THE GENUS *AMYNODON* AND ITS RELATIONSHIP TO OTHER MEMBERS OF THE AMYNODONTIDAE (PERISSODACTYLA, RHINOCEROTOIDEA)

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ABSTRACT—The taxonomy of the late Eocene rhinocerotoid *Amynodon* is revised. Two species of *Amynodon* are recognized: the primitive *A. reedi* and the derived *A. advenus*. *A. intermedius* is regarded as a junior synonym of *A. advenus* because of a demonstrated morphologic gradation between the two. *Amynodon* occupies a phylogenetic position intermediate between the basal amynodont stock and the more derived members of the family (cadurcodonts and metamynodonts). Dental and cranial characters of *Amynodon* are described, and their primitive or derived states determined by comparisons with other amynodontids and primitive ceratomorphs (tapiroids and rhinocerotoids).

INTRODUCTION

THIS paper is the first in an intended series of papers dealing with amynodont systematics. Anatomical and stratigraphic evidence indicate that *Amynodon* is a relatively primitive amynodontid (see Wood, 1941). Some confusion persists, however, regarding the specific and generic relationships of *Amynodon*. My recent systematic revision of the Amynodontidae (Wall, 1981) places *Amynodon* between a primitive amynodont (to be described elsewhere) and the derived cadurcodonts and metamynodonts (Text-fig. 1). The phylogenetic relationships depicted in Text-fig. 1 are based on my observations of a majority of the taxa included in the Amynodontidae, using other ceratomorphs (Tapiroidea and Rhinocerotoidea) for outgroup comparison. The unnamed primitive amynodont is represented by a complete skull and lower jaws (AMNH 107635) from the late Eocene of Asia. This taxon is the primitive sister group of other amynodonts because it retains cranial features typical of primitive ceratomorphs, such as *Heptodon* and *Hyrachyus*.

I include in the cadurcodonts: *Sharamynodon* Kretzoi, 1942; *Amynodontopsis* Stock, 1933; *Sianodon* Xu, 1965; and *Cadurcodon* Kretzoi, 1942. The cadurcodonts are characterized by a large preorbital fossa extending medial to the orbit, and the development of large frontal sinuses. Cadurcodonts exhibit evolutionary trends leading to a tapir-like proboscis in *Cadurcodon* (Wall, 1980), but lack any skeletal modifications for an aquatic life. The genera I include in the metamynodonts are: *Megalamynodon* Wood, 1945; *Paramynodon* Matthew, 1929; *Zaisanamynodon* Beliajaeva, 1971; *Metamynodon* Scott and Osborn, 1887; and *Cadurcotherium* Gervais, 1873. They are united by a reduced preorbital fossa, transversely and dorsoventrally thickened zygomatic arch, and skeletal adaptations for an aquatic life.

Since *Amynodon* occupies a pivotal phylogenetic position, a thorough description of important anatomical characters, together with my interpretation of the derived or primitive nature of these characters, is needed to accurately reconstruct the adaptive radiation of amynodonts. Before this can be accomplished, however, it is necessary to establish taxonomic limits for the genus, and to stabilize its species composition. This paper will therefore present a taxonomic revision of the genus *Amynodon*, followed by comparisons of its dental and cranial characters with those of other amynodonts.

ABBREVIATIONS OF INSTITUTIONS

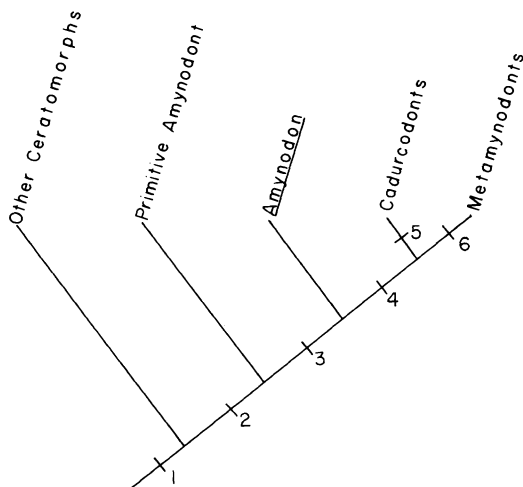AMNH—American Museum of Natural History, New York

CM—Carnegie Museum, Pittsburgh, Pennsylvania

FMNH—Field Museum of Natural History, Chicago, Illinois

LACM—Los Angeles County Museum, Los Angeles, California

MCZ—Museum of Comparative Zoology, Cambridge, Massachusetts

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TEXT-FIG. *1*—Proposed cladistic relationships of amynodontids using other ceratomorphs (tapiroids and rhinocerotoids) to determine character polarities. 1, straight ectolophs and complete crosslophs on upper molars; 2, well-developed, labially-deflected M^3 metastyle, and presence of preorbital fossa; 3, reduction in length of preorbital portion of skull; 4, reduction, or loss, of premaxilla-nasal contact laterally; 5, large preorbital fossa extending medial to orbit; 6, reduced preorbital fossa, increased brachycephaly of skull. For more characters and further discussion on phylogenetic relationships of amynodonts see Wall (1981).

