

CRANIAL EVIDENCE FOR A PROBOSCIS IN *CADURCODON*
AND A REVIEW OF SNOUT STRUCTURE IN THE
FAMILY AMYNODONTIDAE (PERISSODACTYLA,
RHINOCEROTOIDEA)

WILLIAM P. WALL

Department of Zoology, University of Massachusetts, Amherst 01003

ABSTRACT—A detailed comparison of the skulls of *Cadurcodon* (Rhinoceroidea, Arynodontidae) and a recent tapir (*Tapirus pinchaque*) presents strong evidence for the existence of a proboscis in the Oligocene amynodont. A review of other fossil mammals (*Astrapotherium*, *Palaeomastodon*, *Brachycrus*, and *Macrauchenia*) shows the range of variation among probable proboscis bearers and suggests that the key characters indicating a proboscis are the reduction of the nasals, the expansion of the nasal incision, and the presence of large snout muscle scars.

Six genera of amynodonts displaying a range from primitive, intermediate, to advanced grades with regard to snout structure, are described. These grades show a good correlation with the stratigraphic history of the family. The primitive square-lipped pattern is exhibited by AMNH 107635 from the late Eocene of Mongolia. *Sharamynodon* was an early intermediate form which may have had a prehensile upper lip. Two Oligocene genera, *Arynodontopsis* and *Cadurcodon*, represent the line of derived amynodonts which probably had a tapir-like proboscis. The second derived group, the metamynodonts, diverged along a separate adaptive line but retained the prehensile upper lip developed in the intermediate common ancestor of both groups.

INTRODUCTION

THE AMYNODONTS were a group of rhinoceroses which flourished during the mid-Eocene to mid-Oligocene in Asia and North America, reaching Europe during the Oligocene. The known morphologic diversity of Asian amynodonts is greater than the range exhibited by the much more thoroughly collected North American taxa. In spite of this fact, much of the information used to describe the life habits of amynodonts up to the present time has been derived from the two common North American genera, *Arynodon* and *Metamynodon*.

The excellent Asiatic collection at the American Museum of Natural History in New York (AMNH) has provided the major source for my work on functional interpretations of amynodont skeletal structure. This paper deals specifically with cranial modifications of the snout region related to the development of a prehensile upper lip or a proboscis in amynodonts.

An important early contribution to the study of the facial region of amynodonts was by Osborn (1898), who was the first to note the reduced length of the nasals in amynodonts as evidence for either a prehensile upper lip similar to that of tapirs, or a proboscis. Osborn's application of these two terms is different from

that in current usage. I define a prehensile upper lip as an enlarged movable lip which is adapted for seizing or grasping food but does not drastically change the position of the nostrils. The African Black Rhinoceros (*Diceros bicornis*) and the giraffe (*Giraffa camelopardalis*) are examples of recent mammals with prehensile upper lips. A proboscis is a more extreme development of the upper lip, resulting in a long, flexible snout with the nostril opening at its distal end. The best known case of proboscis development is found in the Elephantidae, where the snout forms a long trunk. The several species of tapir, however, present a much better example of the type of proboscis referred to in this paper.

Troxell (1921) suggested that *Metamynodon* probably had a prehensile upper lip, basing his conclusion on the shape of the nasal opening, the large infraorbital canals, and the roughened supraorbital ridge. Troxell also believed that the well developed preorbital fossa, a family characteristic of amynodonts, accommodated the enlarged snout musculature. Gregory (1920a), however, showed that the proboscis musculature of both tapirs and elephants is superficial in position (the function of the preorbital fossa in amynodonts will be discussed in a future paper).

Gromova (1954) believed that some advanced amynodonts may have had a proboscis but she did not discuss the skull adaptations correlated with the presence of such a structure. Also, her reconstruction of *Cadurcodon* does not include a proboscis.

The purpose of this paper is to examine in detail the evidence for a proboscis in one advanced line of amynodonts and to trace the evolutionary history of snout structure in the family Aynodontidae.

SYSTEMATICS

Because of the questionable status of some of the amynodont genera used in this study (see Radinsky, 1969), a brief explanation of the taxonomic arrangement followed in this paper is necessary. A thorough systematic revision of the Aynodontidae is now being prepared by the author.

AMNH 107635 represents a new genus of amynodont to be described and named elsewhere. This specimen, represented by a complete skull and lower jaws, is the most primitive amynodont known. The unusually long preorbital portion of the skull and the primitive state of the dentition set it apart from all other amynodonts.

Kretzoi (1942) believed that the species *Cadurcotherium ardynense* (Osborn, 1923) and *Aynodon mongoliensis* (Osborn, 1936) did not belong in the genera Osborn put them in. Kretzoi proposed the names *Cadurcodon ardynense* and *Sharamynodon mongoliensis* for these two Asian amynodonts. Although neither genus has received total acceptance, I believe both *Cadurcodon* and *Sharamynodon* are valid taxa. In addition a previously undescribed skull used in this study, AMNH 26041, from early Oligocene deposits in Mongolia, is referred to the North American late Eocene genus, *Aynodontopsis*, described by Stock (1933).

None of the currently recognized specimens of *Megalamynodon* (see Wood, 1945) from the upper Eocene Duchesne River Formation include the facial region of the skull. Therefore a reconstruction of the snout of *Megalamynodon* cannot be accomplished at this time.

