilson, 1977b and McDowell, 1979), whereas *M. planifrons* extends to the middle Oligocene in South Dakota. *Metamynodon mckinneyi* n. sp. and *Amynodontopsis bodei* lie in between, with the former closer to 42.9 and the latter closer to 38.6.

A skull of *Sthenodectes* from the Titanothere Hill locality (fig. 1, E) was previously referred by Wilson (1977a) to the Whistler Squat l.f. New faunal and stratigraphic information necessitated a new local fauna, the Serendipity l.f. above the Whistler Squat l.f. and below the Skyline l.f. Material from the Titanothere Hill locality is included in the Serendipity l.f.

Tooth nomenclature is after Osborn but with no implication for origin of the cusp. Measurements of the upper cheek teeth are the greatest length along the ectoloph and the greatest width along the protoloph and metaloph. Lower cheek teeth were measured along greatest length and width. All measurements are in millimeters.

Specimen numbers without prefixes belong to TMM; such numbers preceded by a hyphen are abbreviated, and include the five digit locality number preceding, e.g., 41372-1, -2. Detailed descriptions of localities are on file at the Vertebrate Paleontology Laboratory, Texas Memorial Museum, The University of Texas at Austin.

ABBREVIATIONS

@	measurement approximate
alv	alveolus
AMNH	American Museum of Natural History, New York
AW	width across protoloph
CIT	Carnegie Institute of Technology, Pasadena, CA
CM	Carnegie Museum, Pittsburg, PA
DW	distal width
est	estimate
FMNH	Field Museum of Natural History, Chicago, IL
frag	fragment
L	anteroposterior length
LACM(CIT)	Los Angeles County Museum, California Institute of Technology Collection
l.f.	local fauna
loc.	locality
M	mean
OR	observed range
PU	Princeton University, Princeton, NJ
PW	width across metaloph
PW	proximal width of leg bone
σ	standard deviation
SDSM	South Dakota School of Mines and Technology, Rapid City
TMM	Texas Memorial Museum, The University of Texas at Austin
USNM	United States National Museum
V	coefficient of variation expressed in percent
W	width
YPM	Yale Peabody Museum, New Haven, CN

ACKNOWLEDGMENTS

The Geology Foundation, the Owen-Coates Fund of the Geology Foundation of the Department of Geological Sciences, the University Research Institute, and the Vertebrate Paleontology Laboratory, Texas Memorial Museum of The University of Texas at Austin, have supported the field work, the laboratory preparation, and in part, the cost of publication.

We are especially grateful to Dr. William D. Turnbull and Dr. Rainer Zangerl of the Field Museum of Natural History, Chicago, for the loan of material, information, and photographs concerning metamynodont material in their collection. We acknowledge and express our gratitude for courtesies to Dr. Donald Baird, Earl Manning, Dr. J.H. Ostrom, Dr. D.E. Savage and W.P. Wall. Dr. Ernest L. Lundelius and Melissa Winans were especially helpful concerning statistics. Dr. James B. Stevens and Margaret S. Stevens worked out the stratigraphic sequence in the Agua Fria area, and Mrs. Stevens and Robert H. Rainey collected much of the material herein described. The Whistler Squat Quarry was discovered by Robert H. Rainey and John A. Wilson in 1970 and was extensively worked in 1971. Members of the 1971 field party were Dr. Anne Forsten, Richard P. McCulloch, Robert H. Rainey, Margaret S. Stevens, Sally Rogers Scanlon and Dr. John A. Wilson. Mr. and Mrs. Billy Pat McKinney, the lessees, and J.H. Burton, Sid Burton and Macon Richmond, owners of the Agua Fria Ranch, provided invaluable assistance to field parties. The upper reaches of the Alamo de Cesario extend onto the ranch of Dr. Walter W. Dalquest of Midwestern University, who generously permitted us access to his land. Clegg Fowlkes of Marfa, Texas has been most helpful in giving us access to his ranches in the Green Valley area. This publication is a contribution of the Vertebrate Paleontology Laboratory, Texas Memorial Museum, The University of Texas at Austin.

SYSTEMATIC PALEONTOLOGY

Order	Perissodactyla	Owen 1848
Suborder	Ceratomorpha	Wood 1937
Superfamily	Rhinocerotoidea	Gill 1872
Family	Amynodontidae	Scott & Osborn 1883
Genus	*Amynodon*	Marsh 1877
Synonym	*Orthocynodon*	Scott & Osborn 1882
Type species	*Amynodon advenus*	*(Diceratherium advenum)* (Marsh, 1875)

Included species: *Amynodon advenus, A. reedi.*

Amynodontids have lent their names to prominent stratigraphic marker beds in the Eocene and Oligocene, the *Amynodon* sandstone of the Uinta Basin and the *Metamynodon* channels of the South Dakota Badlands. Yet, in spite of the relative frequency with which one encounters the name *Amynodon* in the paleontologic literature relating to the western interior of the United States, there has been published relatively little descriptive morphology since Osborn (1895). Furthermore, no comprehensive study of the family has been published[3] since Gromova (1954), but she dealt primarily with Mongolian amynodontids.

Four North American species of *Amynodon* have been described from the Rocky Mountain area and one from California. The earliest was *A. advenus* based on an M^3, YPM 11763, first described by Marsh (1875) as *Diceratherium advenum.* Two years later Marsh (1877) described the new genus *Amynodon* and referred to "a nearly perfect skull and various other remains . . . from the Uinta, or *Diplacodon* beds . . . ." Marsh also stated, "The type species is *Amynodon advenus* Marsh, which was provisionally referred to the genus *Diceratherium* when first described."

In 1833, Scott and Osborn named the family Amynodontidae and included within it the genera *Amynodon* and *Orthocynodon.* In the same paper, they described *O. antiquus* which was based on a lower jaw and the posterior portion of a skull (PU 10047), without the snout anterior to P^3. Scott and Osborn (1833, p. 9) used the structure of the third upper premolar to distinguish *Orthocynodon* from *Amynodon,* but in 1887 they referred to *Orthocynodon* as a probable synonym of *Amynodon* and in 1890 Osborn (1890, p. 507) was again doubtful that *A. advenus* and *O. antiquus* were generically distinct. He pointed out that, "A second examination of

[3] Mr. William P. Wall of the University of Massachusetts is currently undertaking a study of the family Amynodontidae.

type specimen recently made brings out several important diagnostic characters . . . . The type of *A. antiquus* is still found to resemble that of *A. advenus* closely, with the important exception that there are four lower premolars instead of three, the first lower premolar being fully functional and bifanged; the first upper premolar is missing." It must be pointed out, however, that the type of *A. antiquus,* PU 10047, is figured in Scott and Osborn (1833, pl. 5). In the side view of the lower jaw, M_3 and a section completely through the lower jaw are shown as restored but on the occlusal view the M_3 is not represented. In the side view of the skull, the nasal region and P^1 and P^2 are shown as restored. Neither of these restored teeth is shown on the occlusal view of the upper dentition. Earl Manning (personal communication, October 5, 1978), of the American Museum of Natural History, who had the type specimen from Princeton University on loan, very kindly confirmed my suspicion that the M_3 in the type lower jaw, PU 10047, is restored and that "there is no evidence of a tooth posterior to the last tooth in the occlusal figure. There is no bone present behind the last tooth in the figured rt. ramus." This changes the interpretation of the lower dental formula of *A. antiquus* to P_2–P_4, M_1–M_3 which is the same as that of other early Uintan North American amynodonts.

The type specimen of *A. antiquus* was collected in the Bitter Creek country of the Washakie Basin of Wyoming. Osborn (1929, fig. 62) showed *Amynodon antiquus* type as coming from the approximate zonal level of Adobe Town. The Adobe Town Member of the Washakie Formation was described by Roehler (1973) and correlated by him with the Wagonhound Member of the Uinta Formation of the Uinta Basin.

Osborn (1890, p. 506) said that, "There are now three skulls known which may be referred to three species. First, the type *Amynodon advenus* from the Uinta beds; second, the type of *A. (Orthocynodon) antiquus, nobis,* from the Washakie beds; third, the type of *A. intermedius* spec. nov., from the Uinta." Osborn (1890) and Scott and Osborn (1887) were wrong in referring to a skull as the type of *A. advenus.* The type of *A. advenus* is the M^3 described by Marsh (1875). However, Osborn (1890) revised Marsh's very brief description (1877) of the referred skull of *A. advenus. A. intermedius* was distinguished by Osborn (1890, p. 507) from *A. advenus* and *A. antiquus* by its much larger size, by the procumbent canines and by retention of a single-fanged first upper premolar. Five years later Osborn (1895, p. 95) modified his description of *A. intermedius* somewhat, based on more material, none of which, to our knowledge, has ever been figured. His diagnosis as of 1895 read: "Dentition: $I\frac{3}{3}$, $C\frac{1}{1}$, $DP\frac{4}{4}$, $M\frac{3}{3}$. Upper canines suboval in section, inclined forwards. Four deciduous premolars in both jaws. Four permanent premolars in the upper jaw? Lower canines erect, triangular."

In the same paper Osborn (1895, p. 75) listed the succession of species in the Uinta Basin. *Amynodon,* AMNH 1878, is listed as having been found in Horizon A–Lower Level; AMNH 1932, 1936, and 1830, also identified as

Amynodon, were from Horizon B–Middle Level; and *Amynodon intermedius,* AMNH 1933, was from Horizon C–Upper Level. This terminology of the stratigraphic units was changed by Osborn (1929, p. 91) and summarized in Wood et al. (1941) and later by Roehler (1973). Osborn (1929) in his valuable section on the stratigraphy of the intermontane basins showed the distribution of *Amynodon* as follows. For the Washakie Basin (p. 89): "*Amynodon antiquus,* type. (First of the amynodonts [aquatic rhinoceroses].)" Washakie B1 and B2 (*Eobasileus-Dolichorhinus* zone). And on p. 90, figure 62, he showed *Amynodon antiquus* type as occurring at the level of Adobe Town. For the Uinta Basin, Osborn (1929, p. 92) clarified the stratigraphic terms as follows: Uinta B2 of Peterson and Osborn: *Dolichorhinus cornutus* zone of Osborn (1895. 98). Amynodon beds of Riggs (1912.1, p. 22). Coarse brownish dacite tuffs and sandstones, capped at the summit by the 'Amynodon sandstone' immediately underlying Uinta C," and in this unit he stated that *Amynodon intermedius* was abundant. On the following page (Osborn, 1929, p. 93) *A. intermedius* is shown as having been found in the "Amynodon sandstone" at the top of Uinta B2 and also in Uinta C1 "*Amynodon* skel. Am Mus. No. 1933."

More information concerning *A. intermedius* was given by Colbert (1938) in his description of *Paramynodon birmanicus.* The former, as the largest species of North American Eocene amynodonts, was compared to the Burmese material. In addition Colbert (1938) very carefully analyzed those characters used by Pilgrim (1925) and Pilgrim and Cotter (1915) to distinguish *P. birmanicus* from *P. cotteri.* Colbert (1938) came to the tentative conclusion that the differences between the two species are due to sexual dimorphism within a single population. Our study of the Texas Eocene amynodonts brings us to a similar conclusion.

In 1921 Troxell described *A. erectus.* Troxell made the skull, mentioned by Marsh (1877) to supplement the description of *A. advenus,* the type of *A. erectus.* Troxell separated *A. erectus* from *A. advenus* on minor differences in size, a stronger cingulum, and a deeper postsinus of the third upper molars.

In addition Troxell (1921) stated that "*A. antiquus* may be distinctly separated from the others, perhaps subgenerically by the presence of both upper and lower functional first premolars, and by a marked difference in the general proportions of the teeth. The new species, *A. erectus,* is small and primitive, and in this respect approaches *A. antiquus,* but it has lost all trace of the first premolars and is of a later geological horizon." The only figures of *A. antiquus* that we can find are those of the type published by Scott and Osborn (1883, pl. V). The dentition of the type specimen, PU 10047, as previously mentioned, can be interpreted as having only three premolars. The upper dentition of the type has only P^3 and ^{4} preserved. There is no evidence for a first premolar, upper or lower, in *A. antiquus.*

Peterson (1919) discussed material of the genus *Amynodon* collected in the Uinta Basin but did not give locality or stratigraphic information. He

(Peterson, 1919, p. 130) said: "This genus is represented by a number of individuals. The material has a considerable range in size and undoubtedly represents two or probably three species. Unfortunately the fragmentary condition of the greater number of the specimens does not admit of an accurate identification. The smaller individuals are therefore provisionally placed in *Amynodon advenum* (Marsh) while the larger are referred to *Amynodon intermedius* Osborn."

Wood, Seton, and Hares (1936) listed *A. advenus* from upper Eocene beds on the north side of the Wind River Basin in the Badwater area. The Badwater fauna (except that from Carnegie Museum locality 20, Krishtalka and Setoguchi, 1977) is considered to be late Uintan or Myton. H.E. Wood II, identifier of the specimen, did not describe it or give the basis for his identification.

Wood (1941, 1949, 1954) published a chart showing the distribution and inferred stratigraphic relationships of American amynodont rhinoceroses. In none of the papers does Wood give any taxonomic, morphologic, or stratigraphic evidence to explain his choice of taxa, and one can only assume that this information would have been given in his long projected, but never completed, study of Tertiary rhinoceroses. Wood (1941) specifically stated "no amynodonts known" in Wasatchian or Bridgerian. In addition, Wood (1941, 1949, 1954) recognized in the western interior only *A. advenus* in Uinta A, *A. advenus* and *A. reedi* in Uinta B, and *A. intermedius* in Uinta C. Neither *A. antiquus* Scott and Osborn (1883) nor *A. erectus* Troxell (1921) are mentioned by Wood, but it is not evident from the literature when he had synonymized either of these species. In all of his charts, Wood recognized *A. reedi* from the Poway and *A. sp.* from the Sespe of California.

References to the occurrence of *Amynodon* in the Rocky Mountain area other than that of Peterson (1919) have been made. Granger (1910) reported on a fine skull of *Amynodon*? *antiquus* from Beaver Divide, Wyoming. The same skull is mentioned in Scott (1945, p. 212) as having been identified by H.E. Wood as *Amynodon advenus.* Wood (1948) referred to the specimen, AMNH 14601 as *A. advenus* "definitely referable to this species, although a slightly progressive variant," and further: "*Amynodon advenus* is a Uintan index fossil, most characteristic of the early Uintan." Emry (1975, p. 17) said, "*Amynodon advenus* and *Protoreodon parvus* from the uppermost part of the Wagon Bed Formation near Wagon Bed Spring indicate more specifically 'Uinta B' temporal equivalence."

Riggs (1912, p. 22) in a section on the stratigraphy of the 'Uintan Group' of the Uinta Basin discussed the Amynodon Beds. "This includes substantially the same vertical series as Horizon B of Peterson and Osborn as far as the writer has been able to interpret them." Riggs (1912, p. 23) did not describe any specimens of *Amynodon,* but said, "However, specimens of *Uintatherium* (?), *Stylinodon* sp., *Amynodon intermedius* and *Protylopus* were recorded" at the Field Museum of Natural History in Chicago. The senior author measured a skull, FMNH 12184, and a lower jaw, FMNH 12191, (see table 3) that were collected by Riggs. They are herein referred to *A. advenus.*

The occurrence of amynodontids in California was first reported by Stock (1933) when he described *Amynodontopsis bodei* based on a very fine skull that, according to Stock, is: "Larger than *Amynodon antiquus, A. advenus* and *A. erectus,* but less robust than *A. intermedius.* Skull dolichocephalic." Stock (1933, p. 767) concluded that: "Possibly the type of *A. intermedius* should be referred to *Amynodontopsis.*" The skull was collected from locality 150 of the California Institute of Technology (loc. LACM [CIT] 150). The collection from this locality was called Pearson Ranch local fauna by Golz (1976) and was correlated by him with the Lapoint of the Uinta Basin. In 1936 Stock referred more material including several fragmentary jaws, teeth, and a lower canine from loc. 150 to *Amynodontopsis bodei.* A lower jaw from locality LACM (CIT) 147, also included in the Pearson Ranch l.f., was referred by Stock (1936) to *Amynodontopsis bodei.* Stock (1939) described *Amynodon reedi* based on a maxillary fragment with P^4–M^3 collected at LACM (CIT) loc. 314. This locality was given by Stock as being in the Poway Conglomerate but the revision of the stratigraphic section in the San Diego area by Kennedy and Moore (1971) would now place the locality in the Friars Fm. of the La Jolla Group. This nomenclature was used in Golz (1976) and Schiebout (1977a). *A. reedi* is: "Smaller than *Amynodon advenus, A. antiquus* and *A. erectus* and resembling *A. sinensis* in size" (Stock, 1939). In addition Stock (1939) identified a single imperfect M^2 as *Amynodon* sp. possibly *advenus* and several parts of dentition referred to *Amynodontopsis bodei* from the "uppermost Eocene, California." We assume this to be LACM (CIT) loc. 150, but Stock (1939) did not say so specifically. Schiebout (1977a) referred a left maxilla with an incomplete M^3 and a right upper canine lacking the right half of the crown to *A. reedi.* Both specimens are from the Friars Fm. Golz (1976) summarized the stratigraphic occurrence of amynodonts in southern California in his table 1. The presence of *Amynodon* cf. *A. intermedius* in southern California was indicated for the first time by Golz and Lillegraven (1977). This is recorded by them as having come from the Santiago Fm. and in their figure 6, "the most likely temporal position of the land vertebrate faunas in the Santiaago Fm. is correlated with Uinta C of Utah. Amynodonts in southern California, therefore, are known from stratigraphic units that have been correlated with Wagonhound Member, the Myton Member, and the Lapoint of Utah.

A poorly-preserved lower jaw, CM 734, was found at Sage Creek, Montana, and identified by Douglas (1903) as *Metamynodon*?. Matthew (Osborn, 1909, p. 99) listed this specimen as "*Metamynodon* sp. (=?*Amynodon*)." Wood (1934, p. 252) said, "The Amynodont, CM 734, . . . seems . . . to be inside the limits of the genus *Amynodon* . . . . It is somewhat advanced over *Amynodon antiquus,* but is comparable in size with *Amynodon intermedius* from the Myton, and is more advanced in the loss of one incisor (I_3?), in the reduction in size of the remaining median incisor (I_1?), in the slightly larger canine and in the loss or extreme reduction of P_2. It is somewhat smaller and more primitive than, but otherwise rather close to, Stock's form from the Sespe Formation of Ventura County, California." Wood must have been referring to *Amynodontopsis bodei* Stock. Later on Wood (1934, p. 255) stated in a footnote that: "Restudy indicates reference to *Amynodon advenus* of the Lower Uinta." The results of further collecting in the Sage Creek area were presented by Hough (1955). She did not find any more amynodont material but referred CM 734 to *Amynodontopsis* cf. *A. bodei.* This was the first identification of that genus from the Rocky Mountain area. Hough (1955) applied the molar index proposed by Stock (1933) to the lower teeth, although she did not use the measurements given by Stock (1936) for a lower jaw that he referred to *A. bodei.*

Bjork (1967) identified *Amynodontopsis bodei* from the Slim Buttes area of northwestern South Dakota. His material consists of associated right and left mandibles and isolated teeth. He disagreed with Hough's identification of the Sage Creek specimen as *Amynodontopsis* and preferred Wood's (1934) reference of CM 734 to *Amynodon.* Bjork (1967, table 4) gave comparative measurements for some late Eocene and early Oligocene amynodonts.