PU—Princeton University, Princeton, New Jersey

TMM—Texas Memorial Museum, Austin, Texas

UCMP—University of California Museum of Paleontology, Berkeley, California

YPM—Yale Peabody Museum, New Haven, Connecticut

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA
Suborder CERATOMORPHA
Superfamily RHINOCEROTOIDEA Gill, 1872
Family AMYNODONTIDAE Scott and Osborn, 1883
Genus AMYNODON Marsh, 1877

Type species.—*Amynodon advenus* Marsh, 1877.

Revised diagnosis.—Dental formula I 3/3, C 1/1, P 3/3, M 3/3; P_2 large and double rooted; length of upper and lower premolar series approximately one half that of molar series; a distinct labial groove separating trigonid and talonid; P^4 large and submolariform; M^3 metastyle less labially deflected than in more derived amynodonts; M_3 width 49–55% of length; premaxilla well developed in lateral extent, excluding maxilla from border of external nares; frontal sinuses not greatly enlarged as in cadurcodonts; preorbital fossa large, but not extending medial to the orbits; preorbital portion of skull reduced compared to ancestral condition, but longer than in more advanced amynodonts; orbits not elevated on the skull; nasal incision ending above the canine-cheek tooth diastema; skull dolichocephalic, with a relatively narrow occiput.

Discussion.—*Amynodon* is the primitive sister taxon of cadurcodonts and metamynodonts (Text-fig. 1). Thus, many of the characters listed above are primitive within the Amynodontidae (a major exception being the submolariform P^4). *Amynodon* shows advances beyond the basal family stock (represented by AMNH 107635) in: reduced length of the preorbital portion of the skull (approximately 35% of total skull length in *Amynodon,* compared to 42% of total skull length in AMNH 107635); shorter premaxilla-nasal contact; and narrower lower molars (M_3 width ranging from 49 to 55% of length, compared to 58% of length in AMNH 107635). Although the above characters link *Amynodon* with the more advanced members of the Amynodontidae, the cadurcodonts and metamynodonts are further derived in these characters. Because of its taxonomic position, the characters exhibited by *Amynodon* are very important for determining character polarities for the remaining members of the family.

Amynodon is represented by more material than any other amynodontid. My examination of a majority of this material indicates a large size range for members of the genus. Failure to recognize this variation, coupled with the long geologic range of the genus (Uinta A through C), led some early workers to recognize several species, and a separate genus, *Orthocynodon* Scott and Osborn (1882). After reexamination of a skull of *Amynodon,* YPM 11453, Osborn (1890) decided that *Orthocynodon* was not a valid taxon, and designated it a separate species of *Amynodon, A. antiquus.* I believe, on the basis of the morphological criteria discussed above, that the genus

Amynodon is restricted to the Uintan Eocene of North America. The Asiatic material referred to *Amynodon* (see Xu, 1966) should either be placed in *Sharamynodon* Kretzoi, 1942, or listed as Amynodontidae *incertae sedis* (Wall, 1981). The following discussion presents my interpretation of species-level taxonomy in *Amynodon*.

AMYNODON REEDI Stock, 1939

Type.—LACM (CIT) 314/2529, a fragmentary left maxilla.

Type locality.—Poway Conglomerate, San Diego, California.

Revised diagnosis.—A small amynodontid considerably smaller than *Amynodon advenus*; lower cheek teeth more primitive than *A. advenus,* with more distinct labial grooves separating trigonids and talonids, and more lingually directed talonids.

Discussion.—Stock (1939) named *A. reedi* because of its much smaller size compared to *A. advenus,* more primitive cheek teeth, and earlier geologic age. The morphologic size gap between *A. reedi* and *A. advenus* is considerable, and, in the absence of intermediate forms, I believe *A. reedi* is a valid species.

Referred specimens.—Several specimens in the American Museum exhibit characters similar to the type specimen, and are included in *A. reedi.* These are: AMNH 1955, a complete but poorly preserved skull still in matrix, from Uinta B, White River, Utah; AMNH 1936, a partial left maxilla with M^{1-3}, from the same locality as AMNH 1955; and AMNH 2099, a partial mandible from Uinta B, Uinta Basin, Utah.