For the purpose of this paper the amynodonts described above can be subdivided into three groups: "primitives," including AMNH 107635, *Aynodon*, and *Sharamynodon*; cad-

urcodonts, composed of *Aynodontopsis* and *Cadurcodon*; and metamynodonts, which includes *Metamynodon* and *Zaisanamynodon*.

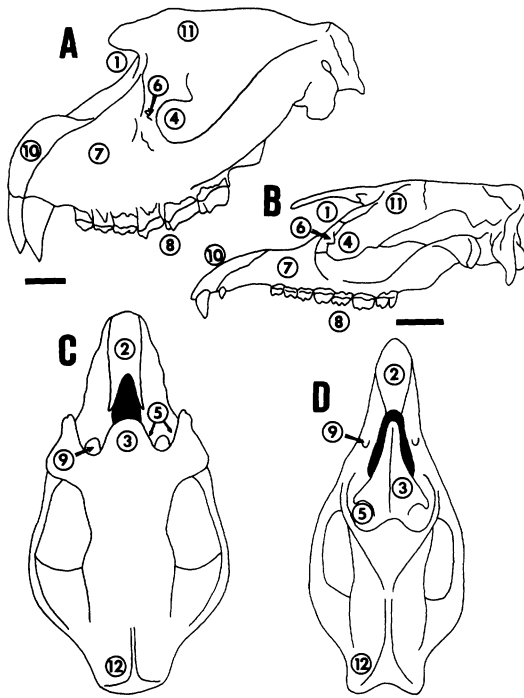
BIOSTRATIGRAPHIC CORRELATION

All of the taxa used in this paper to depict the evolutionary stages of proboscis development are from Mongolia, collected during the 1920's by the American Museum Central Asiatic Expeditions under the directorship of Mr. Roy Chapman Andrews. North American genera are correlated with the evolutionary sequence of the Mongolian forms to produce a complete picture of snout development in the Aynodontidae.

The various stages of amynodont proboscis development compare favorably with the geologic occurrence of the taxa. Therefore a brief review of the amynodont-bearing strata worked by the American Museum Expeditions in Mongolia is necessary (for a more detailed study of pertinent Mongolian geology, including locality maps, see Berkeley and Morris, 1927, and Radinsky, 1964).

The oldest amynodont bearing beds in Mongolia are in the Camp Margetts Region. The lower deposits at Camp Margetts have been weakly correlated with the type locality of the Irdin Manha Formation, but Radinsky (1964) believed that the "Irdin Manha" strata at Camp Margetts might be comparable in age to the Arshanto Formation which he considered to be early late Eocene and older than the type Irdin Manha. According to Romer (1966) the "Arshantan Age" is equivalent to the North American Bridgerian. AMNH 107635 and several specimens of an undetermined amynodont were collected in the "Irdin Manha" beds at Camp Margetts. A biostratigraphic correlation with the Bridgerian would suggest that the "primitive amynodont" (AMNH 107635) is older than *Aynodon* from the North American Uinta Formation (an age which is in agreement with the more highly derived characteristics of *Aynodon*).

The Shara Murun Formation is a highly fossiliferous clay exposed at three localities visited by the American Museum Expeditions. The Shara Murun Formation is very late Eocene in age and is probably temporally more recent than the "Irdin Manha" beds just described (Radinsky, 1964). *Sharamynodon* is



TEXT-FIG. 1.—A, C, lateral and dorsal views of the skulls of *Cadurcodon* (AMNH 26029), right side restored. B, D, *Tapirus pinchaque*. Proboscis characters common to both taxa are indicated by circled numbers which are described in the text. External nares indicated by shading. Skull of *Tapirus* modified from Hatcher (1896). Scale lines equal 5 cm.

the best known amynodont from this formation.

The Ulan Gochu Formation, early Oligocene in age, contains the greatest diversity of amynodonts known. The amynodont taxa from the Ulan Gochu in the American Museum collection are: *Amyndontopsis*, *Cadurcodon*, *Zaisanamynodon*?, and several undescribed metamynodonts. The Ardyn Obo Formation (see map in M. Coombs, 1978) has a fauna similar to that of the Ulan Gochu (see Dawson, 1968, and M. Coombs, 1978). The occurrence of *Cadurcodon ardynense* in the Ardyn Obo Formation and two closely related species (undescribed) from the Ulan Gochu Formation adds to this correlation.

The Oligocene strata above the level of the Ulan Gochu Formation are poorly understood at the present time. At Baron Sog Mesa a thin band of white clays (Baron Sog Beds) rests on

top of the red clays of the Ulan Gochu Formation. At Camp Margetts the "Irdin Manha" clays are unconformably overlain by a sandstone labeled "Houldjin Beds" (Radinsky, 1964). Both the Baron Sog and the "Houldjin Beds" exhibit a great reduction in diversity of amynodont taxa. A large metamynodont (possibly *Zaisanamynodon*) was the only amynodont collected by the American Museum in these two deposits.