Gazin (1956) in his review of the Badwater fauna did not describe or figure the *Amynodon advenus* specimen reported by Wood et al. (1936). Gazin (1956, p. 7), however, used Wood's identification of *A. advenus* to support a temporal correlation between the Sage Creek and Badwater faunas. Gazin also assigned the Badwater fauna, as then known, to the Uintan.

Black and Dawson (1966) listed the genus *Amynodon* as present in Wagonhound, Washakie B, Poway, Myton, Hendry Ranch, Tapo Ranch, and Randlett. The Hendry Ranch amynodont is presumably the one mentioned first by Wood et al. (1935). We are unable to account for the genus in the Randlett other than by their citation. Turnbull (1972) listed *Amynodon* sp. from Washakie B. of the Washakie Basin.

Stock (1939) referred to an amynodont from Uinta A as follows: "Unfortunately, the fauna thus far known from Uinta A is a meager one. It contains, according to Dr. H.E. Wood, II, an amynodont which he recognizes as of the species *Amynodon advenus* (No. 11983 Carnegie Mus.)." This may be the specimen or specimens that Wood (1941, 1949, 1954) used as a basis for the presence of *A. advenus* in Uinta A in his charts. Stock (1939) also referred to a small amynodont in the collection of the American Museum of Natural History (AMNH 1936A) that is the " . . . nearest resemblance in size to *A. reedi* . . . ." This specimen is from Uinta B of Utah and may be the basis of Wood's (1941, 1949, 1954) chart showing *A. reedi* present in Uinta B of the Rocky Mountain basins.

AMYNODON ADVENUS (Marsh) 1877

Figs. 2-13, Tables 1-6, 8, 11, 14, 15.

Type.—YPM 11763 LM^3, M_3. *Diceratherium advenum* Marsh 1877, Uintan, Uinta Basin, Utah.

Synonyms.—*Orthocynodon antiquus* Scott and Osborn 1883, *Amynodon antiquus* Scott and Osborn 1883, *A. intermedius* Osborn 1890, *A. erectus* Troxell 1921.

Material.—Distorted skull (?female) alv I^{1-3}, alv $\underline{C}$, P^2-M^3, 41576-19; somewhat crushed skull (?male) alv I^1, I^{2-3}, $\underline{C}$, alv P^2, P^3-M^3, 41372-416; skull frag (?female) L $\underline{C}$, P^2-M^3, -45; skull frag L P^4-M^3, -72; skull frag M^{2-3}, -101; skull frag R root $\underline{C}$, P^{2-4}, -421; skull frag (?male) R $\underline{C}$, -75; posterior half skull, -410; occiput, -603; skull frag (?female) alv $\underline{C}$, alv P^2, alv P^3, P^4, alv M^1, M^{2-3}, 41576-30; L M^{2-3}, 41372-629; L M^{1-3}, -628.

Isolated upper teeth, numerous incisors of uncertain position; $\underline{C}$, 41372-51, -606; P^2, 41747-85; P^3, -53; P^4, 41372-65, -444, -583; M^1, -430, 41576-29; M^2, 41372-49, -74, -520, -570, -605; M^3, -50, -413, -428, -613, -617.

Uncrushed lower jaw (?male) alv I_1, I_2, alv I_3, $\overline{C}$, P_2-M_3, 41372-451; dentary R alv P_2, P_3-M_3, 41747-75; dentary L P_3-M_3, 41747-76; dentary L alv P_2, P_3-M_3, 41372-99; dentary R M_{2-3}, -46; dentary L P_3-M_1, -602; dentary L P_3-M_1, -612; dentary L P_4, 41747-91; dentary R M_3, 42061-4.

Isolated lower teeth, numerous incisors of uncertain position; $\overline{C}$, 41372-619; P_2, -171; -624; P_3, -66, -207, -600; P_4, -426, -598, 41747-50; M_1, 41372-429; M_2, -441, -442, -594, 41576-16, -24; M_3, 41372-558.

Uncrushed juvenile skull without occiput, alv I^{1-3}, alv $\underline{C}$, P^1, dP^{2-4}, 41747-92. Juvenile lower jaw, alv I_{1-3}, alv $\overline{C}$, dP_{2-4}, 41372-71; alv $\overline{C}$, dP_2-dP_4, 41747-90; d$\underline{C}$, 41372-492; d$\overline{C}$, -544, dP_2, -159; dP_3, -64.

Disarticulated postcranial material.

Stratigraphic position.—Above the basal Tertiary conglomerate, if present, and within the lower 50 ft. (15.2 m) of the Pruett Tuff, Buck Hill Group, Brewster Co., Texas, Whistler Squat l.f. early Uintan (fig. 1).

Revised diagnosis.—Dentition $\frac{3}{2\text{ or }3}\ \frac{1}{1}\ \frac{4}{3}\ \frac{3}{3}$, milk dentition $\frac{3}{3}\ \frac{1}{1}\ \frac{3}{3}$. Medium to moderately large amynodonts. Incisors erect; upper canines semi-procumbent and large (L 27 mm) in males, more vertical and smaller (L 17 mm) in females. Canine to second premolar diastema longer in males (45-48) than in the female (30). Premolar length approximately one-half the molar length. Facial fossae deeper in males. Skull longer in males. Crown height at metacone on unworn M^3 approximately 25-35 mm.

Upper dentition.—Upper incisors or their alveoli are preserved in 41372-416 and 41576-19. In the former, the broken base of right I^2 and I^3 are present. The crown is broken off of I^1, is partly worn off of both I^2 and completely worn off of I^3. Incisors ^{1} and ^{2} are oval in cross section where they emerge from the alveolus; incisor ^{3} at the same position is more nearly circular in cross section. The wear on I^2 has rounded off the apex of the tooth, forming a dull chisel shape with the larger beveled surface facing posteriorly and

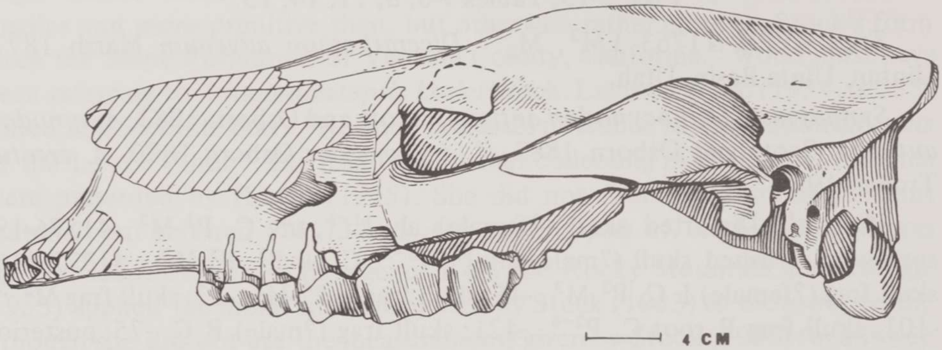

Figure 2. *Amynodon advenus*. Lateral view of skull. Whistler Squat l.f.

curving slightly to the exterior; a smaller beveled surface faces anteriorly. The only enamel left on the tooth is on the anteroexternal surface. The wear on I^3 has been more severe but the result is the formation of a chisel-shaped tooth like that of I^2. The posterior wear surface on I^3 is the larger and was formed by the apex of the lower canine coming between it and the upper canine. The anterior wear surface on I^3 is smaller and is grooved.

In the skull of the young adult, 41576-19 (figs. 2, 3), the alveoli for I^1 are well-preserved. A small unerupted I^2 is present in a small alveolus on the right side. On the left side the alveoli for the three upper incisors are all approximately of equal size. Measurements for the upper teeth are given in table 1.

The right upper canine is in place in the large skull 41372-416. It has an anterior wear surface for the lower canine and what appears to be an anteroexternal wear facet, but without the corresponding lower canines and incisors it is difficult to account for a wear surface in this position. An isolated anterior part of a right premaxillary and maxillary, 41372-75 (fig. 4A), has the canine in place. In both 41372-75 and -416, the enamel has been worn from the front of the tooth. This wear surface for the lower canine is vertical with respect to the plane of the palate. The wear surface for the lower canine (fig. 5) gives the upper canine a triangular cross section with the base of the triangle anterodorsal and, in unworn or little worn upper canines, the apex of the triangle is posteroventral. The apex of the triangle is a ridge of enamel that ends at the base of the enamel. The root of the lower canine is oval in cross section so that when the wear proceeds beyond the enamel, a cross section of the tooth is even more ovate (fig. 5). This is confirmed in an isolated upper canine, 41372-606. As Colbert (1938, p. 323-324) pointed out, the shape of a cross section of the canine depends on where the cross section is made.

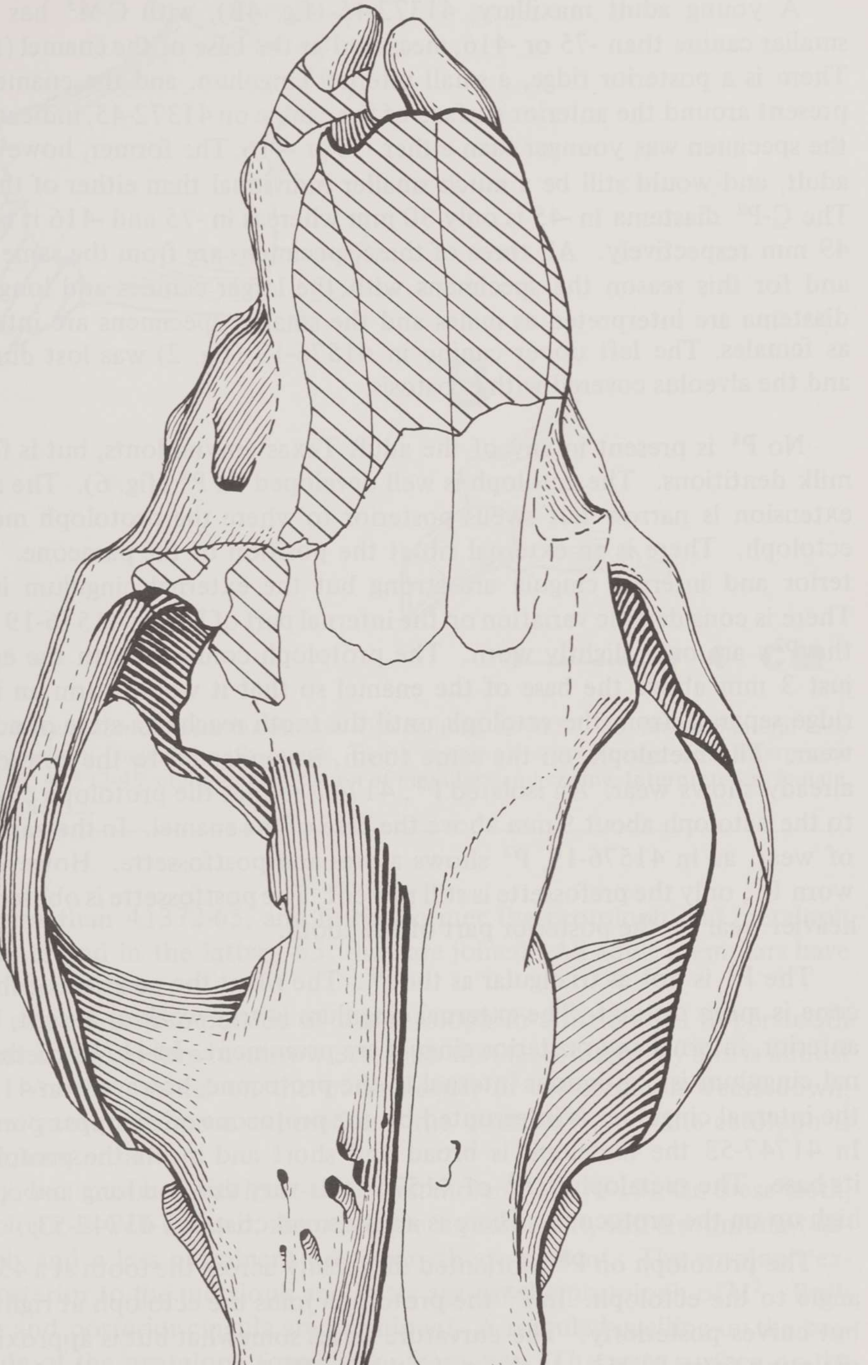

Figure 3. *Amynodon advenus*, 41576-19. Dorsal view of skull. Whistler Squat l.f.

A young adult maxillary, 41372-45 (fig. 4B), with C-M^3 has a much smaller canine than -75 or -416, measured at the base of the enamel (table 1). There is a posterior ridge, a small internal cingulum, and the enamel is still present around the anterior surface of the canine on 41372-45, indicating that the specimen was younger than either -75 or -416. The former, however, is an adult, and would still be a much smaller individual than either of the latter. The $\underline{C}$-P^2 diastema in -45 is only 30 mm whereas in -75 and -416 it is 44 and 49 mm respectively. All three of these specimens are from the same quarry; and for this reason the specimens with the larger canines and longer $\underline{C}$-P^2 diastema are interpreted as males and the smaller specimens are interpreted as females. The left upper canine in 41576-19 (fig. 2) was lost during life and the alveolus covered with exostosis.

No P^1 is present in any of the adult Texas amynodonts, but is found in milk dentitions. The ectoloph is well developed on P^2 (fig. 6). The anterior extension is narrow but swells posterior to where the protoloph meets the ectoloph. There is an external rib at the position of the paracone. The anterior and internal cingula are strong but the external cingulum is weak. There is considerable variation on the internal part of P^2. In 41576-19 (fig. 6), the P^2s are only slightly worn. The protoloph connects with the ectoloph just 3 mm above the base of the enamel so that it would form an isolated ridge separate from the ectoloph until the tooth reached a state of advanced wear. The metaloph, on the same tooth, is connected to the ectoloph and already shows wear. An isolated P^2, 41747-85, has the protoloph connected to the ectoloph about 9 mm above the base of the enamel. In the early stages of wear, as in 41576-19, P^2 shows a pre- and postfossette. However, on a worn P^2, only the prefossette is still present. The postfossette is obliterated by heavier wear on the posterior part of the tooth.

The P^3 is not as triangular as the P^2. The rib at the position of the paracone is more distinct. The external cingulum is very weak or absent, but the anterior, internal and posterior cingula are prominent. In 41747-53 the internal cingulum is continuous internal to the protocone, however, on 41576-19 the internal cingulum is interrupted by the protocone on all upper premolars. In 41747-53 the metaloph is broad and short and meets the protoloph at its base. The metaloph in P^3 of 41576-19 is very thin and long and connects high up on the protocone. There is a very small crista on 41747-53.

The protoloph on P^2 is oriented diagonally across the tooth at a 45 degree angle to the ectoloph. In P^3 the protoloph joins the ectoloph at right angles but curves posteriorly. The curvature varies somewhat but is approximately the same from P^3-M^3. If the metaloph on P^4 joins the protoloph near the base, the two lophs remain separate during much of the wear of the tooth. If they join higher up, however, they form a prefossette early in the wear stage. Of five moderately worn P^4s, three have the protoloph and metaloph connected, and two have them separated. However, 41372-72 and -444 are

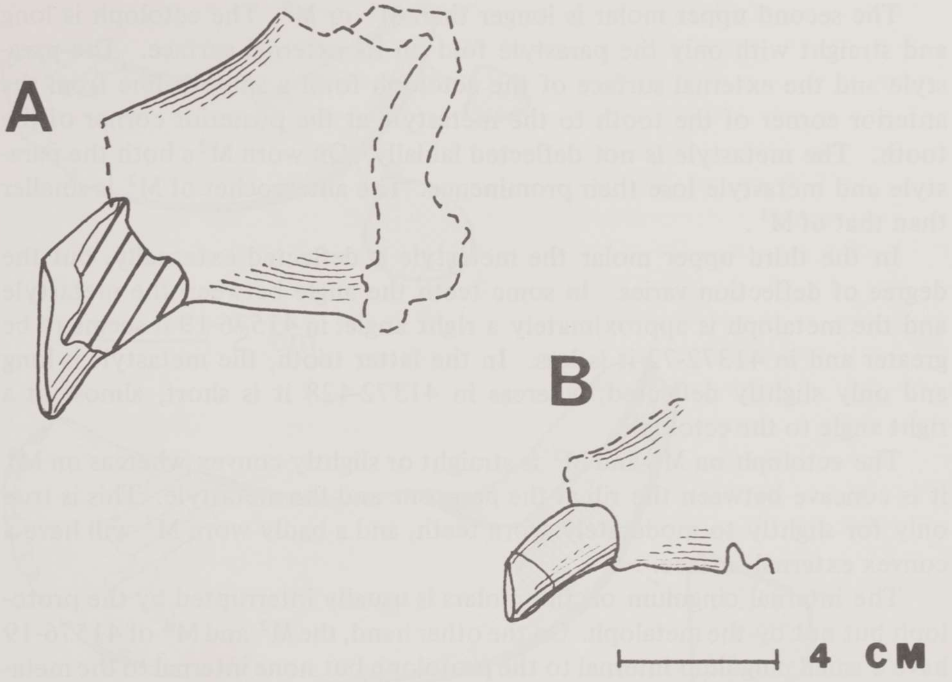

Figure 4. *Amynodon advenus* maxillaries with canines. A. 41372-75, reversed lateral view of right maxillary fragment with canine. Tooth is complete on internal side. Interpreted as a male. B. 41372-45, comparable portion of maxillary and canine. Interpreted as female. Whistler Squat l.f.

more worn than 41372-65, and in the former the protoloph and metaloph are separate and in the latter, -65, they are joined. All adult premolars have a single internal cusp.

The enamel on the outside of the ectoloph in a little-worn upper tooth curves internally to form a narrow ectoloph that faces internally and is almost vertical. As the enamel on the outer border of the ectoloph wears down, more and more dentine is exposed and the wear surface of the ectoloph is closer to horizontal.

Only one specimen has little-worn first molars (41576-19). On these teeth, the ectoloph is well-defined, the parastyle is prominent, and a prominent anterior rib and a less prominent posterior rib are present. The ectoloph extends posterior to the metaloph and butts against the protoloph of M^2. Both anterior and posterior cingula are prominent. A rounded swelling on the posterior side of the protoloph forms an antecrochet. The wear surface on the ectoloph is almost vertical and the medial valley is prominent. In adult first molars most of these characters are worn away. The ribs become faint as the ectoloph is worn down; the external corners of the tooth are rounded off and the median valley eventually becomes a median ridge as the last of the enamel is worn off.

The second upper molar is longer than M^1 or M^3. The ectoloph is long and straight with only the parastyle fold on its external surface. The parastyle and the external surface of the ectoloph form a smooth line from the anterior corner of the tooth to the metastyle at the posterior corner of the tooth. The metastyle is not deflected labially. On worn M^2s both the parastyle and metastyle lose their prominence. The antecrochet of M^2 is smaller than that of M^1.

In the third upper molar the metastyle is deflected externally, but the degree of deflection varies. In some teeth the angle between the metastyle and the metaloph is approximately a right angle; in 41576-19 it seems to be greater and in 41372-72 it is less. In the latter tooth, the metastyle is long and only slightly deflected; whereas in 41372-428 it is short, almost at a right angle to the ectoloph.

The ectoloph on M^1 and M^2 is straight or slightly convex whereas on M^3 it is concave between the rib at the paracone and the metastyle. This is true only for slightly to moderately worn teeth, and a badly worn M^3 will have a convex external surface.

