

**ROSTRIAMYNODON GRANGERI** N. GEN., N. SP. OF AMYNODONTID  
(PERISSODACTYLA, RHINOCEROTOIDEA) WITH COMMENTS ON  
THE PHYLOGENETIC HISTORY OF EOCENE AMYNODONTIDAE

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**ABSTRACT**—A new genus and species of amynodontid rhinoceros, *Rostriamynodon grangeri*, from the early Late Eocene of Inner Mongolia, People's Republic of China, is the most primitive amynodontid recognized to date. *Rostriamynodon* exhibits the major diagnostic characteristics of amynodontids: quadratic M<sup>3</sup>, preorbital fossa, and loss of upper and lower P1. It differs from more advanced members of the family in its long preorbital region and lower cheek tooth morphology. Comparisons with other Eocene ceratomorphs show the crucial position *Rostriamynodon* has in determining phylogenetic relationships between rhinocerotoids and tapiroids. Evidence is presented for the monophyly of the Rhinoceroidea, including amynodontids.

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INTRODUCTION

A PRIMITIVE rhinocerotoid from the early Late Eocene of Inner Mongolia, People's Republic of China is herein identified as a new genus of amynodontid. This new taxon provides useful information on the early separation of amynodontids from other rhinocerotoids. Analysis of the anatomical characters of this new taxon is crucial, not only to an understanding of phylogenetic relationships within the Amynodontidae, but also to questions regarding monophyly of the Rhinoceroidea (see Radinsky, 1969).

Preliminary discussion of the phylogenetic position of this new genus was given by Wall (1982a). Using cladistic methodology, Wall tentatively separated the new taxon from other amynodontids at the subfamily level. A formal diagnosis of this new amynodontid subfamily is presented below. The Amynodontinae (as diagnosed by Wall, 1982a) includes all of the remaining amynodontids. Kretzoi (1942) included only *Amyndon*, *Sharamynodon*, and *Amynodontopsis* in the subfamily Amynodontinae, one of four subfamilies he proposed to subdivide the ten genera of amynodontids into as recognized at that time. The subfamily name Amynodontinae, whenever used in this paper, will follow the usage by Wall (1982a). Kretzoi's Metamynodontinae is reduced to the level of a tribe (Metamynodontini). *Paramynodon* is considered to be a primitive member of the Metamynodontini, thus eliminating the

subfamily Paramynodontinae, and Kretzoi's Cadurcotheriinae is regarded as an artificial and taxonomically invalid assemblage of genera (see Wall, 1981).

AMNH refers to the American Museum of Natural History, New York City; IVPP, to the Institute of Vertebrate Paleontology and Paleoanthropology, Peking, China; MCZ, to the Museum of Comparative Zoology, Harvard University, Cambridge; NMNH, to the National Museum of Natural History, Washington, D.C.; and SDSM to the South Dakota School of Mines, Rapid City.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758  
Order PERISSODACTYLA Owen, 1848  
Superfamily RHINOCEROTOIDEA  
Gill, 1872  
Family AMYNODONTIDAE  
Scott and Osborn, 1883  
Subfamily ROSTRIAMYNODONTINAE  
n. subfam.

*Diagnosis.*—That of the type species described below.

Genus ROSTRIAMYNODON n. gen.

*Type species.*—*Rostriamynodon grangeri* n. sp.

*Diagnosis.*—That of the type species described below.

*Etymology.*—*rostri*, snout, referring to the long preorbital portion of the skull, plus *amynodon*.

## ROSTRIAMYNODON GRANGERI n. sp.

Figures 1-3

*Holotype*.—AMNH 107635, complete skull and mandible. Skull slightly crushed dorsoventrally and upper teeth poorly preserved. Lower jaws laterally compressed but contain a relatively complete dentition.

*Type locality*.—"Irdin Manha Beds," 2 miles East of Camp Margetts, Inner Mongolia, People's Republic of China.

*Horizon and age*.—Li and Ting (1983) consider this locality early Late Eocene in age, comparable in time to either the late Bridgerian or early Uintan of North America.