DISCUSSION

General.—The amynodont genus exhibiting the greatest number of cranial specializations associated with a proboscis is *Cadurcodon*. The best example of such specializations among the three species of *Cadurcodon* is found in the skull, AMNH 26029, one of the two undescribed species of *Cadurcodon* from the Ulan Gochu Formation. Text-figure 1 shows a comparison of AMNH 26029 (Text-fig. 1A, C) with the skull of a recent tapir, *Tapirus pinchaque* (Text-fig. 1B, D). The general shape of the two skulls suggests a similarity in function. One obvious difference between the two genera is the greater length of the diastema in *Tapirus* compared to *Cadurcodon*. The reduced diastema in the amynodont may be correlated with the large size of the canines (see Gromova, 1954).

A detailed analysis of the skulls of *Tapirus* and *Cadurcodon* resulted in the identification of twelve cranial characters related to proboscis function which are present in both genera. The locations of these characters are indicated by circled numbers in Text-fig. 1. They are: 1, the posterior enlargement and expansion of the nasal incision back to the level of the orbit; 2, loss of the ascending process of the premaxilla and its contact with the nasal, resulting in the incorporation of a portion of the maxilla along the border of the external nares; 3, reduction in length of the nasal bone; 4, posterior displacement of the cribriform plate and the turbinal bone (compared to more primitive related taxa) to a position medial to the orbit; 5, development of a lateral concavity on the maxilla medial to the orbit to house the displaced nasal diverticulum; 6, presence of bony knobs on the lacrimal for muscle attachment; 7, reduction in overall length of the preorbital part of the skull; 8, anterior shift of the orbit relative to the cheek teeth; 9, increased di-

ameter of the infraorbital canal; 10, vertical thickening and fusion of premaxillae; 11, presence of an enlarged frontal sinus; and 12, increased width of the occipital region correlated with the development of strong neck musculature.

The first five characters provide space for and allow for the free movement of the proboscis. Radinsky (1965) associated the presence of these five characters in the skull of *Tapirus* with the evolution of the proboscis. The loss of the ascending process of the premaxilla is directly related to the backward expansion of the nasal incision. The reduction in the size of the nasals in *Cadurcodon* is extensive, but a small naso-lacrimal contact is maintained (contact between the nasal and lacrimal is a primitive character for perissodactyls; see Gregory, 1920b). The nasal bones of AMNH 26029 are extremely thick and would have provided a solid base for the proboscis. The naso-lacrimal suture is lost in *Tapirus*, resulting in a contact between the frontal and the maxilla (a derived character which may be useful in tapiroid systematics). The posterior displacement of the cribriform plate and the turbinal bone is associated with the reduction of the facial portion of the skull, but it also has the effect of removing any hindrance to free movement of the proboscis. The nasal diverticulum of mammals lacking a proboscis is usually positioned within the border of the nasal incision (see Gregory, 1920a, for a discussion on some of the exceptions to this generalization). Displacement of the nasal diverticulum into a dorsal groove on either side of the nasal bones in *Tapirus* was correlated with development of the proboscis (see Radinsky, 1965). The preorbital fossa is very well-developed in *Cadurcodon* and extends well medial to the orbit (see number 5 in Text-fig. 1C). Gregory (1920a) believed that the preorbital fossa housed the nasal diverticulum in amynodonts. If this is true, the nasal diverticula of *Cadurcodon* would not have interfered with proboscis movement.

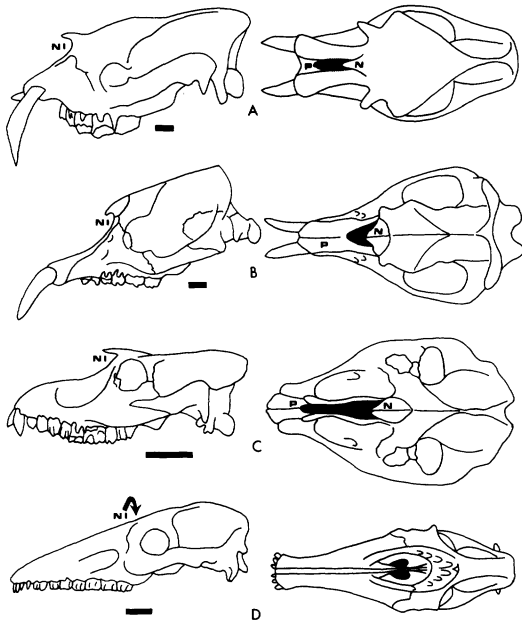
Characters six through eight suggest the presence of well-developed proboscis musculature in both genera. The large bony knobs on the anterior border of the orbit in *Cadurcodon* were the probable site of origin for two of the proboscis muscles, the nasolabialis and the maxillolabialis superior. A third proboscis

muscle, the maxillolabialis inferior, most likely had its origin along the anterior border of the zygomatic arch just below the orbit (reconstruction of proboscis musculature is based on Gregory, 1929). The reduced preorbital portion of the skull and the anterior shift of the orbits both served to reorient the line of action of the proboscis musculature, thereby creating a greater vertical component for these muscles in raising the proboscis. The anterior placement of the orbits also allows for the expansion of the masseter origin on the zygomatic arch over more of the tooth row, thus improving the mechanical advantage of this jaw muscle.

The large diameter of the infraorbital canal, particularly in *Cadurcodon*, allows for the passage of a large infraorbital artery and nerve. The infraorbital artery supplies the nose and upper lip. The infraorbital nerve sends sensory fibers to the integument, the vibrissae of the upper lip, and to the sides of the nose. The increased complexity of a proboscis, and its function as a sensitive tactile organ probably brought about an increase in the size of the infraorbital artery and nerve and therefore of the canal itself.