The internal cingulum on the molars is usually interrupted by the protoloph but not by the metaloph. On the other hand, the M^2 and M^3 of 41576-19 have a small cingulum internal to the protoloph but none internal to the metaloph. There is a thin film of cement on the upper cheek teeth of 41576-19 and on some of the teeth from the Whistler Squat quarry although it is not as evident on the latter. We are unable to distinguish distinct and consistent differences in the upper dentition of amynodonts from the two localities that would imply more than one species. Therefore, we assume the variation is within the range of the age of the individuals or the sex of the individuals within a single population.

Lower dentition.—Only 41372-451 (fig. 7) furnishes evidence concerning the lower incisors. On the right side of this specimen there is part of an incisor and a single alveolus preserved. On the left side, there are three alveoli. Those for LI_1 and LI_2 are of about equal size (W=9.5 mm), but that for I_3 is very small and crowded against the canine. The incisor on the right and the alveolus next to it are larger (W=12.5 mm) than those on the left. We do not attach any taxonomic significance to the absence of one incisor and assume it to be pathologic or individual variation. We consider -451 to be a male because of the large canines and long diastema. Measurements for the lower teeth are given in table 1.

Isolated lower canines are easily distinguished by having the wear surface on the inside of the curve of the tooth. The crown of the tooth is triangular with the apex of the triangle anterior and the base of the triangle posterior. In the canine of a young adult, 41372-619, the apex of the triangle is a ridge of enamel extending to the base of the crown. The root of the canine is oval. The left canine in 41372-451 is in place and unbroken. The wear surface for the upper canine is present on the posterior side of the tooth (fig. 7)

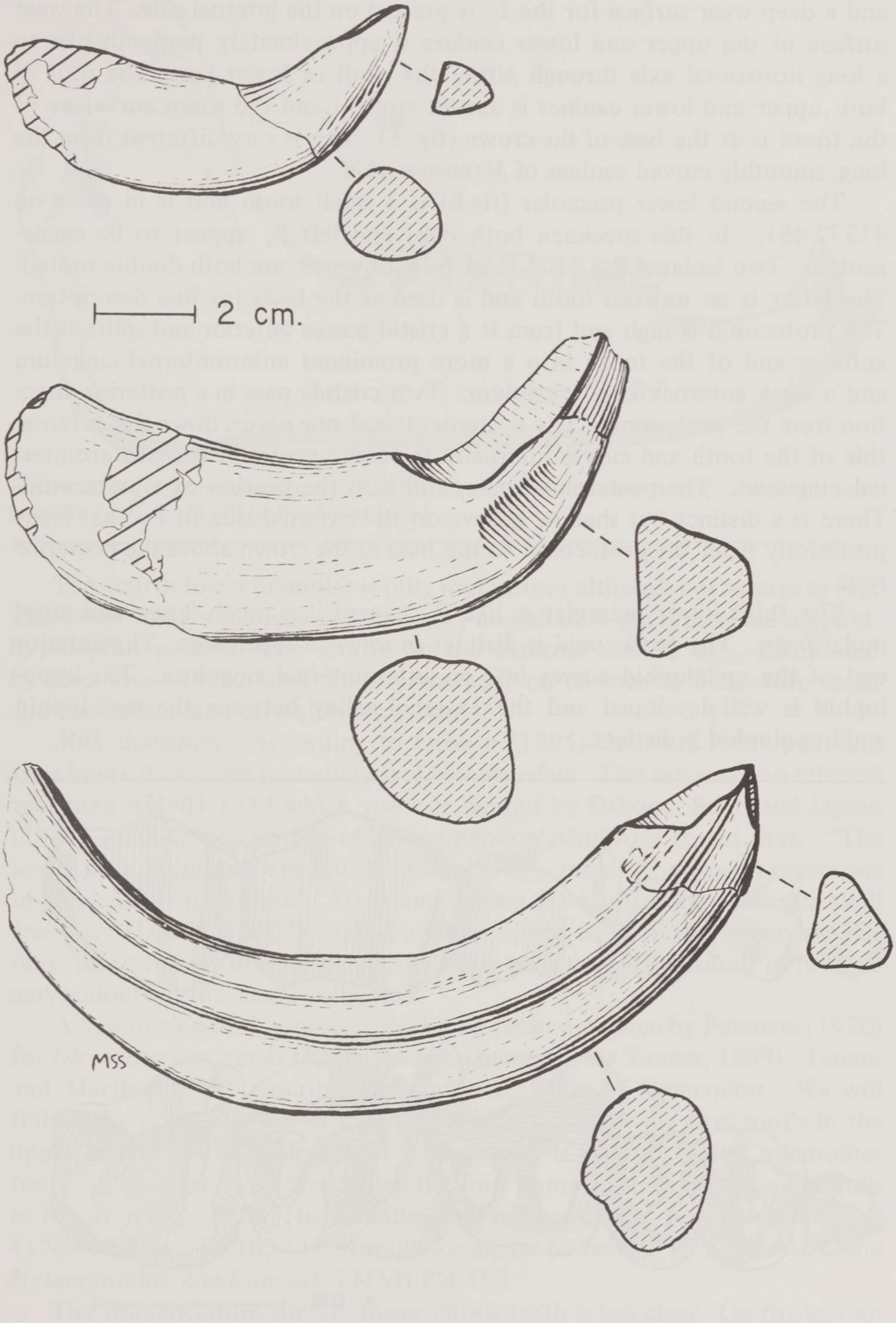

Figure 5. Top, *Amynodon advenus,* left lower canine, 41372-619, Whistler Squat l.f.; *Metamynodon mckinneyi* n. sp., left lower canine, 41723-8, Serendipity l.f.; bottom, *Metamynodon chadronensis,* right lower canine, FMNH PM 161, Porvenir l.f.

and a deep wear surface for the I^3 is present on the internal side. The wear surface of the upper and lower canines is approximately perpendicular to a long horizontal axis through either the skull or lower jaw. The root of both upper and lower canines is almost straight and the sharp curvature of the tooth is at the base of the crown (fig. 5). This is very different from the long, smoothly curved canines of *Metamynodon.*

The second lower premolar (fig.8) is a small tooth and is in place on 41372-451. In this specimen both right and left P_2 appear to be single-rooted. Two isolated P_2s, -171, and -624, however, are both double-rooted. The latter is an unworn tooth and is used as the basis for this description. The protoconid is high and from it a cristid passes anterior and splits at the anterior end of the tooth into a more prominent anterointernal cingulum and a weak anteroexternal cingulum. Two cristids pass in a posterior direction from the protoconid. The posteroexternal one passes down the external side of the tooth and curves internally to form a posterior and posterointernal cingulum. The posterointernal cristid is in the postion of a metaconid. There is a distinct but shallow groove on the external side of P_2 that leads posteriorly from the protoconid to the base of the crown above the posterior root.

The third lower premolar is like P_2 except it is much larger and more molariform. The protoconid is distinct in unworn specimens. The anterior end of the metalophid curves into an anterointernal cingulum. The hypolophid is well developed and the external valley between the metalophid and hypolophid is distinct.

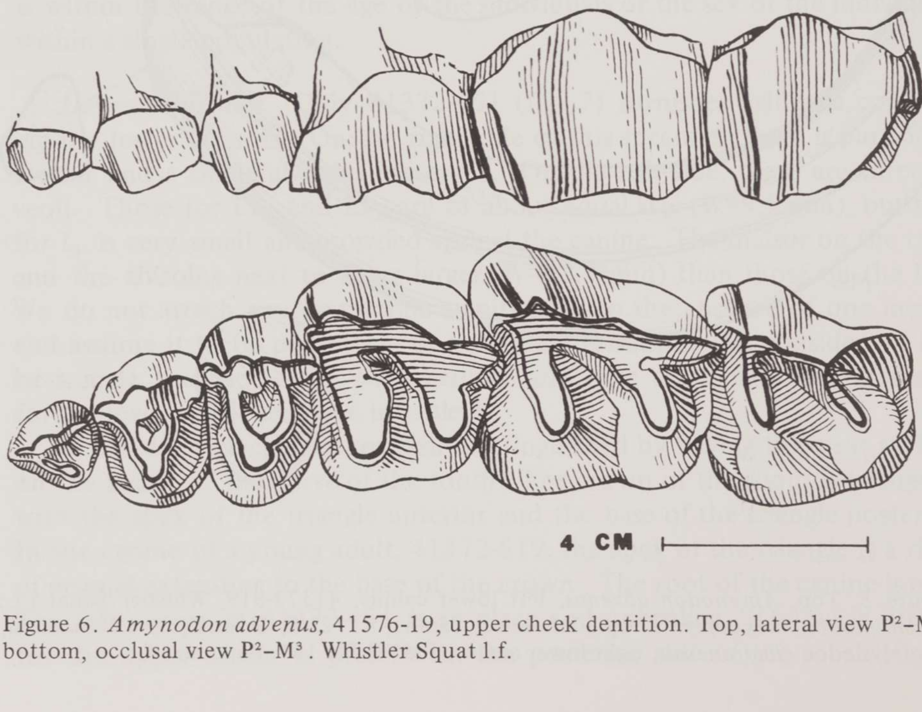

Figure 6. *Amynodon advenus,* 41576-19, upper cheek dentition. Top, lateral view P^2–M^3; bottom, occlusal view P^2–M^3. Whistler Squat l.f.

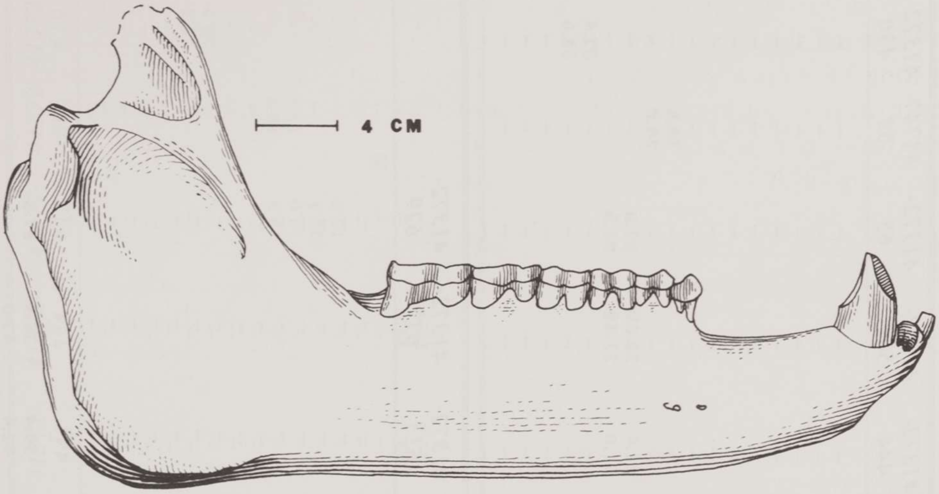

Figure 7. *Amynodon advenus,* 41372-451. Lateral view of lower jaw. I_1, alveolus I_2, and possibly I_3, $\overline{C}$, P_2–M_3. Whistler Squat l.f.

The fourth lower premolar is fully molariform although not as large as M_1. The lower molars increase in size to M_3 and all have the typical metalophid-hypolophid pattern. The groove on the external side of M_{2-3}, mentioned by Gromova (1954, table 1), is prominent on unworn or little-worn teeth and becomes less so on well-worn teeth.

Milk dentition.–According to Osborn (1895) there are four upper and four lower deciduous premolars in *A. intermedius.* This is based on a referred specimen AMNH 1933 which was not figured by Osborn. Scott and Jepsen (1941) in their description of *Metamynodon planifrons* stated that: "The lower milk premolars are four in number, dP_1 and dP_2 having no successors in the second dentition." Scott and Jepsen (1941) figured a juvenile skull and jaws (USNM 10602) that show four cheek teeth in the upper jaw but only three in the lower jaw. This is the same condition found in juvenile amynodonts in the Texas collection.

A description of the succession of milk teeth was given by Peterson (1920) for *Diceratherium cooki* (=*Menoceras arikarense, vide* Tanner, 1969). Tanner and Martin (1972) described the milk dentition of *Hyracodon.* We will follow the nomenclature of Peterson (1920) in which the first tooth in the upper cheek row is designated P^1 because it is not succeeded by another tooth. Therefore, we have labeled the four upper teeth in the juvenile skulls as P^1, dP^2, dP^3, dP^4. The juvenile skulls referred to are *Amynodon advenus,* 41747-92 (figs. 9, 10, 11), *Amynodontopsis bodei* 41715-2 (fig. 16), and *Metamynodon chadronensis* FMNH PM 159.

The nomenclature for the lower cheek teeth is less clear. On the second cheek tooth in both 41372-71 (fig. 12) and 41747-90 there are three cross-lophs. The anterior loph is small but distinct. This tooth also has the most wear. Peterson (1920) identified a similar tooth as dP_3 in *Menoceras cooki.*

Table 1. Measurements of upper and lower teeth of *Amynodon advenus*, Whistler Squat l.f.

UPPER TEETH

	41372-45	*41576-19R*	*41372-416*	*41372-72*	*41576-30*	*41372-75*	*41747-85*	*41372-421*	*41372-444*	*41372-583*	*41372-65*	*41747-53*	*41372-430*
C–M^3	195	232.0	–	–	–	–	–	–	–	–	–	–	–
P^2–M^3	152	173.5	170 est.	–	–	–	–	–	–	–	–	–	–
P^2–P^4	52.3	61.0	56 est.	–	–	–	–	–	–	–	–	–	–
M^1–M^3	104.9	116.0	115.0	115.6	– –	–	–	–	–	–	–	–	–
C L	17.8	–	22.0	–	–	28.2	–	–	–	–	–	–	–
W	16.2	–	21.5	–	–	21.9	–	–	–	–	–	–	–
P^2 L	16.5	12.8	–	–	–	–	15.4	17.0	–	–	–	–	–
W	18.0	16.9	–	–	–	–	18.1	18.6	–	–	–	–	–
P^3 L	17.1	22.0	19.0	–	–	–	–	–	–	–	–	18.8	–
W	26.2	29.1	25.0	–	–	–	–	–	–	–	–	24.0	–
P^4 L	21.0	24.5	20.8	18.9	21.5	–	–	–	21.4	22.0@	22.0	–	–
W	32.5	37.8	33.1	36.5	33.0	–	–	–	31.0	31.8@	31.0	–	–
M^1 L	31.2	41.8	26.9	34.5	–	–	–	–	–	–	–	–	32.4
W	38.4	44.7	37.4	41.3	–	–	–	–	–	–	–	–	38.6
M^2 L	37.8	45.8	38.4	39.0	38.1	–	–	–	–	–	–	–	–
W	43.2	51.0	45.0	47.1	45.6	–	–	–	–	–	–	–	–
M^3 L	34.6	39.5	39.0	41.9	34.4	–	–	–	–	–	–	–	–
W	37.2	45.5	–	46.2	42.4	–	–	–	–	–	–	–	–

	41756-29	*41372-49*	*41372-74*	*41372-570*	*41372-605*	*41372-428*	*41372-413*	*41372-50*	*41372-613*	*41372-617*	*41372-629*
C–M^3	–	–	–	–	–	–	–	–	–	–	–
P^2–M^3	–	–	–	–	–	–	–	–	–	–	–
P^2–P^4	–	–	–	–	–	–	–	–	–	–	–
M^1–M^3	–	–	–	–	–	–	–	–	–	–	–
C L	–	–	–	–	–	–	–	–	–	–	–
W	–	–	–	–	–	–	–	–	–	–	–
P^2 L	–	–	–	–	–	–	–	–	–	–	–
W	–	–	–	–	–	–	–	–	–	–	–
P^3 L	–	–	–	–	–	–	–	–	–	–	–
W	–	–	–	–	–	–	–	–	–	–	–
P^4 L	–	–	–	–	–	–	–	–	–	–	–
W	–	–	–	–	–	–	–	–	–	–	–
M^1 L	40.5	–	–	–	–	–	–	–	–	–	–
W	38.5 @	–	–	–	–	–	–	–	–	–	–
M^2 L	–	45.5	–	44.5	39.3	–	–	–	–	–	–
W	–	47.2	48.1	–	44.2	–	–	–	–	–	–
M^3 L	–	–	–	–	–	32.3	37.7	39.2	39.4	35.5	37.2
W	–	–	–	–	–	40.4	45.3	43.3	42.4	42.0	–

Table 1, cont.

LOWER TEETH

	41372-451	*41372-99*	*41747-75*	*41747-76*	*41372-66*	*41372-598*	*41372-426*	*41372-442*	*41372-441*	*41372-594*	*41372-612*	*41372-600*	*41372-619*
$C–M_3$	247.0	–	–	–	–	–	–	–	–	–	–	–	–
$P_2–M_3$	151.0	–	–	–	–	–	–	–	–	–	–	–	–
$P_2–P_4$	51.4	54 est.	56 est.	–	–	–	–	–	–	–	–	–	–
$M_1–M_3$	100.8	105.5	109.3	–	–	–	–	–	–	–	–	–	–
C L	22.8	–	–	–	–	–	–	–	–	–	–	–	21.5
W	20.3	–	–	–	–	–	–	–	–	–	–	–	20.7
P_2 L	13.0	–	–	–	–	–	–	–	–	–	–	–	–
W	9.2	–	–	–	–	–	–	–	–	–	–	–	–
P_3 L	17.7	18.1 @	19.0	–	17.8	–	–	–	–	–	19.3	18.7	–
W	12.8	–	12.5	–	13.5	–	–	–	–	–	13.0	12.1	–
P_4 L	20.2	23.0	24.6	–	–	22.6	24.4	–	–	–	22.1	–	–
W	15.5	16.4	18.5	–	–	16.1	14.7	–	–	–	15.3	–	–
M_1 L	23.6	–	29.0	–	–	–	–	–	–	–	–	–	–
W	18.7	–	–	–	–	–	–	–	–	–	–	–	–
M_2 L	33.9	36.0 @	38.2	–	–	–	–	38.7	42.3	39.6	–	–	–
W	22.5	23.6	24.4 @	–	–	–	–	19.6	21.4	22.9	–	–	–
M_3 L	43.6	40.1	42.5	43.5	–	–	–	–	–	–	–	–	–
W	22.5	20.5	23.3	20.2	–	–	–	–	–	–	–	–	–

	41372-171	*41372-624*	*41372-207*	*41747-50*	*41576-16*	*41576-24*	*41372-558*	*42061-4*
$C–M_3$	–	–	–	–	–	–	–	–
$P_2–M_3$	–	–	–	–	–	–	–	–
$P_2–P_4$	–	–	–	–	–	–	–	–
$M_1–M_3$	–	–	–	–	–	–	–	–
C L	–	–	–	–	–	–	–	–
W	–	–	–	–	–	–	–	–
P_2 L	11.1	13.5	–	–	–	–	–	–
W	9.1	9.0	–	–	–	–	–	–
P_3 L	–	–	18.9	–	–	–	–	–
W	–	–	12.9	–	–	–	–	–
P_4 L	–	–	–	23.8	–	–	–	–
W	–	–	–	16.0	–	–	–	–
M_1 L	–	–	–	–	–	–	–	–
W	–	–	–	–	–	–	–	–
M_2 L	–	–	–	–	39.1	37.5	–	–
W	–	–	–	–	21.2	20.5	–	–
M_3 L	–	–	–	–	–	–	48.0	42.0
W	–	–	–	–	–	–	23.7	21.8

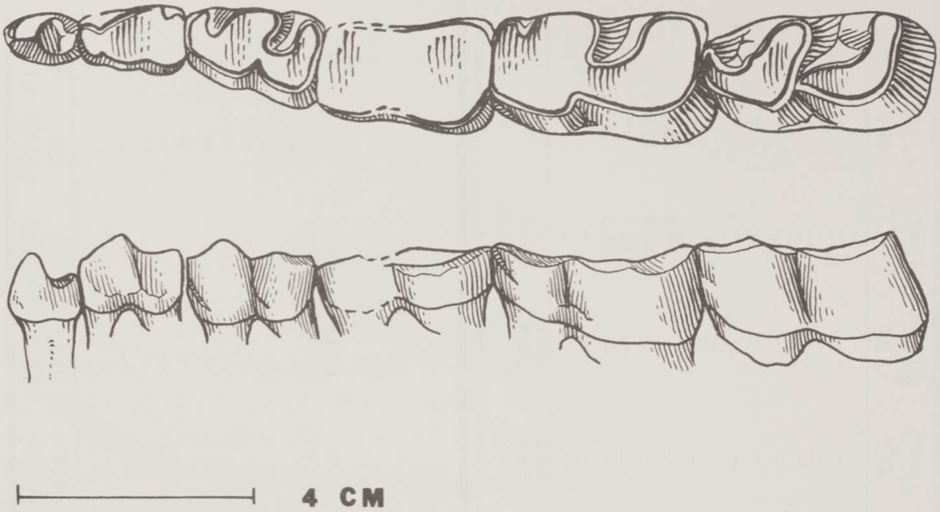

Figure 8. *Amynodon advenus,* 41372-99. Top, occlusal view P_2–M_3 ; bottom, lateral view P_2–M_3 . In both views P_2 is from 41372-451. Whistler Squat l.f.