*Etymology*.—In honor of Walter Granger, chief paleontologist for the American Museum Asiatic Expeditions.

*Diagnosis*.—Dental formula 3/3 1/1 3/3 3/3; incisors with well developed lingual cingulum; canines much larger than incisors and within size range of those of *Amyndodon*; long post-canine diastema; P<sub>2</sub> larger than in other amynodontids and double rooted; P<sub>2</sub>–P<sub>4</sub> less than half the length of M<sub>1</sub>–M<sub>3</sub>; lower molars relatively broad transversely for any amynodontid; large labial groove separating molar trigonid and talonid; anterochet absent; large premaxilla, extending far back laterally between the nasal and maxilla; nasal bones very long, anterior end of the nasals rounded and overhanging external nares slightly; nasal incision small, terminating slightly posterior to the canines; preorbital fossa long and shallow, not extending medial to the orbits; preorbital portion of the skull long; anterior border of the orbit above the anterior end of M<sup>3</sup>; orbits are not elevated on the skull as in metamynodontines; lacrimal bone smooth; external auditory meatus open ventrally; secondary palate slightly concave; occiput narrow; braincase small; infraorbital foramen long but small in diameter; nasal-lacrimal contact present.

*Affinities*.—The quadratic shape of M<sup>3</sup>, loss of upper and lower P<sub>1</sub>, enlargement of the canines, well developed metalophids, and presence of a preorbital fossa are derived characters which place *Rostriamynodon* firmly in the family Amyndontidae. *Rostriamynodon* is primitive in almost all other regards. The early geologic age and primitive nature of *Rostriamynodon* make it an important intermediate form which is useful in

analysis of out-group comparisons for amynodontids. In Wall's cladistic analysis, the subfamily Rostriamynodontinae is the sister group to all other amynodontids. As such, *Rostriamynodon* is also of great value in determining superfamily level relationships for the family. Dental and cranial characters of *Rostriamynodon* will be compared to those of primitive ceratomorphs and other amynodontids to help determine character polarities for more advanced rhinocerotoids.

*Dental characters*.—Three pairs of incisor alveoli are present on the premaxillae (see Figure 1.1) but only the right I<sup>3</sup> is preserved. The I<sup>3</sup> of *Rostriamynodon* has a simple, conical shape, probably a derived condition, compared to the spatulate incisors of *Hep- todon* and *Hyrachyus*. The three pairs of incisors of *Rostriamynodon* radiate backward from the anterior tip of the premaxilla in a manner similar to that in primitive tapiroids. In comparison, the tip of the premaxilla in *Amyndodon* is blunt and the incisors have a more transverse orientation (Wall, 1982b). Based on the size of the incisor alveoli, I<sup>2</sup> was the largest of the three upper incisors. There is a small diastema between I<sup>3</sup> and the upper canine. The lower incisors are better preserved (right and left I<sub>2</sub> and I<sub>3</sub> present) than the uppers (see Figure 1.2). The lower incisors of *Rostriamynodon* are similar to those of *Amyndodon*. I<sub>2</sub> is probably the largest of the three. The lower incisors are spatulate, possess a well developed internal cingulum, and are semiproclumbent. There is no diastema between I<sub>3</sub> and the lower canine.

The upper canines are not preserved but the size of the alveoli indicates that the canines were significantly larger than the incisors. The lower canines are round and stand semierect. There is a well marked wear surface on the posterior border of the canine where the lower canine sheared anterior to the upper, fitting into the diastema between I<sup>3</sup> and the upper canine. A similar situation is seen in the primitive tapiroid *Hep- todon* (MCZ 17670), which had moderately large canines (see Radinsky, 1965). The canines of *Hyrachyus* (NMNH 26309) are only slightly larger than the incisors and there is no diastema between I<sup>3</sup> and the canine (also see Wood, 1934). This same condition is also found in *Hyracodon* and therefore may represent a shared derived character for these