The retention of functional upper incisors and canines resulted in the thickening and fusion of the premaxillae to compensate for strength lost in the enlargement of the nasal incision. The premaxillae of *Cadurcodon* (Text-fig. 1A) are especially thick due to the large size of the canines. The expanded cerebrum of the recent tapir led to changes in brain proportions from *Heptodon* to *Tapirus* which resulted in development of enlarged frontal sinuses in the modern tapir elevating the nasal bones, and increasing the size of the nasal incision (see Radinsky, 1965). The relatively low position of the orbit in *Cadurcodon* is possibly related to the presence of large frontal sinuses in this genus as well (Dr. John Wilson, pers. commun., has found sections of thick spongy bone in the skull roof of some North American amynodonts).

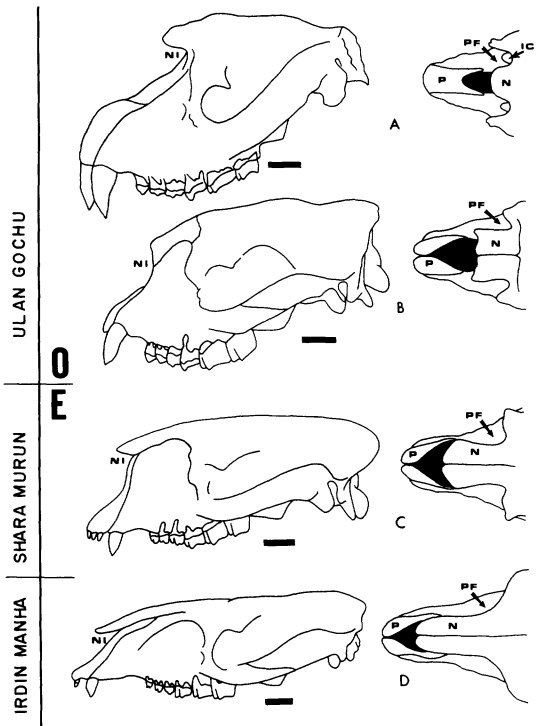
Radinsky (1965) thought that *Tapirus* has more massive neck musculature than *Heptodon* (determined by the greater width of the occipital region in *Tapirus*). He thought the increase in neck musculature was due either to the greater weight of the skull of the recent tapir or to the function of the proboscis. The



TEXT-FIG. 2—Left, lateral and right, dorsal views of skulls of some proboscis bearing fossil mammals. *A*, *Astrapotherium* (after Scott, 1937). *B*, *Palaeomastodon* (after Andrews, 1906). *C*, *Brachycrus* (after Schultz and Falkenback, 1968). *D*, *Macrauchenia* (after W. Coombs, 1975). External nares indicated by shading. Abbreviations: N, nasal; NI, nasal incision; P, premaxilla. The nasals and premaxilla are vestigial in *Macrauchenia*. Scale lines equal 5 cm.

back of the skull of AMNH 26029 is damaged but another specimen of *Cadurcodon*, AMNH 26035, indicates that the width of the lambdoid crest in this genus was relatively greater than in the primitive amynodont, AMNH 107635. Since the skull length of AMNH 26029 (approximately 470 mm) was less than that of AMNH 107635 (560 mm), the contrasting difference in skull widths is significant. It is likely that increased neck musculature added to the usefulness of the proboscis by increasing the maneuverability of the head. An alternative explanation for the increase in size of the neck musculature in *Cadurcodon* is possible if the enlarged canines were used in uprooting tough vegetation (as suggested by Gromova, 1954).

Based on the favorable comparison of the skull of *Cadurcodon* with that of *Tapirus* it is likely that *Cadurcodon* had a short probos-



TEXT-FIG. 3—Structural stages in the evolution of a proboscis in Mongolian representatives of the family Amynodontidae placed in stratigraphic progression. Left, lateral and right, dorsal views of: *A*, *Cadurcodon*; *B*, *Amynodontopsis*; *C*, *Sharamynodon*; and *D*, AMNH 107635 (restored). External nares indicated by shading. Abbreviations: IC, infraorbital canal; N, nasal; NI, nasal incision; P, premaxilla; PF, preorbital fossa. Scale lines equal 5 cm.

cis similar in appearance to that of the recent tapir.

Proboscis development in other fossil mammals.—Amynodonts are just one of several groups of fossil mammals speculated to have developed a proboscis (i.e. astrapotheres, pyrotheres, palaeotheres etc.). Similar cranial structure in these unrelated forms indicates that the acquisition of a proboscis is a strong factor in determining the general shape of the skull. Text-figure 2 illustrates the skulls of some likely proboscis bearing fossil mammals (for others see W. Coombs, 1975). The first two genera, *Astrapotherium* (Text-fig. 2A) and *Palaeomastodon* (Text-fig. 2B) compare most favorably with the pattern seen in *Cadurcodon*

and *Tapirus* above. *Astrapotherium*, a South American ungulate, and *Palaeomastodon*, an early proboscidean, have greatly reduced nasals, enlarged nasal incisions, shortened facial regions, bony knobs on the lacrimal, and enlarged infraorbital canals. The premaxilla in *Palaeomastodon* possesses a thin strip of bone in contact with the nasals, a condition which is retained in more derived proboscideans. The maintenance of a premaxilla-nasal contact in elephants may be associated with the large size of the incisor tusks. The premaxilla of *Astrapotherium* lacks incisors and therefore is greatly reduced (the premaxilla cannot be seen in a lateral view of *Astrapotherium* Text-fig. 2A).