AMYNODON ADVENUS Marsh, 1877

Diceratherium advenum MARSH, 1875, p. 244.
Orthocynodon antiquus SCOTT AND OSBORN, 1882, p. 223–225; SCOTT AND OSBORN, 1883, p. 3–11, fig. 1, Pl. 5.
Amynodon intermedius OSBORN, 1890, p. 506–512, fig. 2, Pl. 10, fig. 10.
Amynodon erectus TROXELL, 1921, p. 28–33, figs. 3–7.

Type and locality.—YPM 11763, an isolated M^3, Uinta Basin, Utah.

Revised diagnosis.—Medium sized amynodont, the smallest members of which are significantly larger than *Amynodon reedi.* M^3 metaloph directed more posteriorly, and lower molar talonids directed more obliquely than in *A. reedi.*

Discussion.—Part of the confusion in species level taxonomy of *Amynodon* is due to Marsh's (1875, 1877) failure to designate a type specimen. Marsh's (1875) diagnosis of "*Diceratherium advenum*" was based primarily on an M^3 (YPM 11763); however, his diagnosis of *Amynodon advenus* (Marsh, 1877) was based on a skull, YPM 11453. According to Troxell (1921), the M^3 is the type of *A. advenus*; he designated the skull as the type of a new species, *A. erectus.* The characteristics that Troxell used to set off his new species are all quite minor, and fall well within the range of variation for *A. advenus* (see discussion in Wilson and Schiebout, 1981).

The key taxonomic characters which supposedly separate *A. antiquus* (=*Orthocynodon antiquus* Scott and Osborn, 1882) from other species of *Amynodon* are the retention of P^1_1, and possession of a molariform P_4. The presence of P^1_1 was a misconception first stated by Scott and Osborn (1882, 1883), and continued by Osborn (1890). The type, PU 10047, is an incomplete skull and lower jaw. The left P^3 to M^3 are preserved on the skull. The lower jaw is broken posteriorly, and Scott and Osborn (1882) identified the cheek teeth present as P_1 to M_2. I believe these teeth represent P_2 to M_3, and the tooth Scott and Osborn considered a molariform P_4 is really M_1. Wood (1938), in a footnote, stated that *Orthocynodon antiquus* is inseparable from *Amynodon advenus,* but he did not give any reasons for his decision.

Amynodon intermedius has generally been regarded as a valid species due to its larger size and supposedly more recent age than *A. advenus.* Wilson and Schiebout (1981) placed *A. intermedius* in synonymy with *A. advenus.* Their decision was based on variation within a sample of Texas *Amynodon* which fell within the range of variation expected for a single species but which was greater than the variation exhibited by a sample of *A. advenus* and *A. intermedius* from Utah and Wyoming. The statistical analyses presented by Wilson and Schiebout (1981), however, are inaccurate. Many of the values for standard deviation and coefficient of variation presented in their table 5 are wrong. My analysis of *Amynodon* dental measurements shows that a sample of *Amynodon* from various localities (including the type specimens of *A. antiquus, A. erectus,* and

TABLE *1*—Statistical data for upper and lower cheek teeth of *Amynodon advenus,* from Whistler Squat local fauna (using data from table 1 of Wilson and Schiebout, 1981) and various localities in Utah and Wyoming. N = sample size; OR = overall range; M = mean; S = standard deviation; V = coefficient of variation in percent.

| | UPPER TEETH | | | | | | | | | |
| | Whistler Squat local fauna | | | | | Utah and Wyoming | | | | |
	N	OR	M	S	V	N	OR	M	S	V
P^2–M^3	—	—	—	—	—	11	141–187	163.1	14.4	8.83
P^2–P^4	—	—	—	—	—	12	49–66	54.3	5.2	9.5
M^1–M^3	—	—	—	—	—	12	93–131	110.3	11.3	10.23
P^2 L	—	—	—	—	—	10	15–21	16.6	2.0	12.1
W	—	—	—	—	—	10	16–22	18.7	2.2	11.55
P^3 L	—	—	—	—	—	14	17–23	18.8	2.0	10.7
W	—	—	—	—	—	14	23–30	26.1	2.1	8.05
P^4 L	8	19–24	21.5	1.6	7.26	19	20–27	22.4	2.1	9.3
W	8	31–38	33.3	2.5	7.54	19	29–38	33.7	2.9	8.6
M^1 L	6	27–42	34.6	5.7	16.5	15	25–46	33.6	6.2	18.4
W	6	37–45	39.8	2.7	6.83	15	35–44	38.6	2.9	7.4
M^2 L	8	38–45	41.1	3.5	8.62	20	36–50	43.2	4.2	9.6
W	8	43–51	46.4	2.5	5.32	20	36–50	43.1	4.4	10.1
M^3 L	11	32–42	37.3	2.8	7.64	16	34–44	37.6	3.5	9.4
W	9	37–46	42.7	2.8	6.58	16	31–47	39.3	4.8	12.1