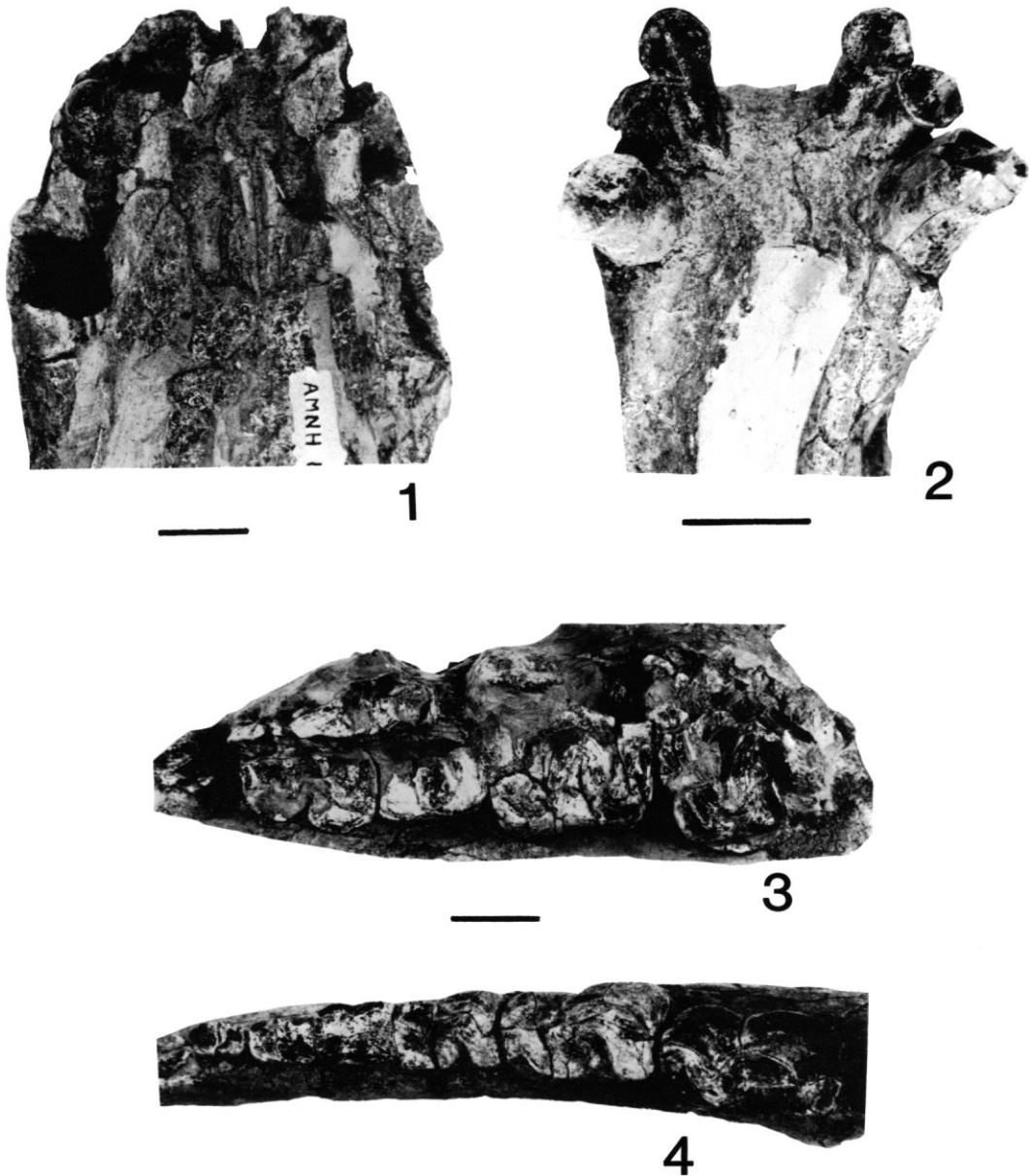


FIGURE 1—*Rostriamynodon grangeri* n. gen., n. sp. 1, ventral view of premaxilla; 2, dorsal view of mandibular symphysis; 3, upper cheek teeth on left side; 4, lower cheek teeth on right side. AMNH 107635. Line equals 2 cm.

two genera. There is a long post-canine diastema on both the upper and lower jaws in *Rostriamynodon*, *Hyrachyus*, *Forstercooperia*, and *Heptodon*, associated with the long preorbital region in all four genera.