Brachycrus (Text-fig. 2C) was a late Miocene oreodont which, according to Schultz and Falkenbach (1968) had a proboscis. Proboscis characters seen in the skull of *Brachycrus* include an anterior reduction in the length of the nasal bone, a large nasal incision, and a bony knob on the lacrimal. *Brachycrus* differs from the scheme seen in the genera described above in the posterior position of the orbit (see Text-fig. 2C). The long facial portion of the skull (anterior border of the orbit above M^3) may be correlated with the retention of a complete set of complex cheek teeth in *Brachycrus*. Since proboscis musculature originates along the anterior border of the orbit, a long muzzle would significantly decrease the vertical component of these muscles, thus reducing maneuverability of the proboscis. The nasal incision in *Brachycrus* has expanded back to the level of the orbits and the anterior border of the nasals is located above M^2 in *Brachycrus*. This change allows fuller use of the proboscis. Increased thickness of the premaxilla was cited above as a characteristic of *Cadurcodon* and *Tapirus*, but the extreme thickness of the premaxilla and maxilla in *Brachycrus* is difficult to explain since the oreodont does not have enlarged canines or incisors.

Macrauchenia (Text-fig. 2D), a litoptern, exhibits the most aberrant cranial structure of any mammal seriously thought to have had a proboscis. This South American ungulate has a relatively longer preorbital region than *Brachycrus* due to the increased size of the cheek teeth. The posterior placement of the nasal incision and nasal bones, and the presence of large snout muscle scars behind the external

nares are, however, strong indications of the presence of a proboscis in *Macrauchenia*.

Study of the above unrelated taxa indicates that two alternative skull configurations can be developed in association with a proboscis. One configuration, exemplified by *Tapirus* and *Cadurcodon*, has reduced the facial portion of the skull. The reduction in the size and/or number of the premolars (a necessary but not a causative factor) and the enlargement of the incisors or canines into tusks (a probable causative factor) also contribute to the small size of the preorbital region in these animals. The second pattern, best seen in *Macrauchenia*, retains a long muzzle associated with the presence of a complete set of well-developed cheek teeth and the absence of tusks. The reduction in the size of the nasals, the posterior expansion of the nasal incision, and the presence of large snout muscle scars are the key proboscis characteristics which both of these skull types possess.

Proboscis development in the family Amyodontidae.—The Mongolian amynodont taxa exhibit a wide range of snout patterns, some of which can be regarded as primitive, intermediate, and advanced stages in the development of a proboscis. Text-figure 3 illustrates four of these stages placed according to their geologic occurrence.

AMNH 107635 (Text-fig. 3D) is the oldest and least specialized representative in the series. This skull shows the primitive condition from which all of the proboscis characters exhibited by *Cadurcodon* are derived. The long snout region, approximately 40% of the entire skull length (measured from the tip of the nasals to the occiput), is a primitive character which AMNH 107635 shares with *Heptodon*, *Hyrachyus*, and other early perissodactyls. The premaxilla is large and extends far back laterally below the nasals. The nasal bones are long and the nasal incision is small, terminating slightly posterior to the canines. The preorbital fossa is long and shallow but it does not extend medial to the orbits (see dorsal view, Text-fig. 3D). The anterior border of the orbit is relatively far back on the skull (above M^3) and the lacrimal bone lacks any rugosities sufficient for strong muscle attachment. The overall appearance of the facial portion of the skull of AMNH 107635 is reminiscent of the Eocene titanotheres *Manteoceras*, which Greg-

ory (1929) reconstructed with a small, non-protrusible upper lip. The primitive amynodont snout, represented by the Eocene "Irdin Manha" skull, was a very simple structure which displayed none of the proboscis modifications characteristic of some of the Oligocene genera.

Sharamynodon (see Text-fig. 3C), from the late Eocene Shara Murun Formation, is a good example of initial modifications of the snout from the primitive condition. Reduction of the facial region from 40% to 31–34% of total skull length in *Sharamynodon* was the result of two processes: first, the orbit shifted anteriorly to a point above M^2 , and second, the anterior end of the snout was reduced. The small size of the diastema and the thinning of the premaxilla laterally are clear evidence of the backward migration of the external nares. Increased size and usage of the canine tusks appear to be the critical factors influencing the reduction of the face at this stage of amynodont history. The backward expansion of the preorbital fossa, producing shallow concavities anteromedial to the orbits (see Text-fig. 3C), may be due to reduction in the length of the facial region without concurrent reduction in the size and function of the preorbital fossa.