| | LOWER TEETH | | | | | | | | | |
| | Whistler Squat local fauna | | | | | Utah and Wyoming | | | | |
	N	OR	M	S	V	N	OR	M	S	V
P_2–M_3	—	—	—	—	—	12	135–169	148.2	11.1	7.47
P_2–P_4	—	—	—	—	—	10	45–52	49.0	2.8	5.69
M_1–M_3	—	—	—	—	—	12	90–117	100.7	7.7	7.63
P_2 L	—	—	—	—	—	7	10–13	11.6	1.4	12.1
W	—	—	—	—	—	7	7–10	8.6	1.0	11.3
P_3 L	7	17–19	18.5	0.6	3.4	12	15–19	16.8	1.9	11.3
W	6	12–13.5	12.8	0.5	3.6	12	9–15	12.2	1.7	13.9
P_4 L	7	20–25	23.0	1.5	6.62	14	18–24	21.2	1.9	8.9
W	7	15–18.5	16.1	1.2	7.51	14	14–19	16.5	1.7	10.54
M_1 L	—	—	—	—	—	16	22–33	27.9	2.6	9.46
W	—	—	—	—	—	16	16–22	19.1	1.8	9.28
M_2 L	8	34–42	38.2	2.5	6.54	17	29–42	34.6	3.3	9.55
W	8	20–25	22.0	1.6	7.36	17	19–25	22.2	1.7	7.8
M_3 L	6	40–48	43.3	2.6	6.1	17	33–43	38.2	2.7	6.9
W	6	20–24	22.9	1.4	6.54	17	18–23	20.4	1.4	6.9

A. intermedius) is more heterogeneous than the single population of *A. advenus* measured by Wilson and Schiebout (1981) from the Whistler Squat local fauna (Table 1).

Wood (1941) believed that *A. advenus* and *A. intermedius* were separated stratigraphically (*A. advenus* from Uinta A and B, and *A. intermedius* from Uinta C). Several specimens from Uinta C, CM 9968 and CM 11960, however, are clearly within the size range of *A. advenus*. Since there is stratigraphic overlap in size, I do not believe the variation presented in Table 1 is high enough to justify species separation for *A. intermedius* on size alone. Osborn's (1890) diagnostic characters of *A. intermedius* are of dubious value. The "P¹" of *A. intermedius,* a character used in his diagnosis of the species, is represented in the type only by a plaster reconstruction. Osborn further stated that the canines are large and semi-procumbent, but in the type, PU 10309, the canines are broken and their original orientation cannot be determined. Variation in canine size can be explained in terms of sexual dimorphism, with the males having larger canines than the females (Wilson and Schiebout, 1981). In the absence of significant differences between the two, I believe *A. intermedius* is a junior synonym of *A. advenus*.

Stock (1933) stated that *Amynodon intermedius* showed the closest approximation in posterior extent to the preorbital fossa in *Amynodontopsis bodei,* and, therefore, *Amynodon intermedius* should be placed in the genus *Amynodontopsis*. Stock based his conclusions on the deep preorbital fossa in the type

skull of *Amynodon intermedius,* PU 10309. However, Stock failed to take into consideration the distortion of the skull. The preorbital fossa on the right side (illustrated by Osborn, 1890, fig. 2) does extend somewhat medial to the orbit, but this is due to crushing. On the left side it does not extend medial to the orbit. I see no justification for placing PU 10309 in *Amynodontopsis.*