Upper and lower P1 are absent in *Rostriamynodon*, a derived condition which separates this genus from other primitive large

ceratomorphs such as *Forstercooperia* (see Lucas et al., 1981). The remaining upper premolars are shortened anteroposteriorly, P<sup>4</sup> having a transverse width over length ratio of 1.7, and the upper premolars are not molariform. The lower premolars exhibit the primitive condition for amynodontids, in the retention of a double rooted P<sub>2</sub>. The sub-

TABLE 1—Dental and cranial measurements (in mm) of various amynodontids. Measurements for individual teeth include width and length (W/L). NA = normally absent; TR = tooth row; CT = cheek teeth.

Taxon	TR	CT	P2	P3	P4	M1	M2	M3	Skull length	Skull width	Snout length
<i>Rostriamynodon</i>											
AMNH 107635											
Uppers	311	172	15/15	28/18	34/20	38/26	46/44	52/47	560	275	241
Lowers	245	159	10/14	13/17	18/20	21/26	26/39	25/43			
<i>Amynodon</i>											
Uppers (AMNH 14601)	235	152		25/17	31/21	35/31	41/41	37/34	459	227	189
Lowers (MCZ 5333)	225	155	10/11	15/18	19/23	22/30	23/35	20/38			
<i>Cadurcodon</i>											
AMNH 26029											
Uppers	250	183	23/20	34/23	43/26	47/34	49/47	48/42	460		172
Lowers	257	171	NA	16/23	22/27	24/35	25/39	23/44			
<i>Metamynodon</i>											
Uppers (SDSM 3645)	310	205	22/16	33/19	46/26	60/37	63/58	61/58	543	305	170
Lowers (AMNH 1100)	297	205	NA	15/21	23/31	27/45	35/59	32/65			

molariform P<sub>4</sub> is an advancement from the primitive ceratomorph condition and is typical of amynodontids.

The molars of *Rostriamynodon* show the basic amynodontid pattern, but in general are primitive. The ectoloph on M<sup>2</sup> is not elongate (as compared to more advanced amynodontids) but the cross lophs are relatively shorter than in *Hyrachyus*, giving this tooth a square appearance (see Figure 1.3). The ectoloph rib is present (even though molars are well worn indicating that the unworn rib was large) and positioned relatively far posteriorly on the ectoloph (a primitive condition which is also found in *Hyrachyus* and *Forstercooperia*). The parastyle of *Rostriamynodon* is large for an amynodontid, but is small compared to the well-developed parastyle of *Hyrachyus*. The cross lophs on the upper molars are approximately equal in size and the edges are smooth.

The lower molars are broad in comparison to those of later amynodontids. *Rostriamynodon* has an M<sub>3</sub> W/L ratio of 58% compared to a maximum of 52% for *Amynodon*. The greater transverse breadth of M<sub>3</sub> in *Rostriamynodon* compared to *Amynodon* is clearly a primitive character since six specimens of *Hyracodon* showed an M<sub>3</sub> ratio of 57–68% and six specimens of *Hyrachyus* had a range of 60–75%. The trigonid and talonid on the lower molars of AMNH 107635 have rounded labial margins, and the cross lophs angle more sharply lingually than in *Amynodon* (see Figure 1.4 and Wall, 1982b). The external groove at the junction of the trigonid and

talonid is large for an amynodontid but is reduced compared to other rhinocerotoids. The molar metalophids are relatively higher than in other primitive rhinocerotoids such as *Forstercooperia* (see figures in Lucas et al., 1981).

In summary, dental characters clearly indicate that *Rostriamynodon* is an amynodontid. More importantly, this genus shows the primitive dental pattern from which later amynodontid dentitions were derived. Comparative measurements are provided in Table 1.