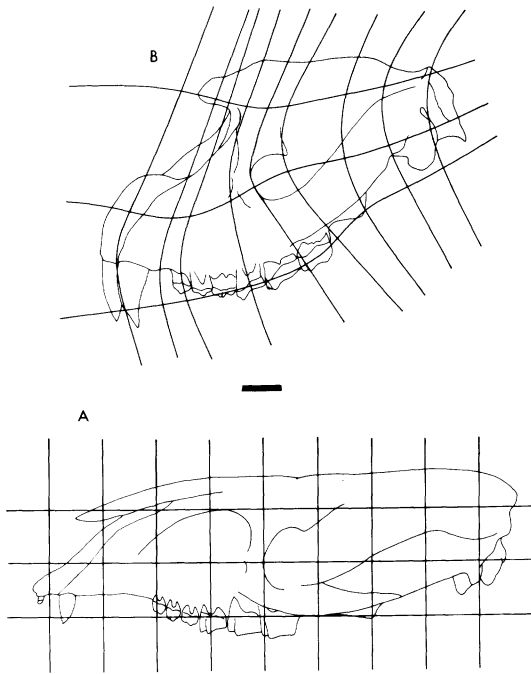
The nasal incision of *Sharamynodon* extends back to a point above the middle of the diastema, which represents an advancement beyond the stage exhibited by AMNH 107635. The lacrimal is more rugose in the Shara Murun genus than it is in the more primitive "Irdin Manha" amynodont, indicating the presence of moderately well-developed snout musculature in *Sharamynodon*. Based on the enlargement of the nasal incision and the rugosity of the lacrimal, *Sharamynodon* probably had a well-developed prehensile upper lip but no proboscis.

Skulls of the North American genus, *Amy-nodon*, from the Uinta Formation (late Eocene) show a reduction in the preorbital region and enlargement of the canines when compared to AMNH 107635 from the "Irdin Manha" beds of Mongolia; but the snout is still less specialized than the condition seen in *Sharamynodon*. Therefore the three species of *Amy-nodon* (*A. reedi*, *A. advenus*, and *A. intermedius* listed in increasing order of complexity) represent transitional grades between the "primitive amynodont" (AMNH 107635) and *Sharamynodon*.

The premaxilla, although greatly reduced laterally compared to AMNH 107635, still contacts the nasal bone in *Amy-nodon* and *Sharamynodon*. A direct connection of the premaxilla with the nasal bone laterally is lost in the next stage of amynodont cranial development (see skull of *Amy-nodontopsis* in Text-fig. 3B). This early Oligocene genus exhibits a tremendous decrease in the length of the face, resulting in the lateral reduction of the premaxilla and a shortening of the diastema. The preorbital region now represents only about 22% of total skull length. The orbit of *Amy-nodontopsis* is still placed above M^2 , the same position attained by *Sharamynodon*; therefore the reduction of the facial region in this genus is due entirely to backward migrations of the nasal incision and the canines. The nasal incision extends back to a point above P^3 and the nasal bones are squared off and reduced anteriorly in the Mongolian representative of *Amy-nodontopsis*. The excavation of the preorbital fossa medial to the orbit is much greater in *Amy-nodontopsis* than in *Sharamynodon* (compare dorsal views, Text-fig. 3B, C). The lacrimal of *Amy-nodontopsis* is highly rugose and the infraorbital canal has a diameter of approximately 20 mm, almost twice that of the infraorbital canal of *Sharamynodon* which is 12 mm (even though the overall skull length of *Amy-nodontopsis* is less than that of *Sharamynodon*). Remnants of the turbinal bones are preserved in one of the Mongolian specimens of *Amy-nodontopsis*, AMNH 26041. In this skull, the turbinals are located far back in the external nares medial to the orbits.

The skull of the type species of *Amy-nodontopsis*, *A. bodei* from North America, shows a higher degree of specialization for a proboscis than the Mongolian species of the same genus. The nasal incision in the North American species extends back to a point above the front of M^1 compared to above P^3 in the Mongolian form. The greater size of the nasal incision in *A. bodei* leaves the nasal bones hanging freely over the external nares in the North American form, similar to the condition in *Cadurcodon*. Stock (1933), in his original description of *Amy-nodontopsis*, noted the overall "tapir-like aspect" of the skull but he made no comment on the presence or absence of a proboscis in this genus.

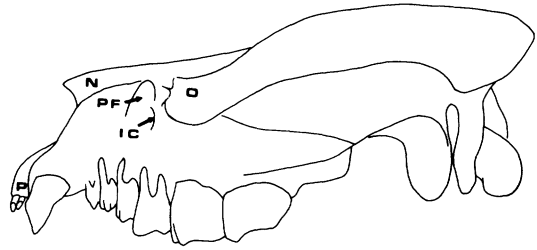
The advanced character of the skull of *A. bodei* represents the only exception to a linear



TEXT-FIG. 4—Distortion grid to show the cranial modifications which took place in the transition from A, the primitive amynodont, AMNH 107635 to B, the more highly derived *Cadurcodon*, AMNH 26029. For a thorough description of the methods used to prepare a distortion grid see Colbert (1935). Scale line equals 5 cm.

geochronological progression for proboscis development in amynodonts. *A. bodei* comes from the uppermost Eocene Sespe deposits of California but has a more highly derived facial region than the *Amyndontopsis* species from the lower Oligocene of Mongolia. Inaccurate stratigraphic correlation of the Mongolian and/or North American beds may be responsible for this minor discrepancy, but even if *A. bodei* is older than the Mongolian *Amyndontopsis* it does not invalidate the overall evolutionary progression seen in the fossil record toward the development of a proboscis in amynodonts. The derived nature of the characters described above points to the existence of a totally functional proboscis in both the Mongolian and North American representatives of *Amyndontopsis*.