If our identification is correct, there is no dP_1 in *Amynodon advenus* and the three cheek teeth in the juvenile lower jaws are dP_2, dP_3, dP_4. Measurements for the juvenile upper and lower dentitions are given in table 2.

Tanner and Martin (1972) described the milk dentition in *Hyracodon.* They showed conclusively that dP_1 is present in that genus and so labeled it, although it is not replaced. Peterson (1920) preferred to identify an unreplaced tooth as a member of the permanent dentition. Plate 1, figure d, in Tanner and Martin (1972) shows both dP_2 and dP_3 with three crosslophs, and dP_3 is the largest tooth in the row. We follow the traditional assumption that the teeth are lost from the anterior end of the premolar row and that in the North American amynodonts dP^1_1 and P_1 are already lost by Uintan time. Unfortunately, the Texas collection does not include young individuals with permanent teeth replacing milk teeth. The lower jaws that do contain the milk dentition belong to very young animals; and, although the jaws were dissected, no trace of the permanent tooth caps could be found.

A juvenile skull, 41747-92 has alveoli for three incisors and a canine. A P^1 is present on the right side (figs. 9, 10). It is a trenchant tooth with cristae leading in anterior and posterior directions from the protocone. There is a single internal cross-ridge at the posterior third of the tooth and a strong internal cingulum. There is no external cingulum. The molariform pattern is well-developed on dP^2, dP^3 and dP^4. The parastyle is strongly developed on all three teeth. The protoloph on dP^2 curves more sharply in a posterior direction than the protolophs on dP^3 and dP^4. A group of folds in the enamel in the position of the crochet are present on dP^4. The wear surfaces are about equal on dP^2 and dP^3; whereas P^1 and dP^4 are unworn, although they are both fully erupted.

Table 2. Measurements of upper and lower deciduous dentitions of *Amynodon advenus*, Whistler Squat l.f.; *Amynodontopsis bodei*, Skyline l.f.; *Metamynodon chadronensis*, Porvenir l.f.

UPPER TEETH

	Amynodon advenus Whistler Squat l.f.		*Amynodontopsis bodei*		*Metamynodon chadronensis*
			Skyline l.f.	Slim Buttes, S. Dak.	Porvenir l.f.
	41747-92	*41372-492*	*41715-2*	*SDSM 10003*	*FMNH PM 159*
P^1-dP^4	75.3	–	82.5	–	94.5
$d\bar{C}$ L	–	13.7	–	6.1	–
W	–	13.2	–	6.0	–
P^1 L	12.7	–	11.2	9.7	15.1
W	8.7	–	8.5	12.8	–
dP^2 L	16.8	–	18.6	18.7	19.3@
W	16.5	–	20.8	20.5	–
dP^3 L	24.0	–	21.5	29.4	–
W	20.9	–	28.9	29.9	–
dP^4 L	30.9	–	36.9	38.0	43.7
W	26.9	–	33.7	37.0	40.0
M^1 L	–	–	38.2@	–	54.2
W	–	–	40.0@	–	50.2
M^2 L	–	–	40.5@	–	67.4
W	–	–	–	–	48.5 @

LOWER TEETH

Amynodon advenus

Whistler Squat l.f.

	41372-71	*41372-64*	*41747-90*	*41372-159*	*41372-492*	*41372-544*
dP_2-dP_4	60.0	–	–	–	–	–
$d\bar{C}$ L	–	–	–	–	12.9	11.4
W	–	–	–	–	13.3	14.5
dP_2 L	14.4	–	14.2	14.9	–	–
W	8.4	–	7.6	8.0	–	–
dP_3 L	21.5	22.2	23.7	–	–	–
W	12.3	11.5	12.5	–	–	–
dP_4 L	25.3@	–	27.1	–	–	–
W	14.2@	–	15.7	–	–	–

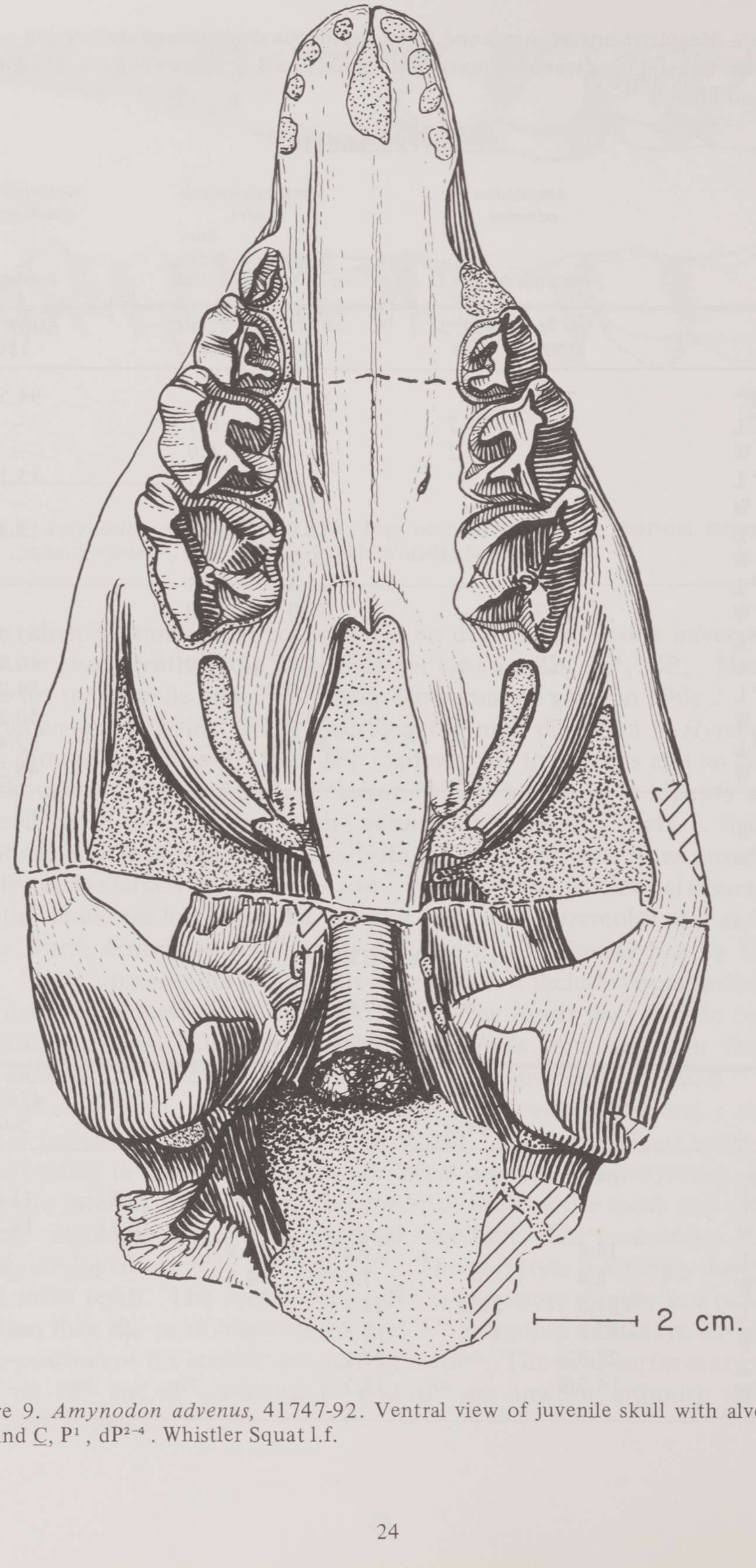

Figure 9. *Amynodon advenus,* 41747-92. Ventral view of juvenile skull with alveoli for I^{1-3} and C̲, P^1, dP^{2-4}. Whistler Squat l.f.

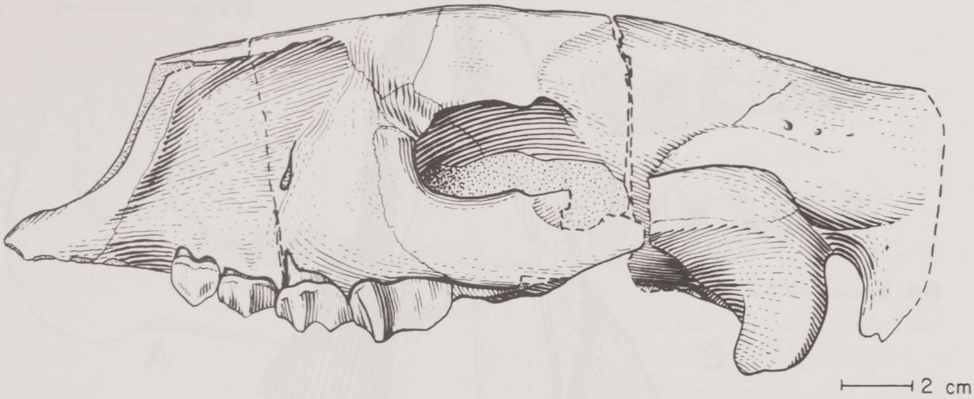

Figure 10. *Amynodon advenus,* 41747-92. Lateral view of juvenile skull with alveoli for I^{1-3} and $\underline{C}$, P^1, dP^{2-4}. Vertical separations are natural beaks and have been left that way. Whistler Squat l.f.

There are two lower jaws of very young individuals in the Texas collection, 41372-71 (figs. 12A, B) and 41747-90. The former has the symphysis complete, but the three incisors and the canine are represented by alveoli. Three deciduous premolars are preserved on the right ramus and two on the left. On 41747-90 only the left ramus is preserved and it carries the same three deciduous premolars. The first cheek tooth, dP_2, is a rather long, narrow, trenchant tooth (14.2 x 7.6 mm). The ridge leading forward from the protoconid is straight and passes over a swelling in the position of a paraconid. There is no anterointernal cingulum on the RdP_2 of 41372-71 and only faint anteroexternal and anterointernal cingula on the dP_3. The metastylid is prominent, curving in a posterior direction and continuing to the base of the tooth. The hypolophid is well-developed.

The second lower cheek premolar, dP_3, is a much larger tooth with three distinct crosslophs. A cristid leads forward from the protoconid in a straight line to the anterior end of the tooth and splits into anteroexternal and anterointernal cingula. There is a prominent paraconid, and a wear surface on it connects with the paracristid at right angles to form the anterior crosscrest. The metalophid is straight and slants posterointernally from the protoconid at an angle of about 45 degress from the long axis of the tooth. The hypolophid has a broad curve to the entoconid. Of the three teeth in the jaw, this tooth is the most worn.

The third deciduous lower cheek tooth, dP_4, is more like an adult molar. A paracristid curves anterointernally from the protoconid and turns posteriorly to join an anterointernal cingulum. The metalophid is directed straight posterointernally as in dP_2. Likewise the hypolophid is similar to that on dP_3 but larger. In both juvenile lower jaws M_1 has not erupted.

Skull. –There are two adult skulls and one juvenile skull from the Whistler Squat local fauna. Although each comes from a different locality, they all occurred at about the same stratigraphic interval. The skull from the Whistler

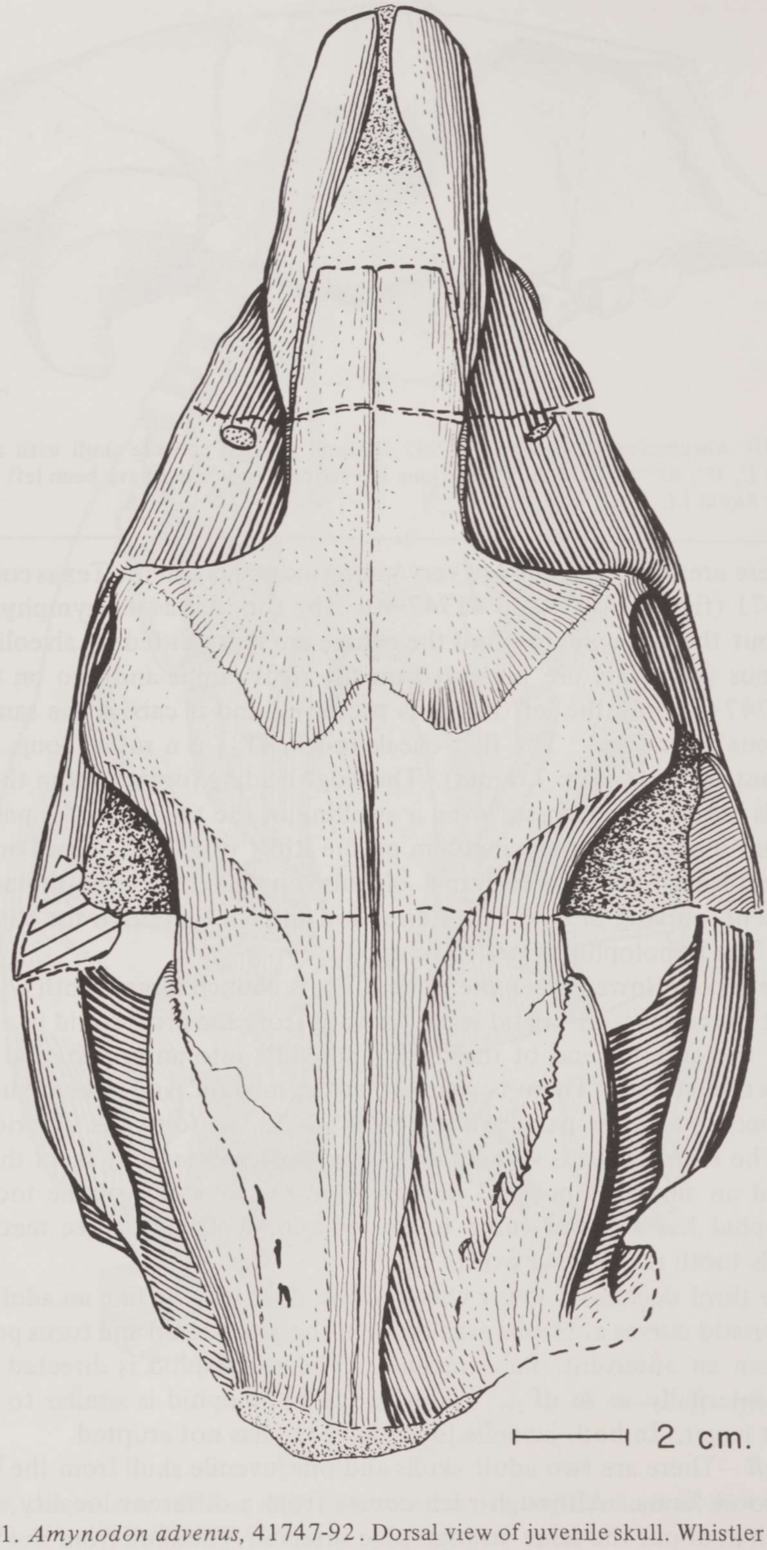

Figure 11. *Amynodon advenus,* 41747-92. Dorsal view of juvenile skull. Whistler Squat l.f.

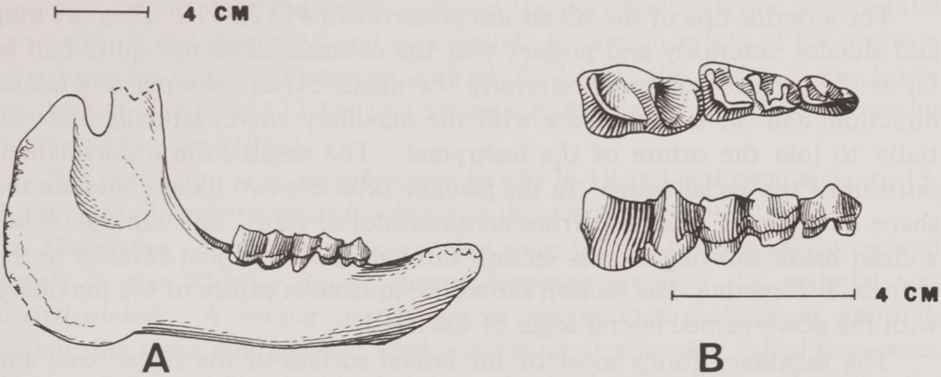

Figure 12. *Amynodon advenus,* 41372-71. A. Lateral view of lower jaw with dP_{2-4} B. Occlusal and lateral view, dP.

Squat quarry 41372-416, the largest, is rather badly distorted but seems to have been a long, narrow skull with large canines and a long post-canine diastema. Another skull, 41576-19 (figs. 2, 3), from near the Wax Camp locality is almost free from distortion but the anterior part of the nasals is missing. Compared with 41372-416, 41576-19 was a shorter skull with smaller canines and a shorter diastema. The latter belonged to a younger individual because the M^3 shows very little wear. The snouts on both skulls are distorted so it is difficult to be sure of the depth of the facial fossae. However, they seem to lack the depth of those of *Amynodontopsis* as illustrated by Stock (1933) and resemble more closely YPM 11453, the type of *Amynodon erectus,* shown in Troxell (1921, table 3). The juvenile skull, 41747-92,(figs. 9, 10, 11), is uncrushed and the snout is well-preserved except for the anterior tip of the nasals. The dorsal part of the snout is sharply constricted just anterior to the orbits (fig. 11) and this constriction passes anteroventrally to the diastema between $\underline{C}$ and P^1. In the juvenile skull the total width from one anterodorsal corner of the orbit to the other is 93 mm. The posterodorsally constricted snout measures only 33 mm just slightly anterior to that line (fig. 11). In none of the three skulls do the facial fossae appear to extend posteriorly to the orbital rim as in the type of *Amynodontopsis.* The posterior edge of the facial fossae is about even with the anterior edge of the antorbital rim.

The premaxillary bones are separate at the midline in both the adult and juvenile skulls. They do not form a median ridge as in *Amynodontopsis,* in which the premaxillaries are united in the midline. The premaxillaries extend forward beyond the anterior tips of the nasals but no more so than on a horse and less than on a cow. Troxell (1921) stated that the premaxillaries are barely visible in a lateral view; however, the anterior end of the snout appears to be incomplete in YPM 11453, the specimen he was describing. Osborn (1890) described the premaxillaries of *A. intermedius* as " . . . rather narrow above and spread inferiorly, rounding and arching forward into a broad incisive border." This is the same condition found in 41576-19, but the premaxillaries are not united on the midline.