*Cranial characters.*—The preorbital portion of the skull of *Rostriamynodon* contains the most significant diagnostic characters. The preorbital region of AMNH 107635 (see Figure 2.1, 2.3, Table 1) is long for an amynodontid (approximately 42% of skull length measured from the tip of the nasals to the back of the occiput). The preorbital region of AMNH 14601, one of the best preserved skulls of *Amynodon* known, is only 32% of entire skull length. *Paramynodon*, an amynodontid considered by Colbert (1938) to have had a long snout, has a preorbital region that is only 33% of skull length (based on a reconstruction by Colbert, 1938). The preorbital regions of the Oligocene amynodontids *Amynodontopsis*, *Cadurcodon*, and *Metamynodon* are only about 20% of total skull length. The skull of the early Eocene ceratomorph *Hyrachyus* (AMNH 12364) has a preorbital region which is 42% of skull length. The skull of *Heptodon* (MCZ 17670) figured

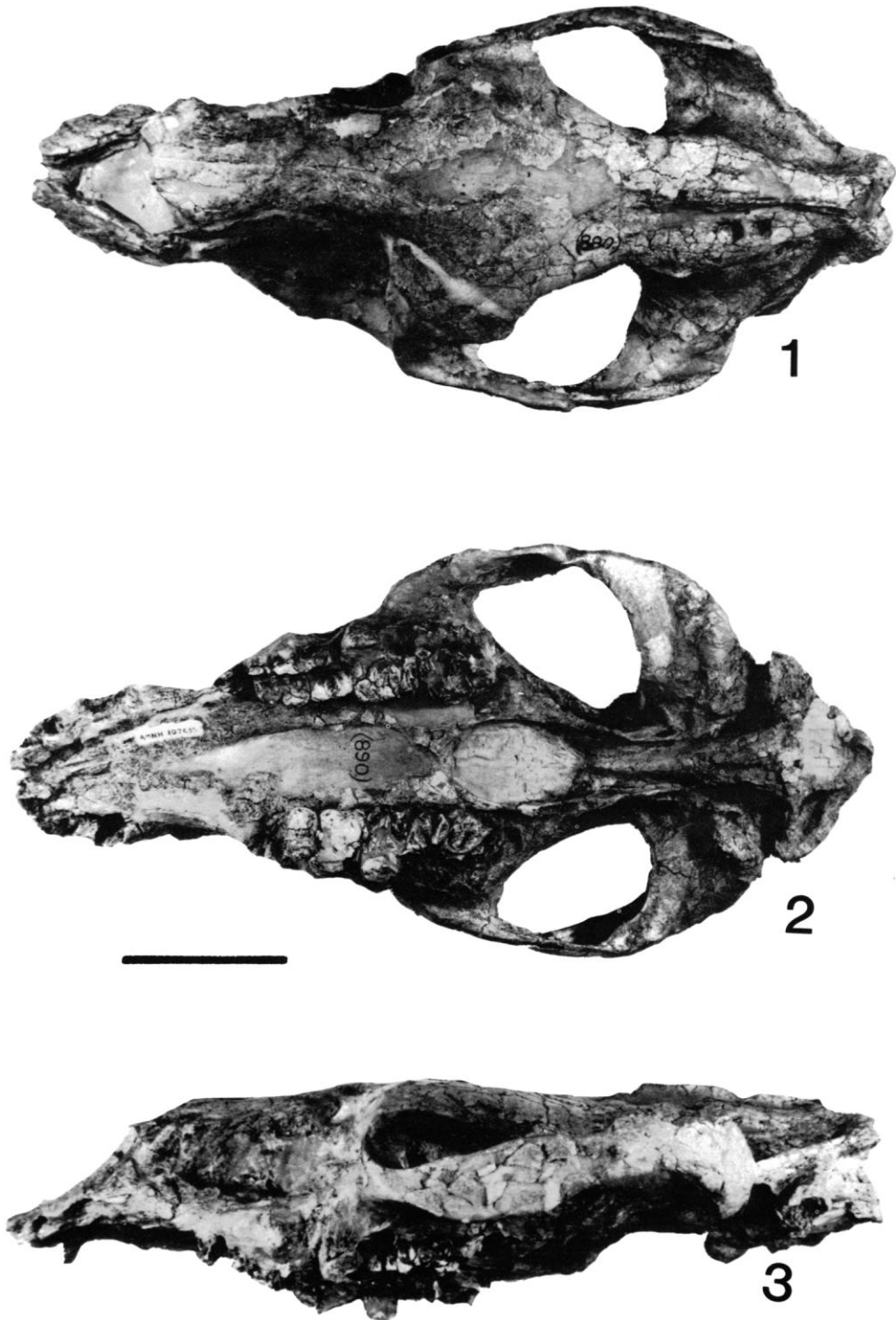


FIGURE 2—*Rostriamynodon grangeri* n. gen., n. sp. 1, dorsal; 2, ventral; and, 3, lateral views of skull. AMNH 107635. Line equals 10 cm.



FIGURE 3—*Rostriamynodon grangeri* n. gen., n. sp. Right lower jaw. AMNH 107635. Line equals 10 cm.

by Radinsky (1965) has a preorbital region 43% of skull length. The preorbital length of *Forstercooperia* (AMNH 26643), one of the earliest hyracodontids, is 43% of skull length. The close similarity of skull proportions in AMNH 107635 to those of primitive ceratomorphs strongly suggests that the long preorbital region of *Rostriamynodon* is a primitive character.

Several other traits are correlated with the long snout region of *Rostriamynodon*. First, the premaxilla is very broad laterally below the nasals, excluding the maxilla from the border of the external nares. The posterior extent of the premaxilla is reduced in all other amynodontids as a consequence of the posterior expansion of the nasal incision (Wall, 1980). Second, the nasal bone of *Rostriamynodon* is very long, 44% of skull length. In *Amynodon* (AMNH 14601) the nasals represented only 38% of skull length. The nasal bones of *Heptodon* are approximately 44% of the length of the entire skull, again suggesting that *Rostriamynodon* is primitive in this regard.