MATERIALS

Specimens of *Amynodon advenus* are far too abundant to include a complete hypodigm for this species. The material listed below by locality represents well-preserved and/or complete specimens, or material which is stratigraphically significant: Uinta B, Uinta Basin, Utah, AMNH 1830, partial mandible; Uinta B, White River, Utah, AMNH 1951, nearly complete mandible, AMNH 2011, right mandible with complete set of teeth and left incisors; Uinta B, Wagon Bed Formation, Beaver Divide, Wyoming, AMNH 14601, complete skull with good teeth; Uinta C, Uinta Basin, Utah, AMNH 1960, skull missing skull roof, but with well-preserved cheek teeth, AMNH 1963, mandible with cheek teeth, CM 2360, juvenile mandible, CM 3200, complete skull, but lacking most teeth, CM 9172, ventral portion of skull with well-preserved dentition; Uinta C, White River, Utah, AMNH 1933, nearly complete skeleton, AMNH 1961, complete forelimb; Uinta C, Uinta Co. Utah, CM 35703, ventral portion of skull; Unspecified Uintan, MCZ 5333, complete mandible with well-preserved teeth, FMNH 12184, complete skull with well-preserved dentition, MCZ 8024, complete skull with poorly preserved ventral surface, PU 10047, partial skull and right mandible, PU 10309, palate with well-preserved cheek teeth, YPM 11453, well-preserved skull; Washakie Formation, Haystack Mtns., Wyoming, UCMP 69378, left maxilla with complete set of cheek teeth; Upper Washakie, Washakie Basin, Wyoming, AMNH 13189, nearly complete skull with teeth; Whistler Squat Quarry, Brewster Co., Texas, TMM 41372-71, juvenile mandible, TMM 41372-410, well-preserved basicranium, TMM 41372-416, complete skull, some crushing, TMM 41372-451, complete mandible; Lower Pruett Formation, Agua Fria Ranch, Brewster Co., Texas, TMM 41747-89, complete juvenile skull, TMM 41747-90, juvenile left lower jaw; Pruett
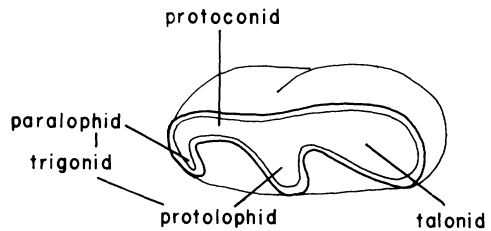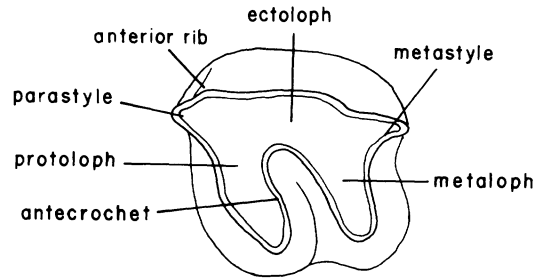

TEXT-FIG. *2*—Diagrammatic representations of upper and lower cheek teeth of *Amynodon,* illustrating the dental terminology used in the text.

Formation, Brewster Co., Texas, TMM 41576-19, complete skull missing premaxilla.

COMPARATIVE MORPHOLOGY

Introduction.—Study of the material listed above provides detailed information on the skeletal and dental anatomy of *Amynodon.* Although specimens have been readily available, a detailed comparison of *Amynodon* to other amynodontids has not been published (see Osborn, 1929, for illustrations of some of the limb elements, and Wilson and Schiebout, 1981, for descriptions of some aspects of cranial and dental anatomy). Because of the relatively primitive position of *Amynodon* within the family, its useful taxonomic characters are also compared with those of selected tapiroids and other rhinocerotoids.

Dentition.—The dental terminology used here is illustrated in Text-fig. 2. Because of its similarity to the dentition of the early tapiroids *Heptodon* and *Hyrachyus,* I believe the dentition of *Amynodon* is primitive, compared to that of cadurcodonts and metamynodonts in the following characters: retention of three pair of large upper and lower incisors; presence of a large, double-rooted P_2; a deep labial groove separating the talonid from the trigonid; broad lower molars; low-crowned cheek teeth; and moderate-sized canines. The den-
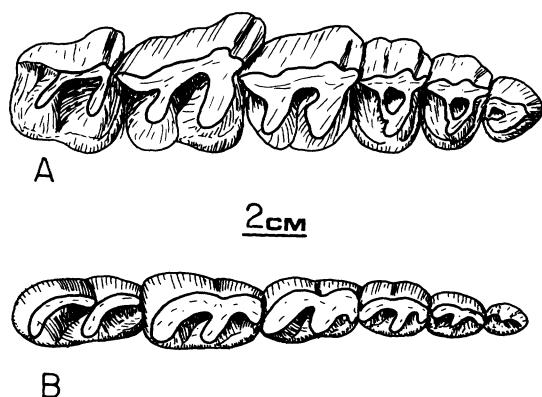
TEXT-FIG. *3*—Dentition of *Amynodon advenus.* A, upper (TMM 41576-19), and B, lower (MCZ 5333).

tition of *Amynodon* is described below in greater detail and illustrated in Text-fig. 3 (for measurements see Table 1).