The level of proboscis development achieved by *Cadurcodon* (see Text-figs. 1, 3A) appears to stem from the same selective forces which molded the skull of *Amyndontopsis* but carried to a greater extreme. The preorbital por-

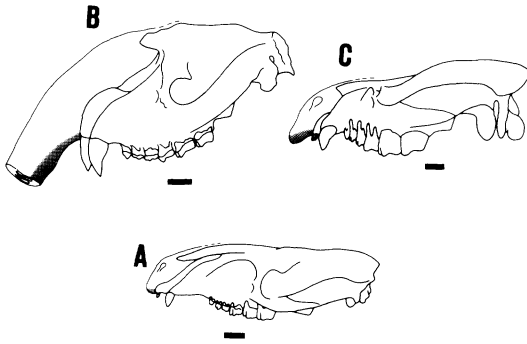


TEXT-FIG. 5—Lateral view of skull of the North American Oligocene genus *Metamynodon* (after Scott and Jepsen, 1941). Abbreviations: IC, infraorbital canal; N, nasal; O, orbit; P, premaxilla; PF, preorbital fossa. Scale line equals 5 cm.

tion of the skull of *Cadurcodon* is only slightly more reduced than that in *Amyndontopsis*. The anterior tip of the nasals to the border of the orbit represents 19% of total skull length in the highly derived skull, AMNH 26029. The nasal incision of *Cadurcodon* extends back to the level of the orbits, above the front of M^2 , a significant increase from the condition reached in *Amyndontopsis*. The loss of bone created by the expansion of the external nares produced a structural weakness in the snout which may have been compensated for by the fusion and thickening of the right and left premaxilla.

The distortion grid presented in Text-figure 4 illustrates the changes in cranial proportions which occurred in the transition from the late Eocene "primitive amynodont," AMNH 107635, to the early Oligocene proboscis bearing amynodont, *Cadurcodon*. The shortness of the face and the enlargement of the nasal incision in *Cadurcodon* are both clearly shown by the line pattern in Text-figure 4B. The vertical height of the anterior part of the skull has also increased greatly. The increased height is related to the development of the large frontal sinuses described earlier. The large external nares in AMNH 26029 allowed complete freedom of movement for the proboscis which would not have been possible in the more primitive form.

Snout structure in metamynodonts.—There are two major derived groups of amynodonts. One branch, represented by *Cadurcodon* and *Amyndontopsis*, was restricted to Asia during the early Oligocene. The second branch, containing several genera commonly referred to as metamynodonts, had a much broader



TEXT-FIG. 6—Summary diagram of snout development in the family Amynodontidae with the outline of the soft part anatomy restored. A, shows the primitive Eocene condition for the family as represented by AMNH 107635. B, C, represent the two derived patterns of amynodont evolution attained in the Oligocene. B, *Cadurcodon*, AMNH 26029 and C, *Metamynodon* (after Scott and Jepsen, 1941). Scale lines equal 5 cm.

geographic distribution in the Oligocene, including taxa from Asia and North America (the poorly known *Cadurcotherium* from Europe and India may also belong in this group).

The low position of the orbit in AMNH 107635, *Sharamynodon*, *Amyndontopsis*, and *Cadurcodon* (see Text-fig. 3) is a primitive character in the Amynodontidae. The elevated position of the orbit in metamynodonts (see Text-fig. 5) is a derived character associated with possible acquisition of semi-aquatic habits in this subgroup (a more thorough discussion on the terrestrial versus semi-aquatic mode of life of amynodonts will be presented in a future paper). In addition, the skull of *Metamynodon* (see Text-fig. 5) shows many other derived characters including: thickened zygomatic arches, high crowned cheek teeth, greatly enlarged canines and a reduced facial region (the premaxilla-nasal contact is reduced), but the metamynodont skull does not exhibit the proboscis modifications seen in *Cadurcodon*. The external nares of *Metamynodon* are not enlarged, the nasal incision reaches only as far back as the diastema, the nasal bones do not extend far over the nares, and the height of the snout is not increased. The preorbital fossa of *Metamynodon* does not extend far back medial to the orbits and as a result is greatly reduced.

The general outline of the face of *Metamynodon* is not significantly different from that of *Sharamynodon* (compare Text-figs. 5, 3C). The greater reduction in length of the preorbital portion of the skull in the metamynodont probably served to bring the large canine tusks into a structurally more advantageous position by reducing the distance between the canines and jaw musculature. The lacrimal bone is only slightly more rugose than in *Sharamynodon*, but it does indicate the presence of moderately well-developed snout musculature.

Based on the overall appearance of the face, *Metamynodon* probably had a well-developed prehensile upper lip similar in structure to the condition in *Sharamynodon*.

CONCLUSIONS

The primitive condition of the snout in the family Amynodontidae is represented by a skull, AMNH 107635, from the late Eocene "Irdin Manha" Formation of Mongolia. A long facial region and the small size of the external nares suggest that the primitive amynodonts were square lipped (see Text-fig. 6A). Later amynodonts diverged along two main evolutionary lines. The *Amyndontopsis-Cadurcodon* group became specialized for a tapir-like existence, utilizing a well-developed proboscis in the location of and manipulation of food (see Text-fig. 6B). The other branch of amynodonts derived from the ancestral condition was the metamynodonts. The metamynodonts had large massive bodies and skulls possibly adapted for a semi-aquatic existence. The general outline of the skull of metamynodonts and evidence from muscle scars of well-developed snout musculature are sufficient evidence for reconstructing the face of *Metamynodon* with a prehensile upper lip (see Text-fig. 6C) rather than a proboscis.