The preorbital fossa of *Rostriamynodon* is large, but due to the great length of the snout region it does not extend medial to the orbits. The medial expansion of the preorbital fossa in cadurcodontines therefore must be a derived character.

The infraorbital canal is long in *Forster-*

*cooperia*, *Hyrachyus*, and *Heptodon*, and the same is true of *Rostriamynodon*. The infraorbital canal in other amynodontids is shortened to a variable extent in conjunction with the shortening of the preorbital region. The small diameter of the infraorbital canal in *Rostriamynodon* is another primitive character which may be associated with the unspecialized snout region of this genus. *Cadurcodon* had a large infraorbital canal, probably to allow for the passage of a complex infraorbital artery and nerve out to the region of the proboscis.

The nasal incision in *Rostriamynodon* is small compared to that of some of the later amynodontids, particularly *Cadurcodon*. The small size of the nasal incision and the lack of strong snout muscle attachment sites on the lacrimal suggest that *Rostriamynodon* did not have a proboscis or a prehensile upper lip (Wall, 1980).

In summary, the skull of *Rostriamynodon* is typical of the early ceratomorph pattern. In particular, it is very similar in appearance to *Forstercooperia*, but it does show specializations toward the amynodontid pattern lacking in other early ceratomorphs.

**Mandible.**—The lower jaw of *Rostriamynodon* (Figure 3) is typical of the early ceratomorph pattern. Two characteristics are of systematic, and probably biomechanical, significance. First, the angle of the jaw is clearly

distinguished from the ventral border of the ramus. *Rostriamynodon* is comparable to *Forstercooperia*, *Hyrachyus*, and *Amyndodon* in this regard. Cadurcodonts reduce the angle of the jaw to the point that it is level with the ventral border of the ramus. In metamynodonts the angle of the jaw is hypertrophied and exhibits well developed muscle scars. The second important character is the transverse thickness of the ramus. *Rostriamynodon* is like *Amyndodon* and the cadurcodonts in having a primitively narrow lower jaw (jaw thickness is only 35–51% of ramus height at  $M_3$ ). The tremendous thickness of metamynodont jaws (jaw thickness up to 83% of ramus height at  $M_3$ ) is clearly a derived characteristic.