The anterior tips of the nasals are preserved in 41372-416. They are long and slender anteriorly and project over the external nares not quite half as far as the incisive border. Posteriorly the nasals expand sharply in a lateral direction, and the lateral suture with the maxillary curves laterally and ventrally to join the suture of the lachrymal. The nasals form a dorsolateral portion of the facial fossae. In the juvenile skull the two nasal bones are the shape of a capital T as seen from an anterodorsal view. This same skull has a clean break showing a cross section through the snout just anterior to the antorbital foramina. The section shows the squamous suture of the maxillary with the down-turned lateral edges of the nasal.

The maxillary forms most of the lateral surface of the facial fossa and shares the posterodorsal surface with the nasal and the lachrymal. The latter bone is very rugose and forms the anterodorsal rim of the orbit. It has a low boss just over the lachrymal foramen. The medial extent of the lachrymal on the external surface of the skull is not as great as within the orbit. The frontals form the dorsal rim of the orbits, and the orbits are broadly open posteriorly. The nasal-frontal suture at the midline is over the approximate center of the orbit on the juvenile skull. The frontal-parietal suture on the midline is above the postglenoid process. This suture is very faint on the juvenile skull and not distinguishable on the adult. Nasals and frontals are about equally long, approximately 100 mm, whereas the parietal is only about 35 mm long in the juvenile skull. This contrasts with Scott and Osborn's (1883) description of "Orthocynodon" in which they said that " . . . the frontals are short and the parietals are elongated."

The malar forms the anteroventral border of the orbit and sweeps back to the zygomatic arch. On the juvenile skull there is a very small rugosity that forms the posteroventral corner of the orbit. In the adult skulls the malar projects laterally and ventrally just above the middle of M^2 and beneath the center of the orbit. The zygomatic arch is broad dorsoventrally in the adult skulls; on 41576-19 it is about 40 mm at its narrowest point and about 55 mm at the broadest.

The sagittal crest is complete in the adult skulls and is a straight, prominent ridge. It is not preserved in the juvenile skull and was probably cartilaginous. Three nutrient foramina are present in each of the parietals in the juvenile skull whereas there are eight on the left side of 41576-19.

The basicranium is well preserved in 41576-19 (fig. 13) and in 41372-410. The auditory meatus is open ventrally, as noted by Scott and Osborn (1833), Osborn (1895) and Troxell (1921). The basicranium and ear region superficially resemble that of the South American tapir. The postglenoid process on both specimens just previously mentioned is medial and its articular surface is oriented posterolaterally as in the tapir but the process in *Amynodon* is much thicker. The post-tympanic process of the squamosal is complete in 41576-19 and is approximately the same height as the postglenoid process. The paroccipital process of the exoccipital extends beyond the post-tympanic process as in the tapir. A very prominent foramen, probably the stylomastoid foramen, opens along the suture between the post-tympanic and paroccipital processes of the squamosal and exoccipital. We are uncertain of the position of sutures for a mastoid bone on skull 41576-19, but the sutures show clearly on the left side of 41372-410 and are essentially the same as those shown by Scott and Osborn (1883).

The ear region is nicely preserved in 41576-19 and is shown in figure 13. A very prominent *processus hyoideus* of the petrosal is present.

Discussion.—Remains of *Amynodon* were the most commonly preserved fossils in the Whistler Squat quarry; however most of the material was disarticulated. A similar occurrence of amynodont material at approximately the same stratigraphic level was found at a locality called Boneanza. This material combined with that from two other localities—all within the lower 50 feet (15.2 m) of the Pruett Fm. and all within a radius of about 4 mi (6.4 km) from Whistler Squat—very likely represents a sample from a single population. The specimens from localities other than the Whistler Squat quarry itself fell within the observed range of specimens from the quarry. The total number of complete teeth, skulls, jaws, and limb bones is small; however there are presently no published data for a comparably large sample of *Amynodon.* The most striking aspect of the sample was the high variability of adult individuals.

A variety of characters has been used in the past to erect new taxa; one of these has been the number of premolars. It can now be shown that in North American amynodonts there are three permanent upper and lower premolars in adult individuals. The number of lower premolars is reduced to two in *Amynodontopsis* and *Metamynodon.* Other characters that have been used to distinguish taxa are the attitude of the canines, whether erect, oblique, or semi-procumbent; stronger or weaker cingula, deeper or shallower facial fossae; presence and number of cristae; and size. In addition, a

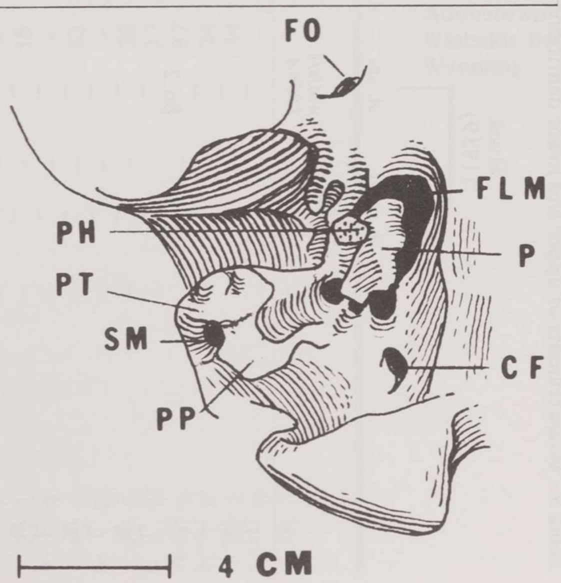

Figure 13. *Amynodon advenus,* 41576-19. Ventral view of basicranium. CF = condylar foramen; FLM = foramen lacerum medius; FO = foramen ovalis; P = petrosal; PH = processus hyoideus of petrosal; PP = paroccipital process; PT = post-tympanic process of squamosal; SM = stylomastoid foramen. Whistler Squat l.f.

Table 3. Measurements of upper and lower dentitions of various amynodonts from deposits of Uintan Age.

	UPPER TEETH									
	Stock (1939)		Troxell (1921)							
	TYPE		TYPE	TYPE						TYPE
	A. reedi	*A. sp.*	*A. antiquus*	*A. erectus*	*A. sp.*	*A. sp.*	*A. intermedius*	*A. sp.*	*A. sp.*	*A. intermedius*
	LACM (CIT) 2529	*AMNH 1936A*	*PU 10047*	*YPM 11453*	*FMNH 12184*	*CM 9421*	*CM 9968*	*CM 11960*	*CM 9172*	*PU 10309*
$C–M^3$	–	–	–	–	–	–	–	197.8 @	–	255 est.
$P^2–M^3$	–	–	–	145	140.8	159.2	–	150.4	–	187
$P^2–P^4$	–	–	–	–	51.1	56.0	–	–	–	65.7
$M^1–M^3$	85.8	86.2	104	96	93.3	111.2	–	102.0	–	130
C L	–	–	–	–	–	–	–	–	–	–
W	–	–	–	–	–	–	–	–	–	–
P^2 L	–	–	–	–	15.5	15.4	–	–	–	19.7
W	–	–	–	–	17.7	18.1	–	–	–	20.8
P^3 L	–	–	–	–	17.7	18.4	–	–	–	23.7
W	–	–	–	–	22.3	23.2	–	25.9	–	30.5
P^4 L	12.0 @	–	22	20	21.1	22.1	–	23.5	27.9	24.5
W	24.7	–	33	32	30.7	32.2	–	31.5	38.5	38.1
M^1 L	25.1	28.2	37	28	27.7	37.1	–	37.0	42.7	46.0
W	29.9	31.5 @	37	39	36.5	46.3	–	37.1	44.8	43.8
M^2 L	29.5	29.7	45	37	33.3	42.2	39.2	41.2	53.6	52.8
W	33.7	34.1	37	42	40.9	42.3	39.4	40.2	52.5	50.6
M^3 L	27.9	32.4	28	36	37.7	36.9	35.8	33.0	43.6	40.6
W	31.1	34.2	30	38	34.5	38.8	36.2	37.4	46.6	46.7
	Santiago Fm., California	Uinta B, Utah	Adobetown Washakie Basin, Wyoming	Uintan White River, Utah	Uinta B, Utah	Adobetown Washakie Basin, Wyoming	Uinta C	Uinta C	Uinta C	Uintan White River, Utah

Table 3, cont.

LOWER TEETH

					CM 9421	CM 3102	CM 3100	CM 3122	CM 3434	
$C\text{–}M_3$	–	–	–	–	–	–	–	–	185.8	–
$P_2\text{–}M_3$	–	–	–	142	–	–	141.4	–	145.2	–
$P_2\text{–}P_4$	–	–	80	46	–	–	51.6	–	52.2	–
$M_1\text{–}M_3$	–	–	–	98	–	–	92.1	–	95.0	–
$\underline{C}$ L	–	–	15	18	17.4	–	–	–	14.0	–
W	–	–	–	–	14.7	–	–	–	13.0	–
P_2 L	–	–	19	10	–	–	15.4	–	13.6	–
W	–	–	–	–	–	–	10.1	–	9.8	–
P_3 L	–	–	23	15	18.3	18.6	17.4	–	17.8	–
W	–	–	–	–	13.3	12.9	–	–	14.8	–
P_4 L	–	–	29	22	21.9	22.5	20.8	23.1	20.2	–
W	–	–	17	16	16.6	15.5	17.2	15.5	15.6	–
M_1 L	–	–	37	29	31.1	32.2	26.5	30.6	24.5	–
W	–	–	24	19	20.4	17.8	20.5	19.2	18.9	–
M_2 L	–	–	44	34	38.4	32.9	32.8	38.2	32.2	–
W	–	–	–	23	22.3	20.5	21.7	21.7	21.6	–
M_3 L	–	–	–	38	–	–	–	–	37.0	–
W	–	–	–	20	–	–	–	–	20.0	–
			Adobetown Washakie Basin, Wyoming	Uintan White River, Utah	Uinta Basin Wagonhound, Utah	Uinta B Wagonhound, Utah	Uinta B Wagonhound, Utah	Uinta B Wagonhound, Utah	Uinta B Wagonhound, Utah	

Table 4. Measurements of skulls and lower jaws of *Amynodon advenus*.

SKULL

	Scott and Osborn (1883) TYPE *A. antiquus*	Troxell (1921) TYPE *A. erectus*								
	PU 10047	*YPM 11453*	*41576-19*	*41372-416*	*41372-410*	*41372-603*	*41372-421*	*41372-75*	*41372-45*	*41576-30*
Total skull L	440	350	510	–	–	–	–	–	–	–
Premaxillary–occipital condyle L	–	–	481	–	–	–	–	–	–	–
Premaxillary–occiput L	–	–	511	–	–	–	–	–	–	–
Premaxillary–M^3 L	–	–	277	295 @	–	–	–	–	–	–
Premaxillary–post-narial notch	–	–	230	284 @	–	–	–	–	–	–
Across $\underline{C}$ W	–	–	92	–	74 est.	–	–	–	–	–
Across zygoma W	–	–	281	–	–	–	–	–	–	–
Across condyles W	–	–	109	–	111	131	–	–	–	–
Across palate at M^3 W	–	–	67	–	–	–	–	–	–	–
Post $\underline{C}$ diastema L	–	–	40 @	50.3	–	–	62.5	45.1	30.3	14.1@
P^2–M^3	–	145	173.5	170 est.	–	–	–	–	152	–
P^3–M^3	–	–	158	151 @	–	–	–	–	139	–
P^2–P^4	–	–	59	–	–	–	–	–	52.3	–
M^1–M^3	104	96	116	115	–	–	–	–	104.9	–

LOWER JAW

	PU 10047	*YPM 11453*	*41372-451*	*41372-99*	*41747-75*	*41747-76*	*41372-46*	*42061-4*
I-angle	–	356	440 @	–	–	–	–	–
Ramus below M_3	–	–	92	84	81	72	79	–
$\overline{C}$–P_2 diastema L	40.0	34	69	–	–	–	–	–
Height ramus	–	–	184	192 @	199	196	178	175 est.
W across $\overline{C}$	–	–	67	–	–	–	–	–

deep facial fossa and dolichocephaly has been used to separate the genus *Amynodontopsis* from *Amynodon*. Within the sample from the Whistler Squat quarry are individuals with erect upper canines, erect lower canines, semi-procumbent upper canines, strong and weak cingula. One M^2 has a prominent crista, the rest do not. The range in size, as shown in tables 1, 3, 4, and 5, overlaps *A. advenus, A. antiquus, A. intermedius* and *A. erectus.* Of the two skulls preserved in the Texas collection, both from approximately the same stratigraphic level, one is dolichocephalic with deep facial fossae and the other more brachycephalic with shallow facial fossae. One skull has a large canine; and another maxillary, a small one.

If the samples of amynodonts from the Whistler Squat quarry and nearby localities at approximately the same stratigraphic level constitute a single population, that population shows a high degree of individual variation (tables 4, 5).

It was not the intention of the authors to revise the late Eocene amynodonts of North America, but when the opportunity to measure the amynodont material at the Carnegie Museum was presented, we were able to compare our Texas sample (table 2) with the one mostly from the Uinta Basin (table 3). A comparison of the statistics is given in table 5. Despite the northern sample's being drawn from different sedimentary basins, Washakie and Uinta, and from different stratigraphic levels, early and late Uintan, it is more homogenous than the sample from Texas. The northern sample also contains the types of three different species, *A. antiquus, A. erectus* and *A. intermedius.*

In order to test our surmise that the amynodonts from the Whistler Squat l.f. belong to a single population, we compared what elements we could with those from large samples found elsewhere. A large sample of *Trigonias* skulls from a single quarry in Colorado was described by Gregory and Cook (1928). They gave measurements (their table 1) and within this sample identified seven different taxa, not all at the species level, however. Such an interpretation is characteristic of the paleontology of that time. Another large sample of rhinoceros material was described by Hooijer (1972) and identified as belonging to the single species *Ceratotherium praecox* from the Pliocene of Langebaanweg, South Africa. He also gave measurements for the sample and stated, "The data provided in the present paper show the amount of individual variation within a single species of Pliocene rhinoceros. It is not saying too much now that *C. praecox* odontologically and osteologically is better known than its extant descendant . . . ." From the data given by Gregory and Cook (1928) and Hooijer (1972) we calculated the standard deviation and the percentage of variation (tables 8, 9).

A combined sample of astragali from the Whistler Squat quarry and from the Boneanza locality (table 6) was large enough to compare with the sample from Langebaanweg (table 7). In addition, we calculated the statistical data for M^2 and M^3 from the Whistler Squat l.f. and compared it with similar data from the South African sample (table 8) and the Colorado sample of *Trigonias*

Table 5. Statistical data for upper and lower teeth of *Amynodon advenus*, Whistler Squat l.f. and various localities in Utah and Wyoming.

UPPER TEETH

	Whistler Squat l.f.					Various localities in Utah and Wyoming (from table 3)				
	N	*OR*	*M*	σ	*V*	*N*	*OR*	*M*	σ	*V*
C–M_3	2	195 -232	213.5	–	–	–	–	–	–	–
P_2–M_3	3	152 -173.5	165.1	–	–	–	–	–	–	–
P_2–P_4	3	52.3–61.0	56.4	–	–	–	–	–	–	–
M_1–M_3	4	104.9–116	112.8	–	–	–	–	–	–	–
$\underline{C}$ L	3	17.8–28.2	22.6	–	–	–	–	–	–	–
W	3	16.2–21.9	19.8	–	–	–	–	–	–	–
P_2 L	3	12.8–17.0	15.4	–	–	–	–	–	–	–
W	3	16.9–18.6	17.8	–	–	–	–	–	–	–
P_3 L	7	17.1–22.0	20.5	2.00	9.8	–	–	–	–	–
W	7	24.0–31.8	28.3	3.19	11.3	–	–	–	–	–
P_4 L	5	18.9–24.5	21.3	–	–	7	20 -27.9	23.0	5.9	2.4
W	5	31.2–37.8	24.5	–	–	7	30.9–38.5	33.7	8.7	2.9
M_1 L	7	26.9–41.8	35.3	5.58	15.7	7	28 -46.0	36.5	39.9	6.3
W	6	37.4–44.7	39.8	–	–	7	36.5–46.3	40.6	15.0	3.9
M_2 L	10	41.1–53.0	45.1	4.15	15.8	8	33.3–53.6	43.0	45.1	6.7
W	10	42.5–51.9	45.0	3.02	6.7	8	37 -52.5	43.1	26.3	5.1
M_3 L	10	32.8–44.0	37.7	3.34	8.9	8	28 -43.6	36.5	19.3	4.4
W	10	37.8–48.2	42.6	3.02	7.1	8	30 -46.7	38.5	28.5	5.3

Table 5, cont.

LOWER TEETH

	N	OR	M	σ	V	N	OR	M	σ	V
C–M^3	1	247.0	–	–	–	–	–	–	–	–
P^2–M^3	1	151.0	–	–	–	–	–	–	–	–
P^2–P^4	1	51.4	–	–	–	–	–	–	–	–
M^1–M^3	3	100.8–109.3	105.2	–	–	–	–	–	–	–
$\underline{C}$ L	2	21.5–22.8	22.1	–	–	–	–	–	–	–
W	2	20.3–20.7	20.5	–	–	–	–	–	–	–
P^2 L	3	11.1–13.5	12.5	–	–	–	–	–	–	–
W	3	9.0–9.2	9.1	–	–	–	–	–	–	–
P^3 L	7	17.7–19.3	18.5	0.629	3.4	6	15 –23	18.4	5.7	2.4
W	6	12.1–13.5	12.8	0.473	3.7	3	12.9–14.8	13.7	0.7	0.8
P^4 L	7	20.2–24.6	22.9	1.52	6.6	7	20.2–29	22.8	7.3	2.7
W	7	15.3–18.5	16.0	1.21	7.6	7	15.5–17.2	16.2	0.5	0.7
M^1 L	2	23.6–29.0	26.3	–	–	7	24.5–37	30.1	14.1	3.8
W	1	18.7	–	–	–	7	17.8–24	20.0	3.4	1.9
M^2 L	8	33.9–42.3	38.1	2.49	6.5	7	32.2–44	36.1	16.1	4.0
W	8	19.6–24.4	22.0	1.62	7.4	6	20.5–23	21.8	0.6	0.8
M^3 L	6	40.1–48.0	43.2	2.63	6.1	–	–	–	–	–
W	6	20.2–23.7	21.6	1.43	6.6	–	–	–	–	–

Table 6. Measurements and statistical data for astragalus of *Amynodon advenus*, Whistler Squat l.f.