ACKNOWLEDGMENTS

I thank Dr. Margery C. Coombs, Ms. Carolyn J. Gamble, Mr. Thomas A. Griffiths, Ms. Jeanne M. Bertoni, Dr. Philip R. Bjork and Dr. David Klingener for their very useful comments and criticisms on various portions of this manuscript. In addition I thank Dr. Malcolm C. McKenna and Mr. Earl Manning for the opportunity to study the excellent collection of amynodonts at the American Museum

of Natural History, and Dr. Walter P. Coombs for the use of facilities at Pratt Museum, Amherst College. I also thank Dr. John Wilson for the personal communication.

REFERENCES

- Andrews, C. W. 1906. A Descriptive Catalogue of the Tertiary Vertebrates of the Fayum, Egypt. Br. Mus. Nat. Hist., Lond., 324 p.
- Berkey, C. P. and F. K. Morris. 1927. Geology of Mongolia. *In*, Natural History of Central Asia, vol. 2., Am. Mus. Nat. Hist., New York, 475 p.
- Colbert, E. H. 1935. Siwalik mammals in the American Museum of Natural History. Trans. Am. Phil. Soc. 26:1-401.
- Coombs, M. C. 1978. Additional *Schizotherium* material from China, and a review of *Schizotherium* dentitions (Perissodactyla, Chalicotheriidae). Am. Mus. Nat. Hist. Novit. 2647:1-18.
- Coombs, W. P. 1975. Sauropod habits and habitats. Palaeogeogr., Palaeoclimatol., Palaeoecol. 17:1-33.
- Dawson, M. R. 1968. Oligocene rodents (Mammalia) from East Mesa, Inner Mongolia. Am. Mus. Nat. Hist. Novit. 2324:1-12.
- Gregory, W. K. 1920a. Studies in comparative myology and osteology, No. V.—On the anatomy of the preorbital fossae of Equidae and other ungulates. Bull. Am. Mus. Nat. Hist. 42:265-284.
- . 1920b. Studies in comparative myology and osteology: No. IV.—A review of the evolution of the lachrymal bone of vertebrates with special reference to that of mammals. Bull. Am. Mus. Nat. Hist. 42:95-263.
- . 1929. The muscular anatomy and the restoration of the titanotheres. *In*, H. F. Osborn, The titanotheres of ancient Wyoming, Dakota, and Nebraska (Chapter 8). U.S. Geol. Surv. Monogr. 55:1-953.
- Gromova, V. 1954. Boltnye nosorogi (Amynodontidae) Mongolii. Trudi Paleontol. Inst., Akad. Nauk SSSR 55:85-189 (in Russian).
- Hatcher, J. B. 1896. Recent and fossil tapirs. Am. J. Sci., 4th series 1:161-180.
- Kretzoi, M. 1942. Ausländische säugetierfossilien der Ungarischen Museen. Foldt. Kozl. 72(1-3):139-148.
- Osborn, H. F. 1898. The extinct rhinoceroses. Mem. Am. Mus. Nat. Hist. 1:75-164.
- . 1923. *Cadurcotherium* from Mongolia. Am. Mus. Nat. Hist. Novit. 92:1-2.
- . 1936. *Amynodon mongoliensis* from the Upper Eocene of Mongolia. Am. Mus. Nat. Hist. Novit. 859:1-9.
- Radinsky, L. B. 1964. Notes on Eocene and Oligocene fossil localities in Inner Mongolia. Am. Mus. Nat. Hist. Novit. 2180:1-11.
- . 1965. Evolution of the tapiroid skeleton from *Heptodon* to *Tapirus*. Bull. Mus. Comp. Zool. 134:69-106.
- . 1969. The early evolution of the Perissodactyla. Evolution 23:308-328.
- Romer, A. S. 1966. Vertebrate Paleontology. Univ. Chic. Press, Chicago, 468 p.
- Schultz, C. B. and C. H. Falkenbach. 1968. The phylogeny of the oreodonts, Parts 1 and 2. Bull. Am. Mus. Nat. Hist. 139:1-498.
- Scott, W. B. 1937. The Astrapotheria. Proc. Am. Phil. Soc. 77:309-394.
- and G. L. Jepsen. 1941. The mammalian fauna of the White River Oligocene. Part 5, Perissodactyla. Trans. Am. Phil. Soc. 28:747-980.
- Stock, C. 1933. An amynodont skull from the Sespe deposits, California. Proc. Nat. Acad. Sci. U.S. 19:762-767.
- Troxell, E. L. 1921. New amynodonts in the Marsh collection. Am. J. Sci. 5th series 2:21-34.
- Wood, H. E. 1945. Family Amynodontidae. *In*, W. B. Scott, The Mammalia of the Duchesne River Oligocene. Trans. Am. Phil. Soc. 34:209-252.

MANUSCRIPT RECEIVED JUNE 31, 1979

REVISED MANUSCRIPT RECEIVED AUGUST 20, 1979