#### DISCUSSION

*Review of Eocene Asiatic amynodontids.* — Li and Ting (1983) list one amynodontid species, *Euryodon minimus*, from the Middle Eocene and seven genera with 23 species of amynodontids from the Late Eocene of China. More specifically, two taxa are approximately synchronous in time with *Rostriamynodon*, *Lushiamynodon menchiapuensis* and *Sianodon honanensis*; however, no amynodontids are previously recorded from the Camp Margetts Irudin Manha Fauna. In addition to these, two other genera, *Teilhardia* and *Caenolophus*, require discussion. Radinsky (1969) placed *Teilhardia* and *Caenolophus* in the Amyndontidae based on presumed dental similarities. Li and Ting (1983), however, continue to classify these two genera in the Hyracodontidae. *Teilhardia* (Matthew and Granger, 1926) is known only from a single lower jaw (AMNH 20299), which is not sufficiently different from *Caenolophus* to justify generic separation in our opinion. *Caenolophus* has a large  $M^3$  metastyle, but it is not strongly deflected labially; however, it approaches the amynodontid condition more closely than it does the hyracodontid in which the  $M^3$  metastyle is reduced. Matthew and Granger (1925) never explained why they placed *Caenolophus* in the Hyracodontidae, but probably based taxonomic assignment on the small size of the specimens ( $M^{1-3}$  length of AMNH 20297 is 43 mm). The type of *E. minimus* (Xu et al., 1979) (IVPP 5375), a fragmentary left maxilla with  $M^{2-3}$ , is essen-

tially indistinguishable from *Caenolophus*, making *Euryodon* a junior synonym of *Caenolophus*. The phylogenetic relationships of *Caenolophus* remain uncertain because of the lack of well preserved material. It is believed, however, that *Caenolophus* is anatomically intermediate between amynodontids and more primitive ceratomorphs such as *Hyrachyus*.

The seven genera of amynodontids from the Late Eocene of Asia are: *Gigantamynodon*, *Paramynodon*, ?*Metamynodon*, *Amyndodon*, *Lushiamynodon*, *Sianodon*, and *Huananodon*. A detailed discussion on the status of most of these genera is given by Wall (1981) but a review of that discussion here will help clarify the early radiation of amynodontids.

The type species of *Gigantamynodon* (Gromova, 1954) is based on a left jaw fragment with a partial  $M_3$  from the early or medial Oligocene of Mongolia. Gromova's diagnosis of *Gigantamynodon* is based on the relatively small size of the  $M_3$  relative to other elements (a few isolated upper premolars that are not associated with the type specimen) and the large size of the specimen overall. Her illustration shows that  $M_3$  is broken anteriorly, yet her measurements and ratios are presented as if the tooth were complete. Much of the diagnosis is therefore invalid, leaving only the specimen's large size as a character. Large size immediately suggests *Zaisanamynodon* (Beliajeva, 1971). If *Zaisanamynodon* and *Gigantamynodon* represent the same taxon, then *Zaisanamynodon* would be a junior synonym of *Gigantamynodon* (an unfortunate occurrence considering the poor diagnosis of Gromova's type species). In any event, the specimens referred to *Gigantamynodon* are of a moderately derived metamynodontine comparable to *Zaisanamynodon*.

*Paramynodon* (Matthew, 1929) is a valid taxon showing characteristics that clearly identify it as an early representative of the Metamynodontini. Since the only reference to *Metamynodon* in Asia comes by way of a faunal list without further discussion or illustration by Xu and Chan-Siang (1962), the presence of *Metamynodon* in Asia cannot be confirmed.