MEASUREMENTS

	41372-14	*41372-93*	*41372-330*	*41372-334*	*41372-335*	*41372-358*	*41372-414*	*41372-461*	*41372-497*	*41372-535*
1. Lateral height	58.8	–	56.5	55.8	54.6	–	55.1	54.6	61.0	–
2. Medial height	65.0	61.5	53.1	57.8	60.7	63.4	61.5	60.9	61.9	61.9
3. Total width	–	80.5	59.5	78.4	72.6	77.5	74.4	74.8	80.2	67.4
4. Ratio meas. 2/3	–	0.76	0.89	0.73	0.83	0.81	0.82	0.81	0.77	0.91
5. Trochlea width	–	61.8	44.7 @	57.7	54.7	57.4	57.4	56.0	59.1	53.8
6. Width distal facets	–	57.5	44.1 @	53.0	54.7	55.0	54.3	56.1	59.1	54.3

	41372-556	*41372-567*	*41372-571*	*41747-1*	*41747-4*	*41747-73*	*41747-74*	*41747-31*	*41747-82*
1. Lateral height	55.7	50.3	49.6	52.3	51.5	58.5	–	–	55.0
2. Medial height	59.8	56.1	57.0	–	57.7	62.6	–	66.8	62.8
3. Total width	74.4	72.8	58.3	72.3	74.9	78.0	–	80.6'	75.7
4. Ratio meas. 2/3	0.8	0.77	0.97	–	0.77	0.80	–	0.82	0.82
5. Trochlea width	53.7	54.1	–	53.0	56.5	59.0	–	60.0	55.6
6. Width distal facets	54.0	51.8	–	53.0	53.0	57.6	53.6	56.4	56.5

STATISTICAL DATA

	N	*OR*	*M*	*σ*	*V*
1. Lateral height	14	50.3–61.0	54.9	3.24	5.90
2. Medial height	17	53.1–66.8	60.6	3.40	5.61
3. Total width	17	58.3–80.6	73.6	6.52	8.85
4. Ratio meas. 2/3	–	–	–	–	–
5. Trochlea width	16	44.7–61.8	55.9	3.89	6.95
6. Width distal facets	17	44.1–59.1	54.3	3.29	6.05

Table 7. Statistical data for astragalus of *Ceratotherium praecox* Hooijer and Patterson. Measurements from Hooijer (1972, table 39).

	N	*OR*	*M*	*σ*	*V*
1. Lateral height	65	77–105	89.1	4.74	5.31
2. Medial height	67	80–96	88.5	4.49	5.07
3. Total width	67	98–122	109.4	5.78	5.28
4. Ratio meas. $^2/_3$	–	–	–	–	–
5. Trochlea width	67	87–108	97.1	4.98	5.12
6. Width distal facets	67	77–103	87.1	5.67	6.50

(table 9). A comparison of these data with that calculated from Hooijer (1950, table 1A) for a series of skulls of the living *Hippopotamus* is very interesting. The measurements on the hippo skulls were of specimens from various museums in the Netherlands and represented both zoo and wild animals from different localities, but all identified by Hooijer as *Hippopotamus amphibius.* Statistical data calculated from Hooijer (1950, table 1A) are given in our table 10. Amynodonts are often described as having lived in a similar environment to that of the hippos; and both developed large canine tusks and semi-procumbent incisors. Note that in Hooijer's (1950) measurements, the males have consistently larger lower canines and that this is the only measurement based on teeth wherein there is no overlap between males and females. The difference in the observed ranges of the size of the canines of the Texas amynodonts is no greater than for the modern male and female hippos. We therefore find it reasonable to assume that the variation found in the amynodonts of the Whistler Squat l.f. is no greater than that expected to be found in a single population. The most variable area seems to have been the anterior part of the snout and lower jaws. The large size of the canines associated with a long $\underline{C}$-P^2 diastema is characteristic of males. There is as much as 10 mm difference in the canines and a 20 mm difference in the length of the $\underline{C}$-P^2 diastema.

The authors feel certain that, on the basis of samples presently known, only two species of *Amynodon* were living in the western United States during late Eocene time, *A. reedi* and *A. advenus.* The variability within what we believe to be a sample from a single population of *A. advenus* in Texas is greater than that of a similar number of individuals, including three type specimens from Wyoming and Utah. For this reason we synonomize *A. antiquus, A. intermedius* and *A. erectus* with *A. advenus.*

Gromova (1954) separated males from females of *Cadurcodon ardynensis* on the basis of several measurements that showed size differentiation. She contrasted differences in lower jaws of her figure 2 (male) and figure 3 (female) in the incisors, figure 6, and in the isolated canines in plate 3. She contrasted sizes of canines in her table 7 for males and females. The greatest measure across the crown of the upper canine for a sample of males is 26-28 mm with

Table 8. Measurements and statistical data for M^2 and M^3 of *Amynodon advenus* from Whistler Squat l.f. and statistical data for M^2 and M^3 of *Ceratotherium praecox* from Langebaanweg. Measurements for *C. praecox* from Hooijer (1972, tables 8 and 9).

MEASUREMENTS

Amynodon advenus
Whistler Squat l.f.

	41372-45	*41372-416*	*41576-19*	*41372-72*	*41372-49*	*41576-30*	*41372-520*	*41372-570*	*41372-605*	*41372-628*
M^2 L	37.8	38.4	45.8	39.0	45.5	38.1	41.0	44.5@	39.3	43.9
AW	43.2	45.0	51.0	47.1	47.2	45.6	43.9	–	44.2	47.5
PW	35.3	36.0	41.2	38.0	38.2	38.7	34.1	–	31.3	–

	41372-416	*41576-19*	*41372-72*	*41372-428*	*41372-413*	*41372-50*	*41576-30*	*41372-613*	*41372-617*	*41372-628*	*41372-45*
M^3 L	39.0	39.5	41.9	32.3	37.7	39.2	34.4	39.4	35.5	37.2	34.6
AW	–	45.5	46.2	40.4	45.3	43.3	42.4	42.4	42.0	–	37.2
PW	–	32.5	36.8	28.3	28.2	31.0	33.1	30.0	31.9	–	29.8

STATISTICAL DATA

	Amynodon advenus Whistler Squat l.f.					*Ceratotherium praecox* Langebaanweg				
	N	*OR*	*M*	σ	*V*	*N*	*OR*	*M*	σ	*V*
M^2 L	10	37.8–45.8	41.3	3.25	7.86	19	50–67	60.3	4.76	7.89
AW	9	43.2–51.0	46.7	2.41	5.16	22	70–82	76.2	3.46	4.54
PW	8	31.3–41.2	36.6	3.08	8.41	20	65–75	69.1	2.90	4.19
M^3 L	11	32.3–41.9	37.3	2.84	7.61	16	56–72	61.3	4.26	6.94
AW	9	37.2–46.2	42.7	2.80	6.55	16	65–75	70.2	3.53	5.02
PW	9	28.2–36.8	31.2	2.69	8.62	17	68–81	74.9	3.97	5.30

Table 9. Statistical data for M^2 and M^3 of *Trigonias*. Measurements from Gregory and Cook (1928, table 1).

	N	*OR*	*M*	σ	*V*
M^2 L	18	33–41	38.1	2.12	4.50
W	18	42–54	48.9	3.05	9.32
M^3 L	17	34–48	38.8	4.12	17.00
W	17	41–49	45.5	2.17	4.72

Table 10. Statistical data for *Hippopotamus amphibius* from measurements in Hooijer (1950, table 1A, measurements 9, 10, 12, 25, 26).

	♂					♀				
	N	*OR*	*M*	σ	*V*	*N*	*OR*	*M*	σ	*V*
Greater diam. $\overline{C}$	11	62–73	66.91	3.91	5.84	7	38–49	44.57	4.47	10.03
Smaller diam. $\overline{C}$	12	40–51	42.33	5.12	12.10	7	25–33	30.57	3.10	10.14
P_2–$\overline{C}$ diastema	15	97–154	120.67	14.91	12.36	9	95–135	116.33	14.08	12.10
P_2–M_3 L	10	260–296	281.30	13.04	4.64	6	232–298	265.50	22.46	8.46
P^2–M^3 L	9	235–278	256.33	16.96	6.62	7	213–258	240.00	14.46	6.03
M^1 L	19	37–52	46.21	4.25	9.20	9	37–50	44.44	4.93	11.09
W	21	37–48	42.52	2.82	6.63	9	36–46	40.67	3.46	8.51
M^2 L	17	45–62	52.53	4.43	8.43	8	47–60	52.38	4.37	8.34
W	16	41–58	49.56	4.66	9.40	9	44–53	49.66	2.55	5.13
M^3 L	10	53–62	54.50	4.45	8.17	8	47–56	53.00	3.12	5.89
W	8	45–58	52.00	4.60	8.85	5	49–51	50.20	0.84	1.67
Zygomatic W	21	331–483	408.52	32.13	7.86	10	327–411	388.50	20.44	7.08
Condylo-basal L	16	495–770	674.44	52.81	7.83	5	577–690	639.80	42.19	6.59

Table 11. Measurements of postcranial bones of *Amynodon advenus*, Whistler Squat l.f., *A. intermedius*, and *Metamynodon planifrons.*

		Amynodon advenus						*Amynodon intermedius* Osborn (1895)	*Metamynodon planifrons* Scott and Jepsen (1941)	
		41372-539						*AMNH 1933*	*No Number*	*PU 1097*
Atlas	W	230						–	300	314
		41372-599								*PU 548*
Humerus	L	355						302	415	454
		42061-1	*41372-359*	*41372-551*	*41372-577*	*41372-596*	*41372-354*			
Radius	L	341	370	–	–	333	–	305	–	385
	PW	70	77	72	73	72	–	–	99	123
	DW	79	80	77	–	–	75	–	101	120
		41372-533	*41372-537*	*42061-2*						
Femur	L	–	–	444@	–	–	–	360	438	–
	PW	163	–	160+	–	–	–	–	144	–
	DW	–	150 est.	–	–	–	–	–	140	–
		41372-501	*41372-52*							
Patella	L	81.4	84 est.	–	–	–	–	–	92	–
	W	71	73	–	–	–	–	–	82	–

Table 11, cont.

		41372-5	*41372-604*	*41372-512*						
Tibia	L	317	326	–	–	–	–	280	–	–
	PW	92	120	–	–	–	–	–	–	–
	DW	72	77	75	–	–	–	–	–	–
Fibula	L	333	–	–	–	–	–	–	–	–
	PW	–	–	–	–	–	–	–	–	–
	DW	–	–	–	–	–	–	–	–	–
		41372-452	*41372-93*	*41372-352*						
Calcaneum	L	133	122	117	–	–	–	–	–	–
PW tuber		49.4	40.2	31@	–	–	–	–	–	–
		42061-3								*PU 1104*
Scapula		–	–	–	–	–	–	–	–	265
Ant.-Post.	W	–	–	–	–	–	–	–	–	306
Dorso-Vent. Height		290+	–	–	–	–	–	–	–	104
Ant.-Post-Glenoid		65@	–	–	–	–	–	–	–	–
		41372-453	*41372-552*	*41372-458*					*PU 10886*	
Metacarpal III	L	167	156	–	–	–	–	163	142	–
Proximal	W	42.2	37.6	37.8	–	–	–	–	53	–
Midshaft	W	–	30.8	–	–	–	–	–	40	–
Distal	W	33.5	28.0	–	–	–	–	–	45	–

a mean of 27.8; for four females 14.5-18 mm with a mean of 16.4. Comparable measures for Texas *A. advenus* are 17.8 mm and 22.0 for females and 28.2 for a male.

Not all the postcranial material of *Amynodon advenus* from the Whistler Squat l.f. has been prepared. Measurements for the presently available material are given in table 11 and compared with measurements given by Scott and Jepsen (1941) for *Metamynodon planifrons.*

Later Amynodontids

The amynodontids that occur higher in the stratigraphic section in West Texas are represented by much smaller samples than those found in and near the quarry at Whistler Squat. Some of the material is as well preserved but it does not occur in sufficient quantity at any one level to enable us to identify males and females within a population. For this reason, we are forced to rely on a more typological approach to our identifications.

The highest occurrence of amynodontids in West Texas is in the Porvenir local fauna of the Vieja area. Two skulls and a lower jaw are clearly referable to *Metamynodon chadronensis.* An amynodontid larger than *M. chadronensis,* however, occurs much lower in the Serendipity local fauna of early Myton age. In between, smaller amynodontids, comparable in size to *Amynodontopsis bodei,* occur in the Skyline and Cotter channel deposits. Amynodontids from the later part of the Uintan in the Uinta Basin and surrounding areas are even less well known than those from the early Uintan.

AMYNODONTOPSIS Stock 1933

AMYNODONTOPSIS BODEI Stock 1933

Figs. 14–16, Tables 2, 12–15

Type.—Skull with P^3-M^3, loc. LACM (CIT) 1087; from the Sespe upper Eocene, north of Simi Valley, Ventura County, California; loc. LACM (CIT) 150.

Material.—Crushed juvenile skull with LP^1, dP^{2-4}, erupting M^1, RdP^{3-4}, erupting M^{1-2} 41715-2; uncrushed lower jaw with $LI_{1,2}$, alv I_3, RI_1, alv I_{2-3}, $RL\bar{C}$, P_3-M_3, 41668-8; RM_1, 41580-6, all from Skyline channels. Skull frag with basicranium and partial LM_2, M_3, 41853-9, from Cotter channels.

Stratigraphic position.—Skyline channels (fig. 1, loc. 1G) approximately 700–750 feet above the base of the Pruett Tuff, Brewster County, Texas. Skyline l.f. latest Eocene, and Cotter channels (fig. 1, loc. 1H), approximately 100 feet above the Skyline channels, earliest Oligocene (fig. 1).

Description.—The Texas lower jaw, 41668-8, (figs. 14, 15, table 13) has two permanent premolars but is a much smaller form than *Metamynodon mckinneyi* n. sp. It is best compared with the uncrushed lower jaw of *Amynodon advenus,* 41372-451 (fig. 7) from the Whistler Squat l.f., but the latter has three permanent lower premolars and is a longer, bigger lower jaw. The depth of the symphysis at the middle of the diastema is shallower in

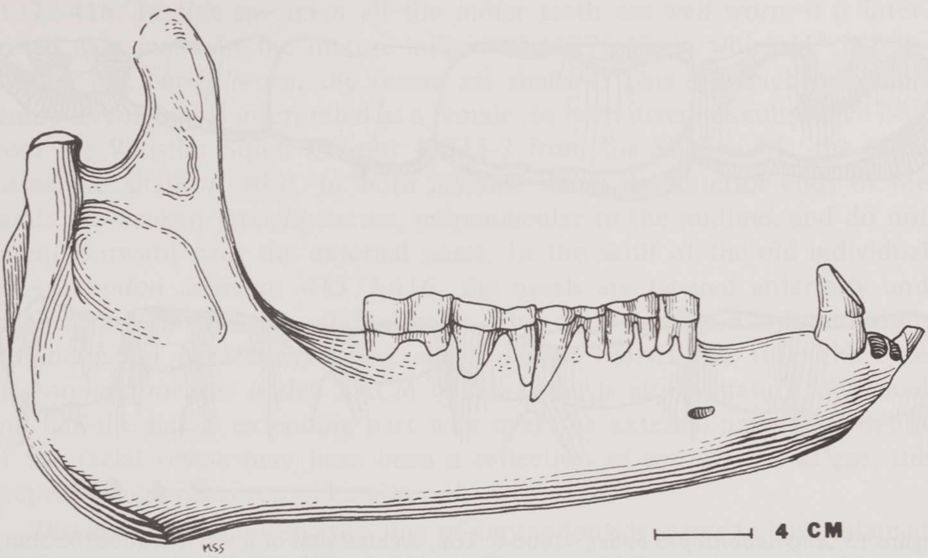

Figure 14. *Amynodontopsis bodei,* 41668-8. Lateral view of lower jaw with I_1, alveoli for I_{2-3}, $\overline{C}$, P_3–M_3. Skyline l.f.

the Skyline specimen; 44 mm versus 58 mm for the Whistler Squat specimen. The depth of the lower jaw just behind M_3 is 74 mm versus 94 mm in the same specimens.

The specimens of *Amynodon advenus* and *Amynodontopsis bodei* are a considerable distance apart stratigraphically and temporally; and, unfortunately, the sample at the upper level consists of only one lower jaw, a crushed juvenile skull, and a skull fragment. There are, however, amynodontids of closely comparable size elsewhere at approximately this time/stratigraphic level. *Amynodontopsis bodei* was described by Stock (1933, 1936, 1939) and is known from an excellent skull (Stock, 1933), most of a lower jaw (Stock, 1936), and some isolated teeth. In addition, Bjork (1967) described a lower jaw from the uppermost Eocene of the Slim Buttes of South Dakota that he referred to *Amynodontopsis bodei.* Measurements (table 13) of individual teeth for the lower jaws from the Skyline channels (41668-8), the Sespe of California [LACM (CIT) 2000] and the Slim Buttes (SDSM 59163) all fall within the observed ranges of the comparable premolars and molars of *Amynodon advenus* from Whistler Squat (tables 5, 15). The measurement of the M_{1-3} of the specimen from the Skyline channels also falls within the observed range of three M_{1-3} measurements of lower jaws from Whistler Squat. In fact, it is to the smaller side of the mean and would be the size of a female in the Whistler Squat population. The maxillary fragment 41372-45 from the Whistler Squat quarry, presumably a female, has about the same proportions as the Skyline lower jaw.

A partial skull, 41853-9, with part of LM^2, all of LM^3, and most of the left side of the basicranium, was collected from the Cotter channels (fig. 1).

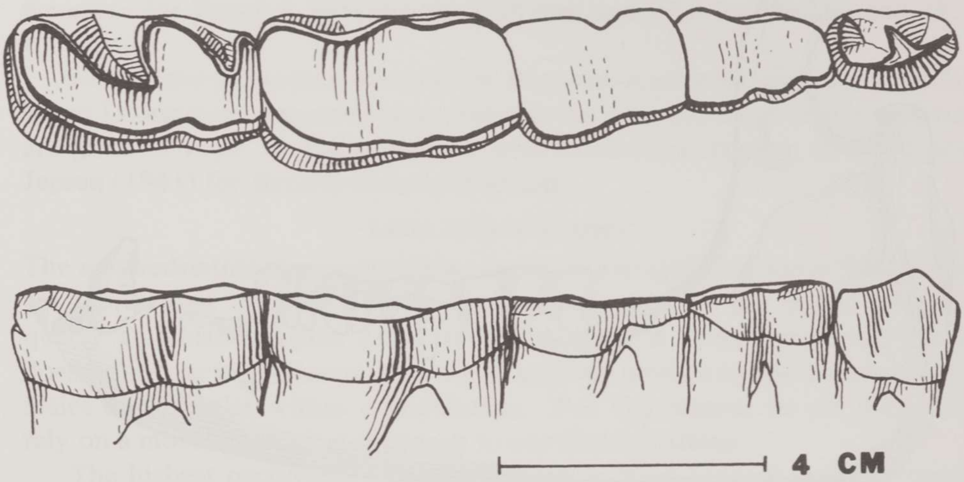

Figure 15. *Amynodontopsis bodei,* 41668-8. Top, occlusal view of lower dentition; bottom, lateral view of lower dentition. P_3 reversed in both figures. Skyline l.f.

The skull is broken in such a way that it shows a sagittal section a little to the right of the midline from M^1 to the right-ear region. The only useful measurements are those of M^3 (table 12). From its relatively small size and stratigraphic position in the Skyline l.f., it is tentatively referred to *Amynodontopsis bodei.*

A juvenile skull, 41715-2 from the Skyline channels (fig. 1), is also referred, tentatively, to *Amynodontopsis bodei* because of its size (table 2). In figure 16 a well-worn P^1 is present on the left side, followed by dP^2, dP^3, dP^4, erupting M^1 and M^2. Measurements for the teeth are given in table 2. Both M^1 and M^2 are smaller than the corresponding teeth in *Amynodon intermedius* (table 12) and would appear to be smaller than upper teeth would be for *Metamnydon mckinneyi* n. sp. Dr. P.R. Bjork of the South Dakota School of Mines and Technology kindly furnished us with a cast of a maxillary of a juvenile *Amynodontopsis bodei* from Slim Buttes, South Dakota. The measurements of the teeth are given in table 2 for comparison with those of the skull of the juvenile from Texas.