The anterior cutting teeth of *Amynodon* are basically primitive, differing from the ancestral pattern primarily in the moderate increase in relative size of the canines, and in shape of the incisors. All incisors are retained, and are subequal (in some individuals upper and lower I2 are larger than the other incisors). The incisors are more conical than in *Heptodon* or *Hyrachyus*. *Amynodon* shares this character with the primitive amynodont, AMNH 107635, and with more derived amynodonts. There is generally a short diastema between I³ and the upper canine to accomodate the lower canine. However, a few adult specimens, such as TMM 41372-451, have no diastema, and the lower canine has a large medial wear facet produced by contact with I³. This diastema is probably derived in amynodonts because related taxa (such as *Hyrachyus* and *Hyracodon*) with small canines lack a diastema. A diastema between I³ and the canine is present in the primitive tapiroid *Heptodon* (MCZ 17670) which has moderately large canines. The canines in *Amynodon* are large, semi-erect tusks, but they do not approach the relative size of the canines in metamynodonts. The lower canines shear anterior to the uppers, creating smooth wear facets along the points of contact. The postcanine diastema in *Amynodon* is longer than in cadurcodonts and metamynodonts, but, because of some reduction in snout length, the diastema is reduced

compared to *Hyrachyus, Heptodon,* and the primitive amynodontid AMNH 107635.

The premolars of *Amynodon* are non-molariform, and molarization of the premolars does not occur in amynodontids. The premolar series is only about half the length of the molar series, but it is even less, primarily because of the elongation of molar ectolophs, in more derived taxa. P² is small, and its long axis is oriented posterolingually. A blunt anterior rib is variably developed along the labial side of the ectoloph. The P² protoloph angles sharply posteriorly, and is usually joined posterolingually by a small metaloph. The hypocone is small or absent. P³ is larger, more complex, and its long axis is more transversely oriented than in P². P³ has a large parastyle, distinct anterior rib, and small posterior rib along the ectoloph. The protoloph is higher than in P², and does not angle as sharply posteriorly. The metaloph is small, but, occasionally, it remains separate from the protoloph. A lingual cingulum is generally present. P⁴ is relatively large for an amynodont (P⁴ represents about 42% of total premolar series length in *Amynodon,* whereas, in most other amynodontids, P⁴ is consistently around 37% the length of the premolar series). The *Amynodon* P⁴ has a pronounced parastyle, anterior rib, and a posterior rib more highly developed than on any of the other cheek teeth. The P⁴ metaloph is relatively larger than that of P³, and it generally remains distinct from the protoloph. The protoloph extends far lingually, and, as a result, interrupts the lingual cingulum.

The upper molars of amynodontids are relatively simpler than the corresponding teeth of rhinocerotids. The molars in *Amynodon* lack distinct crista and crochet, while the antecrochet is variably developed (but never as pronounced as in *Amynodontopsis*). M¹ and M² of *Amynodon* are similar except that M² is larger, and M¹ has a better developed antecrochet. The molar parastyles are reduced compared to those of the premolars, but are still relatively larger than in more derived amynodonts. The anterior ectoloph ribs are placed far forward, but are still separate from the parastyles; the posterior ribs are small, but distinct. The ectolophs are long and relatively straight, and there are large metastyles in line with the rest of the ectolophs. M³ is typical of amynodontids in having a large, somewhat labially-deflected metastyle, forming with the

metaloph a border for the large posterior valley. The resulting quadratic outline of M^3 is an important derived character of amynodontids, separating the family from all other rhinocerotoids. The M^3 ectoloph is relatively shorter than that of M^2. Development of cingula on the cheek teeth is highly variable in *Amynodon,* and, thus, should not be used as a taxonomic character.

In *Amynodon* the lower premolar series ranges from 45 to 50% of the length of the lower molar series. P_2 is relatively large for an amynodontid; it is double rooted, but not molariform. In more highly derived amynodontids, P_2 is either greatly reduced (*Sharamynodon*), occasionally present (*Amynodontopsis*), or completely lost (*Sianodon, Cadurcodon,* and all of the metamynodonts). The protoconid forms the major portion of the P_2 in *Amynodon,* but small paralophid, protolophid, and talonid are present. P_3 is much larger than P_2, and is submolariform. The protoconid still forms a major portion of the tooth, but the paralophid, protolophid, and talonid are enlarged. The talonid basin, however, is still small compared to the same structure in P_4. The P_4 is intermediate in size between P_3 and M_1, and is submolariform. Although the protoconid is still large it does not dominate the tooth to the same extent as in P_2 and P_3. The paraconid is well developed, and the trigonid basin is distinct. The talonid and talonid basin are large.

All the lower molars are similar, with M_3 largest and M_1 smallest. The lingual openings of the talonid and trigonid basins are restricted in M_1, but more broadly open in M_2 and M_3. M_3 is relatively narrower than the other molars due to the more oblique orientation of the hypolophid.