We believe that the Asiatic specimens re-

ferred to the genus *Amyrnodon* are more correctly placed in the genus *Sharamynodon* (Kretzoi, 1942), an early representative of the Cadurcodontini (see Wall, 1982a). *Lushiamynodon* is clearly a relatively primitive amynodontid, but the diagnosis provided by Chow and Xu (1965) does not include any distinctive features to justify a separate generic status. We believe that *Lushiamynodon* is inseparable from *Sharamynodon* but until a thorough study of the relevant material can be made we prefer not to synonymize it formally. *Sianodon* (Xu, 1966) is an advanced cadurcodontine and is probably the primitive sister taxon to *Cadurcodon* (see cladogram in Wall, 1982a). *Huananodon* is a poorly known taxon described by You (1977), who recognized two species, *H. hypsodonta* and *H. hui*. Both are based on extremely poor specimens (isolated upper premolars), which are not clearly identifiable as amynodontid. *Rostriamynodon* is distinct from any of these previously mentioned Eocene amynodontids.

Based solely on species numbers it would appear that the radiation of amynodontids during the Eocene was greater in Asia than in North America. The taxonomic difference between the two continents, however, may be more apparent than real. For example, it is not very likely that seven species of *Lushiamynodon* and six species of *Sianodon* coexisted during the Late Eocene in Asia. Each continent contains a relatively primitive form: *Rostriamynodon* in Asia and *Amyrnodon* in North America; cadurcodontines, *Sharamynodon* and *Sianodon* in Asia and *Amyrnodontopsis* in North America; and metamynodontines, *Paramynodon* in Asia and *Megalaminodon* in North America. The validity of several of the Asiatic genera is questionable (systematic revisions of cadurcodontines and metamynodontines are currently under preparation by the senior author). The evidence does indicate, however, that the major adaptive shifts in amynodontid evolution occurred fairly rapidly during the Late Eocene. The early Oligocene amynodontids then diverged gradually with increasing specialization but without any major adaptive shifts.

*Relationships with other rhinocerotoids.*—Family status for amynodontids is solidly based on a series of shared, derived charac-

ters, the most important of which are: quadratic shape of M<sup>3</sup>; loss of upper and lower P1; enlargement of upper and lower canines; elongation of the molar talonids; reduction or loss of the labial groove separating trigonid from talonid; and presence of a preorbital fossa.

Taxonomic assignments within the Rhinoceroidea are very unstable, however. Radinsky (1969) stated that since amynodontids exhibit "divergent dental characters" from other rhinocerotoids, they probably evolved from an independent tapiroid stock. As Radinsky pointed out, several unrelated tapiroids, such as *Lophialetes*, *Lophiodon*, and *Hyrachyus*, approached a rhinocerotoid pattern. For this reason it is conceivable that amynodontids were independently derived from tapiroids and should not therefore be included in the Rhinoceroidea. We believe, however, that evidence is equally strong for deriving all of the rhinocerotoids, including amynodontids, from hyrachyid tapiroids. The upper molar pattern in *Hyrachyus* is sufficiently primitive to allow different selection pressures acting on it to produce both the quadratic M3 of amynodontids and the triangular M3 of other rhinocerotoids (see Wall, 1982a). The lower molars of *Hyrachyus*, however, are more like those of hyracodontids than amynodontids; therefore *Hyrachyus* itself cannot be regarded as ancestral to the entire Rhinoceroidea.

Superfamily placement of the hyrachyids is a crucial question to be answered before the monophyletic status of the Rhinoceroidea can be verified. Since *Hyrachyus* is probably more closely related to hyracodontids than are amynodontids, placement of hyrachyids in the Tapiroidea would invalidate inclusion of amynodontids in the Rhinoceroidea. Inclusion of hyrachyids within the Rhinoceroidea would solve this problem, but Radinsky (1966) has argued against this interpretation. A thorough reexamination of helaetid tapiroids, hyrachyids, and hyracodontids is necessary to solve the problem, but that goes far beyond the scope of this work. At present, monophyly of the Rhinoceroidea, including the amynodontids, can be based on the following possibly shared derived characters: reduction in size of molar parastyle; increased height of the paralophid



and metalophid on the lower molars; and presence of an elongate, flat metacone on M<sup>1</sup> and M<sup>2</sup>.

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*Note.*—The opinions on the phylogenetic relationships of *Caenolophus* and *Hyrachyus* presented in the discussion are those of the senior author alone.