Stock (1933), writing about the facial fossae, said: "It appears improbable that the differences between *Amynodontopsis* and *Amynodon* in depth and extent of the facial fossae can be interpreted as due entirely to individual age. The Simi skull, as shown by wear of the teeth and by the closing of a number of the cranial sutures, evidently belonged to an old individual. The type of *Amynodon intermedius* represents, however, a mature but younger individual than No. 1087. No. 14601 represents a younger but nevertheless a fully adult individual. The type specimen of *A. erectus* likewise represents a fully mature individual." In the Texas specimens of *Amynodon advenus* the facial fossae are deepest in the old individual

41372-416. In this specimen all the molar teeth are well worn; it is interpreted as a male. In the mature individual 41576-19, in which M^3 is fully erupted but barely worn, the fossae are shallow. This specimen has small canine alveoli and is interpreted as a female. In both juvenile skulls, 41747-89 from the Whistler Squat l.f. and 41715-2 from the Skyline l.f., the facial fossae are shallow. Also, in both juvenile skulls the anterior ends of the nasals are broken straight across, perpendicular to the midline, and do not extend forward over the external nares. In the skull of the old individual of *Amynodon advenus,* 41372-416, the nasals are tapered anteriorly and extend forward over the external nares. This same condition is found in an old individual of *Metamynodon chadronensis,* FMNH PM 160. The type of *Amynodontopsis bodei,* LACM (CIT) 1087, is also a mature individual and has the nasals extending part way over the external nares. The depth of the facial fossae may have been a reflection of sex as well as age, the deepest being present on old males.

Discussion.—A conservative line of amynodontids seems to have retained smaller proportions through the latest Eocene, while a more robust group branched toward *Metamynodon.*

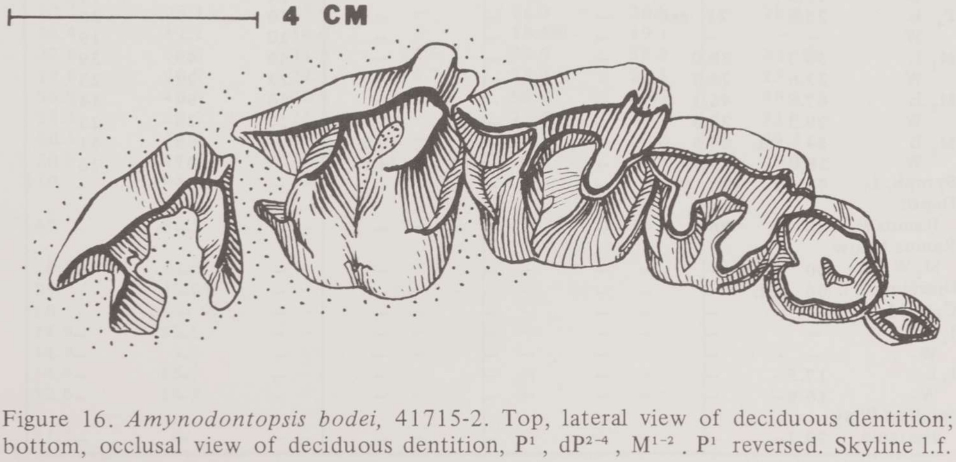

Figure 16. *Amynodontopsis bodei,* 41715-2. Top, lateral view of deciduous dentition; bottom, occlusal view of deciduous dentition, P^1, dP^{2-4}, M^{1-2}. P^1 reversed. Skyline l.f.

Table 12. Measurements of upper teeth of amynodontids of late Eocene and earliest Oligocene.

	?*Metamynodon mckinneyi* n. sp. Candelaria l.f.		*Amynodon intermedius*	*Megalamynodon regalis* Scott (1945)			*Amynodontopsis bodei* Stock (1939)	
			TYPE				TYPE	
	31281-36	*40498-2*	*PU 10309*	*CM 9961*	*CM 11958*	*CM 11953*	*LACM(CIT) 1087*	*LACM(CIT) 2530*
$\underline{C}$-M^3	–	–	255 est.	–	–	–	–	–
P^2-M^3	–	–	187	–	–	204	160.6@	–
P^2-P^4	–	–	65.7	–	–	73	47	–
M^1-M^3	–	–	130	–	147	144	116	–
$\underline{C}$ L	–	–	–	–	–	–	–	19.4
W	–	–	–	–	–	–	–	15.1
P^2 L	–	–	19.7	20	–	20	–	–
W	–	–	20.8	22	–	26	–	–
P^3 L	–	–	23.7	25	26	26	–	–
W	–	–	30.5	28	38	31	–	–
P^4 L	–	–	24.5	34	31	31	–	–
W	–	–	38.1	37	45	40	–	–
M^1 L	–	–	46.0	48	50	46	–	–
W	–	–	43.8	41	49	42	–	–
M^2 L	54.9	52.5	52.8	57	59	53	–	–
W	50.5	–	50.6	48	55	44	–	–
M^3 L	–	–	40.6	–	51	49	–	–
W	–	–	46.7	–	44	46		

Table 13. Measurements of lower teeth of amynodontids of late Eocene and earliest Oligocene.

	Metamynodon mckinneyi					*Megalamynodon regalis* Scott (1945), amended by Wall (personal communication)		
	TYPE							TYPE
	41723-5	*41723-10*	*41723-9*	*41723-8*	*41549-1*	*CM 9961*	*CM 11958*	*CM 11953*
$\overline{C}$-M_3	–	–	–	–	–	–	–	–
P_3-M_3	185 @	–	–	–	–	–	–	185
P_3-P_4	46.2@	–	–	–	–	–	–	52
M_1-M_3	140 @	–	–	–	–	–	141	134
$\overline{C}$ L	–	–	34.4	36.4	–	–	–	24
W	–	–	33.5	32.8	–	–	–	16
P_3 L	20.7	–	–	–	–	21	–	22
W	14.2	–	–	–	–	14	–	17.5
P_4 L	25.8	21 est	–	–	–	30	–	30
W	–	–	–	–	–	20	–	19
M_1 L	36.3	38.0	–	–	–	39	49	39
W	23.6	24.7	–	–	–	23	21	23
M_2 L	47.8	46.1	–	–	–	48	54	44
W	29.3	27.3	–	–	–	27	22	25
M_3 L	54 est.	47.5	–	–	48.5	–	53	51
W	28.0	25.9	–	–	28.5	–	27	26
Symph. L	44 @	128 @	–	–	–	–	–	–
Depth Ramus M_1	80 @	76.0	–	–	–	–	–	–
Ramus below M_2 W	40	–	–	–	–	–	–	–
Diastema L	66 est.	–	–	–	–	–	–	–
$\overline{C}$alv-M_3	–	–	–	–	–	–	–	–
I_1 L	–	–	–	–	–	–	–	–
W	–	–	–	–	–	–	–	–
I_2 L	17.5	–	–	–	–	–	–	–
W	16.9	–	–	–	–	–	–	–
Smallest W at diastema	79.3	–	–	–	–	–	–	–

Table 12, cont.

A. bodei Stock (1939) (cont.)				*A. bodei* Cotter channels	*Metamynodon chadronensis* Porvenir l.f.		
LACM (CIT) 2531	*LACM (CIT) 2532*	*LACM (CIT) 1089*	*LACM (CIT) 2535*	*41853-9*	*FMNHPM 160*	*FMNHPM 161R*	*FMNHPM 161L*
–	–	–	–	–	273	–	–
–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–
–	–	–	–	–	22.2	–	–
–	–	–	–	–	23.3	–	–
15.2	–	–	–	–	17.6	–	–
15.1	–	–	–	–	22.0	–	–
16.6	16.4	–	–	–	–	–	–
20.7	21.1	–	–	–	–	–	–
–	20.0	–	–	–	34.9	–	–
–	26.2	–	–	–	28.8@	–	–
–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–
–	–	42.8	–	–	54.0	–	–
–	–	31.4	–	–	60.9	–	–
–	–	–	38.1	40.3	57.5	44.2	46.1
–	–	–	36.5	44.5	58.0	54.6	56.6

Table 13, cont.

Skyline l.f.	*Amynodontopsis bodei* Stock (1936)	Bjork (1967)		*Metamynodon chadronensis* Wood (1937) TYPE			
41668-8	*LACM(CIT) 2000*	*SDSM 59163*	*41580-6*	*AMNH 11866R*	*AMNH 11866L*	*FMNH PM 160*	*FMNH PM 161*
127.0	–	–	–	–	–	–	–
139.2	–	153.2	–	183.5	–	180	–
38.0	39.8	38.6	–	40.4	–	45	–
102.5	119.5	115.1	–	144.1	141.8	135	–
17.5	–	–	–	–	–	25 @	30.3
16.5	–	–	–	–	–	–	27.9
17.5	17.7	17.5	–	18.8	17.1	19.2	–
12.3	12.8	13.4	–	13.3	13.0	14.9	–
23.2	23.1	23.4	–	26.3	26.8	28.4	–
16.4	17.1	16.4	–	18.5@	19.1	–	–
27.0	31.5	31.2	26.6	33.9	33.5	33 @	–
19.8	20.7	22.1	16.7	25.4	23.5	25	–
35.9	40.0	40.4	–	50.2	47.4	48.1	–
23.3	23.0	24.8	–	27.8	27.7	31	–
40.5	44.3	44.0	–	59.0	59.3	54.5	–
20.5	21.4	24.8	–	24.9	25.8	29.2	–
110	108.5	–	–	–	–	–	–
65	65.5	–	–	–	–	–	–
28.5	24.6	–	–	–	–	–	–
51	48.5@	–	–	–	–	–	–
216	230 @	–	–	–	–	–	–
11.9	10.6	–	–	–	–	–	–
11.9	9.9	–	–	–	–	–	–
14.4	15.7	–	–	–	–	–	–
12.8	14.9	–	–	–	–	–	–
51.5	–	–	–	–	–	–	–

METAMYNODON MCKINNEYI[4] new species

Figs. 5, 17, 18, 19, 20; Tables 12, 13, 15

Type.—Lower jaw with alv I_1, I_2, alv I_3, alv $\overline{C}$, P_3–M_3. 41723-5; Upper Eocene, Uintan.

Material.—Lower jaw symphysis with alv I_1, I_2, alv I_3, R$\overline{C}$, 41723-9; lower jaw with R alv P_3, frag P_4, $M_{1\text{-}3}$, L$M_{1\text{-}3}$, 41723-10; right $\overline{C}$, -8; lower jaw frag with M_3, 41549-1. Questionable reference, LM^2, 31281-36; RM^2 frag, 40498-2.

Stratigraphic position.—Titanothere channels (fig. 1, loc. E), approximately 200 feet (60.8m) above base of Pruett Tuff, Buck Hill Group, Brewster County, Texas. Serendipity l.f., late Uintan (Myton), The M^2s are from the lower sorted facies, lower 50 ft. (15.2 m) Colemena Tuff, Candelaria l.f., late Uintan (Myton), Presidio County, Texas (Wilson, 1977b, table 2).

Diagnosis.—A metamynodont with large procumbent lower incisors (figs. 17, 18), large curved lower canines that erupt to be semi-procumbent but curve into a vertical position (fig. 19) and occlude against the anterior surface of the upper canine. Lower canines with greater diameter at base of enamel than those of *M. chadronensis,* lower jaw more massive than *M. chadronensis,* post-canine diastema longer and breadth of lower jaw between canines wider than in *M. planifrons.* Lower molars higher crowned than those of *Amynodon advenus* and *Amynodontopsis bodei.* Permanent lower dentition P_3–P_4, $M_{1\text{-}3}$. Total premolar length about one-third that of the total molar length (table 15). P_3 is premolariform.

Description.—*M. mckinneyi* has only two lower premolars (fig. 20), and their combined length is only about one-third the length of the $M_{1\text{-}3}$. The referred specimens of *A. advenus,* on the other hand, have three lower premolars and their combined length is about half that of the molars. In other respects, the differences are those of proportion; *M. mckinneyi* has a much more massive lower jaw. Unfortunately, our sample from the Titanothere channels is so small that we cannot tell whether it belonged to a male or a female. Because of the large size we are tempted to call them male, but this is only because of the contrast with the sample from the Whistler Squat l.f.

The middle incisor on the symphysis, 41723-9 (figs. 18, 19), is the largest. The alveolus for the right I_1 is oval, the left I_1, more rounded. Incisor$_2$ is worn on the anterior face. There is also a wear facet at the external base of the tooth for the I^3. The alveolus for the right I_3 is small and for the left I_3 even smaller (4 mm across).

The symphysis, 41723-9, has the right canine complete, although broken, and the base of the left canine. In addition, 41723-8, an isolated left canine, is complete (fig. 5). The latter shows a prominent wear facet for the I^3. It tapers to a blunt posterior end and therefore was probably not a continuously growing tooth.

[4] Named for the B.P. McKinney family, of the Agua Fria Ranch, Brewster County, Texas, who have been most helpful to University of Texas field parties.

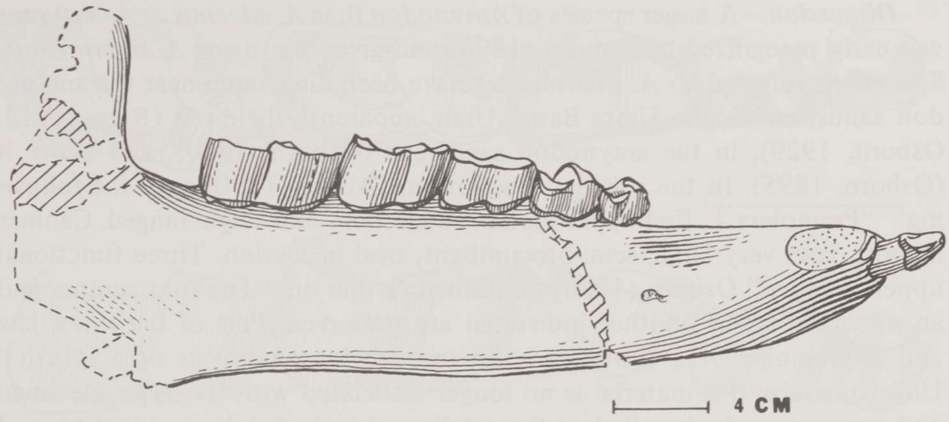

Figure 17. *Metamynodon mckinneyi* n. sp., type 41723-5. Lateral view of lower jaw. I_2, alveolus I_3, alveolus $\overline{C}$ (reversed), P_{3-4}, M_1, reversed, M_{2-3}. Serendipity l.f.

The premolars and molars are higher crowned in *M. mckinneyi* than in amynodonts. The P_3 is triangular and has a well-developed paraconid and hypolophid. An M_3, showing comparable wear to *A. advenus,* has a crown height of 15 mm, whereas one of *M. mckinneyi* has 24.5 measured at the hypolophid on each tooth.

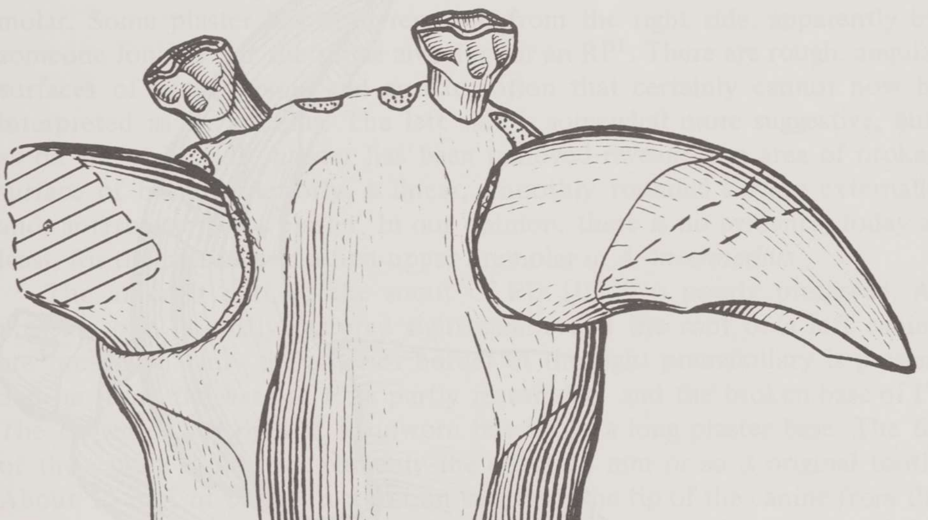

Figure 18. *Metamynodon mckinneyi* n. sp., 41723-9. Dorsal view of symphysis with alveolus I_1, I_2 and alveolus I_3, $\overline{C}$. Right canine restored from offsetting fractures. Serendipity l.f.

Discussion.—A larger species of *Amynodon* than *A. advenus* or *A. antiquus* was early recognized by Osborn (1890) and given the name *A. intermedius.* Specimens referred to *A. intermedius* have been discovered near the amynodon sandstone in the Uinta Basin, Utah, apparently below it (Riggs, 1912; Osborn, 1929), in the amynodon sandstone (Osborn, 1929), and above it (Osborn, 1895). In the original description, Osborn (1890) gave the following: "Premolars $\frac{4}{?}$, first upper molar rudimentary and single fanged. Canines in both jaws very large, semi-procumbent, oval in section. Three functional upper incisors." Osborn (1890) continued farther on, "The four canines and an upper molar of another individual are preserved. Part of the lower jaw and a premolar of a third, and the mandibular symphysis of a fourth." Unfortunately, this material is no longer associated with the type specimen and can now only be cited as "uncatalogued and of dubious identity, and unlocated in the [Princeton] collection" according to a personal communication from Dr. Donald Baird dated 15 May 1979.

At first we thought the very large lower jaw, 41723-5, might be referred to *A. intermedius,* but the lack of lower jaw material directly associated with the type made such a reference seem uncertain. However, Wilson borrowed the type of *A. intermedius,* PU 10309, through the courtesy of Dr. Baird.

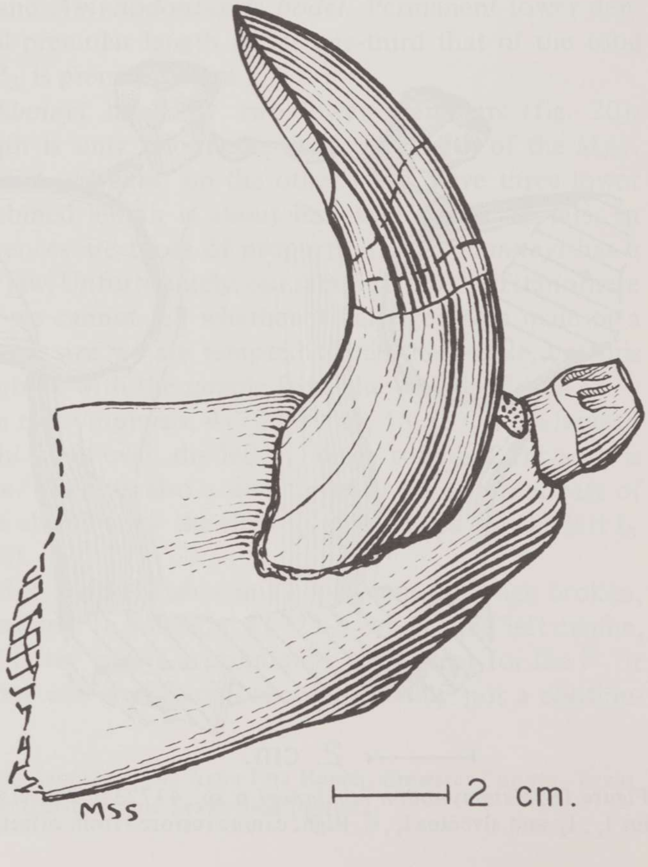

Figure 19. *Metamynodon mckinneyi* n. sp., 41372-9. Lateral view of symphysis with I_2, alv I_3, $\overline{C}$. Canine restored from offsetting fractures. Serendipity l.f.