In summary, the major dental characters of *Amynodon* are consistent with the evolutionary trends typified by later members of the family, namely: enlargement of the canines; decreased importance of the premolars; and increased emphasis on molar ectoloph shear, with corresponding simplicity of the molar crosslophs. These characters are not exhibited by any other ceratomorph group, and are, therefore, useful for uniting the various taxa within the Amynodontidae.

Cranium, introduction.—A number of well-preserved skulls of *Amynodon* (all regarded by the author as *A. advenus*) are available for study, making this species one of the better known anatomically. Wilson and Schiebout (1981) give a detailed description of an individual skull (TMM 41576-19), and, therefore, I shall present only a general overview of pertinent skull characters here (refer to Text-fig. 4 for comparison with discussion below). This description is based on six specimens, AMNH 1933, AMNH 14601, FMNH 12184, TMM 41372-416, TMM 41576-19, and YPM 11453.

Cranium, lateral view.—The premaxillae are not thickened dorsoventrally, nor fused with each other, as in some cadurcodonts, but they do extend far back laterally below the nasals. The extensive premaxilla-nasal contact in *Amynodon* is a primitive character for amynodonts (only AMNH 107635 has a longer premaxilla-nasal contact than *Amynodon*). All other primitive ceratomorphs, for example, *Heptodon, Hyrachyus,* and *Hyracodon,* have long premaxilla-nasal contacts; therefore the reduction of this contact in advanced cadurcodonts and metamynodonts is a derived condition. The length of the premaxilla-nasal contact is closely correlated with the relative length of the preorbital portion of the skull. A major trend in amynodontid evolution is a shortening of the snout region. The basal amynodontid pattern is seen in AMNH 107635, where the preorbital portion of the skull is 42% of skull length (from the tip of the nasals to the back of the occiput). These same skull proportions are also found in the tapiroids *Heptodon* and *Hyrachyus. Amynodon* exhibits a considerable reduction in snout length (32% of skull length in AMNH 14601, ranging up to 35% in other skulls). Reduced snout length is the major character uniting *Amynodon* with the more advanced cadurcodonts and metamynodonts (Text-fig. 1).

Compared to cadurcodonts and metamynodonts, however, *Amynodon* is primitive in the following characters: the nasal incision ends above the canine-cheek tooth diastema, and is partially roofed by the nasals; the preorbital fossa of *Amynodon* is large, but does not extend medial to the orbit; skull height is not increased as in cadurcodonts; and the orbit is not elevated as in metamynodonts. Another character of taxonomic importance is that the zygomatic arch of *Amynodon* exhibits the primitive condition for size and shape in amy-