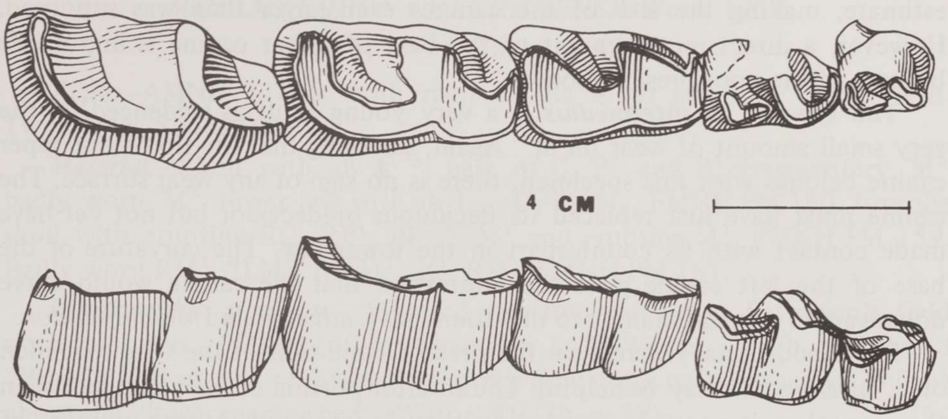

Figure 20. *Metamynodon mckinneyi* n. sp., type, 41723-5. Top, occlusal view P_3–M_3 ; bottom, lateral view P_3–M_3. M_1 reversed in both views. Serendipity l.f.

Several characters that were difficult to make out from the illustrations needed investigation in view of later knowledge about amynodonts, and that new information is added here. One was evidence for the presence of an upper first premolar; and another, the peculiar position of the upper canines as illustrated by Osborn (1890). The specimen does not presently show alveoli in the position that would have been occupied by a first premolar. Some plaster has been removed from the right side, apparently by someone looking for the single alveolus for an RP^1. There are rough, angular surfaces of broken bone and an excavation that certainly cannot now be interpreted as an alveolus. The left side is somewhat more suggestive, but, as on the right side, plaster has been removed revealing an area of broken surface of bone posteriorly, a linear, smoothly rounded surface externally and, anterointernally, plaster. In our opinion, there is no evidence, today at least, for the presence of a first upper premolar in *A. intermedius.*

The anterior part of the snout of PU 10309 is poorly preserved. At present, only a partly restored right canine and the root of a left canine are preserved. Only the anterior border of the right premaxillary is present and on it are the base of I^3, a partly restored I^2 and the broken base of I^1. The crown of the right I^2 is unworn but it has a long plaster base. The tip of the canine is unworn but only the outer 25 mm or so is original tooth. About 15 mm of plaster restoration separates the tip of the canine from the anteroexternal part of the base of the tooth. Assuming that the tip of this tooth belongs to this specimen–which is hard to prove now in the absence of a direct contact–the angle of inclination of the tip with respect to the base is certainly open to question. In addition, Osborn's (1890, p. 509) measurement of 31 mm for the fore and aft diameter of crown of upper canine at base is in error because that measurement is from plaster to plaster, and the plaster restoration does not extend over the entire base of the tooth. At least 7 or 8 mm could be added to that measurement as a conservative estimate, making the size of the canines even larger than was supposed. However, a direct measurement of the base of either canine is impossible because of the poor preservation.

The type of *A. intermedius* is a very young adult as evidenced by the very small amount of wear on M^3. Again, assuming that the tip of the upper canine belongs with this specimen, there is no sign of any wear surface. The canine must have just replaced its deciduous predecessor but not yet have made contact with its counterpart in the lower jaw. The curvature of the base of the left canine gives the impression that the canine would curve downward in a similar manner to that found in *A. advenus* and *Metamynodon*.

Some additional remarks on the present condition of the type specimen of *A. intermedius* may be helpful. The anterior portion of the palate between the premolars is uncrushed and only slightly fractured. A measurement of 67.8 mm between the internal cingula of the second premolars is valid. We therefore agree with Osborn (1890) that the palate is very broad.

Osborn (1890) stated that "There is a considerable diastema." The distance from the left P^2 to the base of C is 24 mm but there is some restoration on both sides so the measurement may not be reliable. In my opinion, the diastema is short, even shorter than in female *A. advenus*. It may be that when some associated skulls and lower jaws are discovered, the lower diastema will be found to be consistently longer than the upper to accommodate the overlap of the lower canine.

The tooth row of the type of *A. intermedius* and the lower jaw of *M. mckinneyi* occlude very well and it was tempting to combine the two in a single taxon. However, lower jaws referred to *A. intermedius* have three premolars, for example, AMNH 1963. It would take a search of the older collections from the Uintan to discover whether there are undescribed lower jaws with very large canines and with only two premolars. This is beyond the scope of our project.

Also, the total upper premolar length is about 40% of the total upper molar length in *Metamynodon* (table 14) whereas in *Amynodon* it is about 50%. In *A. intermedius* it is slightly above 50% and closer to *Amynodon* than *Metamynodon*.

The loss of the P_2, the decrease in length of premolars in proportion to the length of the molars and the increase in size separates *Metamynodon* from *Amynodon advenus*. Whether *M. mckinneyi* can be determined as a transitional form between *A. advenus* and *M. chadronensis* or as a migrant will have to await discovery of better samples in the Uintan.

METAMYNODON CHADRONENSIS Wood 1957

Figs. 5, 21–35; Tables 2, 12–15

Type.—AMNH 11866; both rami of the lower jaw with cheek teeth. Twin Draw, South Dakota.

Material.—Skull with alv I^{1-3}, base of $\underline{C}$, P^2 and P^4 fragmentary, M^2 badly worn, M^3, lower jaw with alv I_{1-3}, $\bar{C}$, P_3–M_3, FMNH PM 160. Juvenile skull with erupting R$\underline{C}$, RP^1, dP^{2-4}, M^1 and erupting M^2, FMNH PM 159. Badly worn RM^1, ?LM^2, RL M^3, 2$\bar{C}$, R$\bar{M}_2$, FMNH PM 161.

Stratigraphic position.—"Big red horizon" of Bryan Patterson's field notes or lower 100 feet (30 m) Chambers Tuff (Wilson, 1977b, p. 18) and "Blue Cliff Horizon" of Bryan Patterson's field notes or 0–88 feet (0–26.7 m) above the "lower marker bed" (Wilson, 1977b, p. 18).

Diagnosis.—Wood (1937) gave the following diagnosis for *M. chadronensis:* "$I_?$, $C_?$, P_2, M_3; considerable smaller than *M. planifrons,* a shade larger than *Paramynodon cotteri;* lower molars smaller, more brachyodont, flattened laterally, and more primitive in pattern, than in *M. planifrons;* thin layer of cement on lateral surfaces of cheek teeth." To this can be added $I^3_?$, C^1_1, P^3_2, M^3_3.

Description.—The measurements of the skull and lower jaw from the Porvenir l.f. of the Vieja area are lower than the observed range of measurements given by Scott and Jepsen (1941) for *M. planifrons.* However, the measurements of the type of *M. chadronensis* (table 13) are close to those of FMNH PM 160 and, primarily on this basis, we refer the Vieja material to *M. chadronensis.*

Figure 21. *Metamynodon chadronensis,* FMNH PM 160. Lateral view of skull. Premaxillary-condylar length 56.2 cm. Porvenir l.f.

Figure 22. *Metamynodon chadronensis,* FMNH PM 160. Dorsal view of skull. Porvenir l.f.

Figure 23. *Metamynodon chadronensis,* FMNH PM 160. Ventral view of skull. Alveoli for I_{1-3}, alv. $\underline{C}$, P^2, alv. P^3, P^4, alv. M^1, M^{2-3}. Porvenir l.f.

Figure 24. *Metamynodon chadronensis,* FMNH PM 160. Lateral view of lower jaw. $\overline{C}$, P_{3-4}, M_{1-3}. Porvenir l.f.

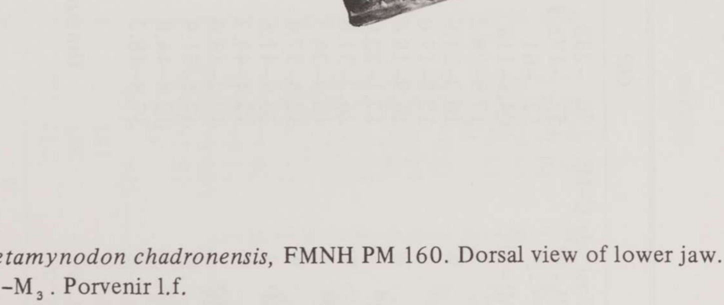

Figure 25. *Metamynodon chadronensis,* FMNH PM 160. Dorsal view of lower jaw. Alveoli for I_{1-3}, $\overline{C}$, P_3–M_3. Porvenir l.f.

Table 14. Observed ranges of measurements of upper teeth of amynodontids arranged in stratigraphic order.

	Amynodon advenus Whistler Squat l.f.		*Amynodon intermedius* TYPE		*Megalamynodon regalis* Scott (1945)		*Amynodontopsis bodei* Stock (1933, 1936, 1939)		*Metamynodon chadronensis*		*Metamynodon planifrons* Scott and Jepsen (1941) Troxell (1921)	
	OR	*N*	*OR*	*N*	*OR*	*N*	*OR*	*N*	*OR*	*N*	*OR*	*N*
Post. alv C–M^3	170 -233	4	214	1	–	–	–	–	273 @	1	–	–
P^2–M^3	152 -173.5	3	187	1	204	1	160.6@	1	–	–	202 -235	4
P^2–P^4	52 -61	3	65.7	1	73	1	47	1	–	–	61 -71	4
M^1–M^3	104.9–116	4	130	1	144–147	2	116	1	–	–	140 -172	4
C L	17.8–28.2	3	–	–	–	–	19.4	1	22.2	1	26.8–35	3
W	16.2–21.9	3	–	–	–	–	15.1	1	23.3	1	35 -36	2
P^2 L	12.8–17.0	4	19.7	1	20	2	15.2	1	17.6	1	17 -21	2
W	16.9–18.6	4	20.8	1	22–26	2	15.1	1	22.0	1	21 -25.5	2
P^3 L	17.1–22.0	6	23.7	1	25–26	3	16.4–16.6	2	19.3	1	21 -21.5	2
W	26.2–31.8	6	30.5	1	28–38	3	20.7–21.1	2	–	–	33.5–35	2
P^4 L	18.9–24.5	6	24.5	1	31–34	3	20	1	34.9	1	23 -30	4
W	32.8–37.8	6	38.1	1	37–45	3	26.2	1	–	–	43.4–47	4
M^1 L	26.9–41.8	6	46.0	1	46–50	3	–	–	43.7–50.2	2	36 -51	4
W	37.4–44.7	6	43.8	1	41–49	3	–	–	52.5	1	56 -58	3
M^2 L	47.2–53.0	9	52.8	1	53–59	3	42.8	1	54.0–65.4	2	59 -68	2
W	42.5–51.9	8	50.6	1	44–55	3	31.4	1	50.2–60.9	2	72	1
M^3 L	32.8–44.0	11	40.6	1	49–51	2	38.1–40.3	2	50.0–67.4	2	58 -70	4
W	37.8–48.2	9	46.7	1	44–46	2	36.5–44.5	2	48.5–58.0	2	60 -64	3
	Uintan		Uintan		Randlett Brennan Basin		Cotter channels (Skyline l.f.), LACM (CIT) Loc. 150		Porvenir l.f.		Brule	
$\frac{\text{Ave. } P^2\text{–}P^4}{\text{Ave. } M^1\text{–}M^3} \times 100$	50.0		50.5		50.17				39.40		42.21	

Table 15. Observed ranges of measurements of lower teeth of amynodontids in stratigraphic order.

		Amynodon advenus Whistler Squat l.f.	*N*	*Metamynodon mckinneyi* n. sp.	*N*	*Megalomynodon regalis* (Scott, 1945)	*N*	*Amynodontopsis bodei* (Stock, 1933, 1936, 1939)	*N*	*Metamynodon chadronensis*	*N*	*Metamynodon planifrons* (Scott and Jepsen, 1941)	*N*
I_3–M_3		272 est.	1	280	1	290	1	–	–	–	–	–	–
$\overline{C}$–M_3		247	1	–	–	–	–	127.0	1	–	–	–	–
P_2–M_3		151	1	–	–	–	–	–	–	–	–	–	–
P_3–M_3		134 -143	–	185 @	1	185	1	139 -153	2	180 -183.5	2	212–215	2
P_2–P_4		51.4	1	–	–	–	–	–	–	–	–	–	–
P_3–P_4		38.2–41.5	3	46.2@	1	52	1	38.0–39.8	3	40.4–45.0	2	49–55	2
M_1–M_3		100.8–109.3	3	140 @	1	134–141	2	102.5–115.1	3	135 -141.8	3	157–163	2
$\overline{C}$	L	21.5–22.8	2	34.4–36.4	2	24	–	17.5	1	25 -30.3	2	37–39	2
	W	20.3–20.7	2	32.8–33.5	2	16	–	16.5	1	27.9	1	31–34	2
P_2	L	11.1–13.5	3	–	–	–	–	–	–	–	–	–	–
	W	9.0–9.2	3	–	–	–	–	–	–	–	–	–	–
P_3	L	17.7–19.3	7	20.7	1	21–22	2	17.5–17.7	3	17.1–18.8	3	21–28	2
	W	12.1–13.5	6	14.2	1	14–17.5	2	12.3–13.4	3	13.0–14.9	3	15–20	2
P_4	L	20.2–24.6	7	25.8	1	30	2	23.1–23.4	3	26.3–28.4	3	29–33	2
	W	14.7–18.5	7	–	–	19–20	2	16.4–17.1	3	18.5–19.1	2	21–27	2
M_1	L	23.6–29.0	2	36.3–38.0	2	39–49	3	26.6–31.5	4	33 -33.9	3	42–43	2
	W	18.7	1	23.6–24.7	2	21–23	3	16.7–22.1	4	23.5–25.4	3	24	1
M_2	L	33.9–42.3	8	46.1–47.8	2	44–54	3	35.9–40.4	3	47.4–50.2	3	53–58	2
	W	19.6–24.4	8	27.3–29.3	2	22–27	3	23.0–24.8	3	27.7–31.0	3	54	1
M_3	L	40.1–48.0	6	47.5–54.0	3	51–53	2	40.5–44.3	3	54.5–59.3	3	57–60	2
	W	20.2–23.7	6	25.9–28.5	3	26–27	2	20.5–24.8	3	24.9–29.2	3	32	1
		Uintan		Uintan		Randlett Brennan Basin		Cotter channels (Skyline l.f.) and LACM (CIT) LOC 147, Slim Buttes Fm.		Porvenir l.f. and Chadron Fm.		Brule	
$\frac{\text{Ave. } P_2 \text{ or } P_3\text{–}P_4}{\text{Ave. } M_1\text{-}M_3} \times 100$		48.8		33.0		37.8		34.5		30.8		32.5	

Upper dentition.—The adult skull (figs. 21, 22) has alveoli for three upper incisors per side (fig. 23), but the snout is broken on the juvenile skull. In the former the premolars and the first and second molars are so badly worn or broken off that nothing can be seen of their pattern. The third molar on the skull is badly worn but is better preserved in FMNH 161. These third molars are worn but still preserve the outer concave ectoloph and the rib at the paracone.

Lower dentition.—A full dentition is preserved on the left ramus (figs. 24, 25) of FMNH PM 160. It is somewhat more worn than the type, AMNH 11866, but shows no morphologic differences.

Upper milk dentition.—The juvenile skull FMNH PM 159 has P^1, dP^2, dP^3, dP^4, M^1 and M^2 preserved (table 2). The first molar was erupted and M^2 was excavated by preparation. The occlusal pattern is worn off of P_1 and dP^{2-3} and the anterior corner is broken off dP_4. Their general shape is like that of the milk premolars of *A. advenus* but they are much larger. The M^1 of *M. chadronensis* is larger and higher crowned than that of the type of *A. intermedius.* The crown height measured at the paracone is 44 mm in *M. chadronensis* and about 37 mm in *A. intermedius.* The second molar, which has not erupted in FMNH PM 161, is an enormous tooth approximately 67 mm as measured along the ectoloph.

Discussion.—*Metamynodon chadronensis* is a rare form in the Porvenir local fauna of the Vieja area. A reduction in the back-levee swamp environment in the Vieja may account for this. The climate seems to have gradually shifted from a more moist condition to a drier, perhaps more open savannah condition from early late Eocene time to early Oligocene time.

SUMMARY AND CONCLUSIONS

A sample of amynodonts, referred to *A. advenus,* from a quarry at Whistler Squat, Brewster County, Texas, is sufficiently large for estimating the size of males and females in a single population. The males have large canines and longer $\overline{C}$–P^2 diastemas. The variation in tooth size is no greater than that given by Hooijer (1950) for the modern *Hippopotamus.* The variation of measurements of M^2 and M^3 and the astragali from the Whistler Squat quarry are comparable to that found by Hooijer (1972) for the Pliocene rhinoceros, *Ceratotherium praecox,* from a quarry at Langebaanweg, South Africa. *Amynodon antiquus, A. intermedius* and *A. erectus* are synonymized with *A. advenus.*

A new species of *Metamynodon, M. mckinneyi,* has very large lower canines and only two lower premolars. It is referred with confidence to that genus. *Metamynodon mckinneyi* is associated with a Myton late Eocene fauna.

Metamynodon bodei occurs still higher in the stratigraphic section in the Skyline and Cotter channels. Because of the association of *Amynodontopsis bodei* and *Hyaenodon* cf. *vetus,* the fauna of the Skyline and Cotter channels is correlated with that of the Lapoint member of the Duchesne River Formation.

Metamynodon chadronensis is identified in the Porvenir local fauna, early Oligocene, of the Vieja area.

The samples of *Metamynodon mckinneyi* n. sp. and *Amynodontopsis* are small and nowhere have they been found together. For this reason we have referred them to the aforementioned genera knowing full well that further synonymization may be possible when large samples are available.

There is no evidence on the type specimen of *Amynodon antiquus* for the presence of P_1 nor on the type specimen of *Amynodon intermedius* for P^1. The formula for the adult cheek dentition in *Amynodon,* as presently known, is P^{2-4}_{2-4}, M^{1-3}_{1-3}. The depth of facial fossae may be a function of sex and individual age and the preservation of the anterior ends of the nasals may be a function of age.

Amynodon advenus is the common Uintan form and is now well represented by the collection from Whistler Squat. Whether *Amynodon advenus, Megalamynodon regalis,* and *Metamynodon chadronensis* all represent a monophyletic series as Wood (1949) proposed will have to await larger samples. The more slender form, *Amynodontopsis bodei,* seems to have been widespread in North America and, so far at least, has not been found directly associated with the robust forms.

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