5 cm
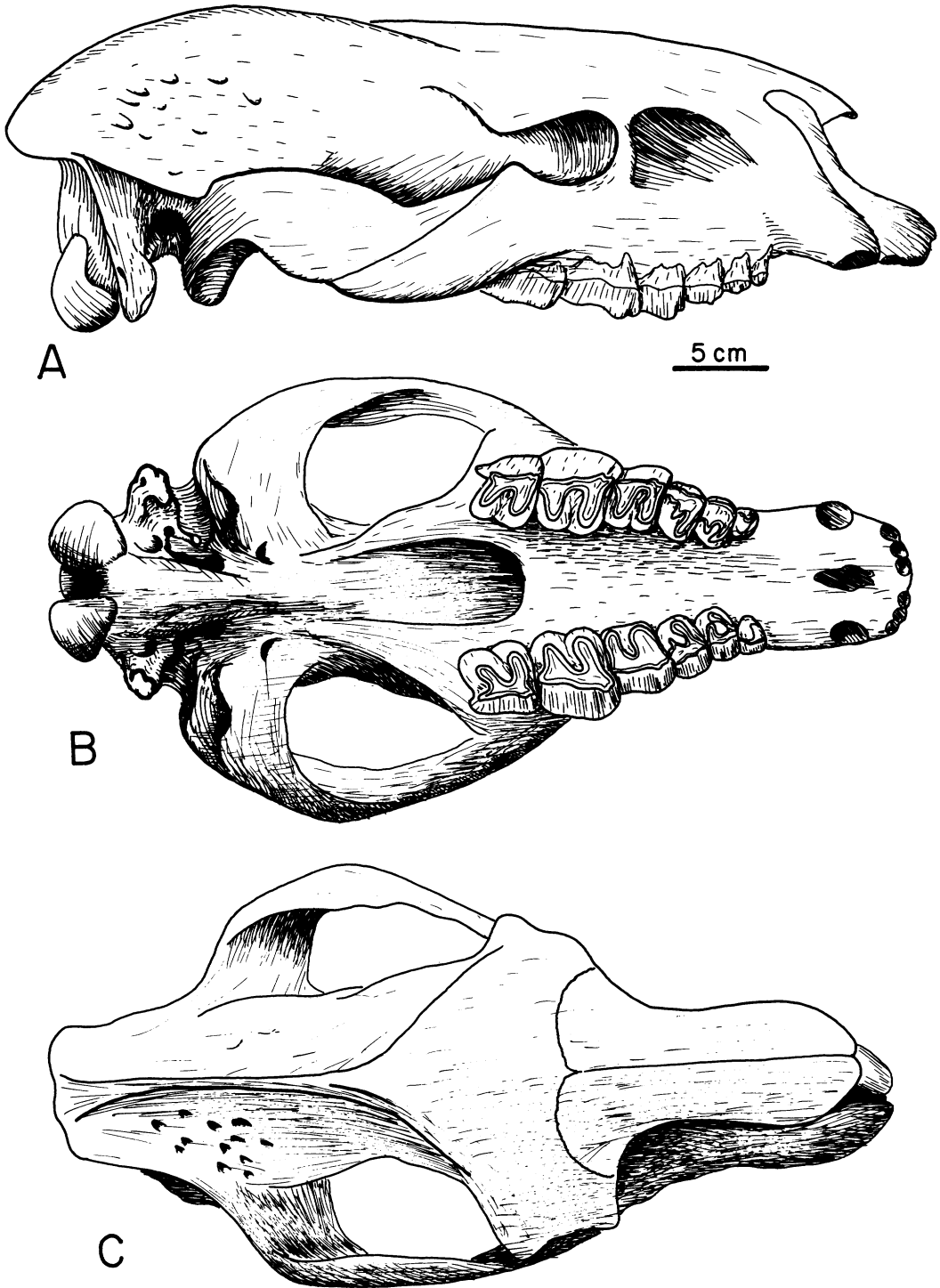
TEXT-FIG. *4—A,* lateral; *B,* ventral; and *C,* dorsal views of restored skull of *Amynodon advenus,* based primarily on AMNH 14601.

nodontids. The zygomatic arch in *Amynodon* either lacks a postorbital process or has only a poorly developed one. Two different derived conditions are found in more advanced amynodontids. In the Asiatic species of *amynodontopsis* (Wall, 1980), the zygomatic arches are reduced in height and thickness. The metamynodonts, on the other hand, all show a tremendous increase in size (in all dimensions) of the zygomatic arch, particularly *Metamynodon*.

Cranium, ventral view.—Amynodon is similar to AMNH 107635 in palatal and basicranial characters. The characters listed here are therefore primitive for the family. The secondary palate of *Amynodon* is moderately concave, and extends back to a point in line with the M^3 protoloph. The pterygoid hamulus is large and solid. The long axis of the glenoid fossa is transversely oriented, and not enlarged. The postglenoid process is angled anteromedially, and bears an articular surface for the mandibular condyle. The external auditory opening is broadly open ventrally. Basicranial foramina are illustrated by Wilson and Schiebout (1981). Cadurcodonts are similar to *Amynodon* with regard to basicranial characters. Metamynodonts, however, have an expanded pterygoid hamulus, and, in advanced forms, such as *Metamynodon,* the external auditory opening is closed ventrally.

Cranium, dorsal view.—Amynodon is moderately dolichocephalic, having a skull width ranging from 49 to 54% of length. Cadurcodonts are even more dolichocephalic, skull width is reduced to only 45 to 50% of length. Because of their wide zygomatic arches, metamynodonts are more brachycephalic, the skull width ranging from 55 to 70% of skull length (*Zaisanamynodon* is the most brachycephalic).

Amynodon exhibits the primitive amynodontid pattern for the following skull characters: the nasal bones are long, rounded anteriorly, and expanded posteriorly where they contact the frontals and lacrimals; there is a distinct postorbital constriction because of the small size of the braincase; the frontals are transversely expanded anteriorly to produce large postorbital processes; numerous nutrient foramina are present in the lateral walls of the braincase; the occiput is relatively narrow; and the sagittal crest is well-developed.

CONCLUSIONS

Amynodon exhibits all of the major characters of the family Amynodontidae (two important ones being the quadratic M^3 and the presence of a preorbital fossa). Because of numerous cranial and dental similarities to primitive ceratomorphs and the basal amynodont stock, *Amynodon* is regarded here as the primitive sister group to later members of the family. Character states in cadurcodonts and metamynodonts are regarded as derived if they show a change from the pattern seen in *Amynodon* (Text-fig. 1).

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