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AN EARLY OLIGOCENE RHINOCEROS JAW FROM THE MARINE BYRAM FORMATION OF MISSISSIPPI

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ABSTRACT

A nearly complete lower jaw of the primitive hornless rhinoceros *Subhyracodon occidentalis*, well known from the American High Plains, has been recovered from MGS locality 106 in the lower Oligocene (32-33 Ma) Byram Formation, upper Vicksburg Group, of west-central Mississippi. It is the first record of a rhinoceros from Mississippi, the first record of *Subhyracodon* east of the Mississippi River, and one of very few Oligocene rhinos from anywhere on the Gulf or Atlantic Coastal Plain. This is the second terrestrial mammal from marine locality 106; the first was a well preserved skull of the amynodont *Metamynodon planifrons*, reported by Manning et al. in 1986. Both animals are thought to have floated out into the Gulf of Mexico as bloated carcasses.

MGS locality 106 had previously been assigned to the Chadronian Land Mammal "Age" (now dated as late Eocene), but current correlation of marine calcareous nannoplankton Zone NP22 places the Byram in the more recent Orellan Land Mammal "Age." A comparison of the jaw to specimens from the High Plains suggests that it belongs to the early (but not earliest) Orellan fauna. The two Byram rhinocerotoids are

apparently the only Orellan terrestrial mammals yet recovered from any marine bed. They help establish a surprisingly close link between the marine Byram Formation of Mississippi and the terrestrial *Metamynodon* Channels of the Scenic Member of the Brule Formation, White River Group, of the White River Badlands of southwestern South Dakota.

INTRODUCTION

In mid-July of 1988, Daniel C. Dear of Jackson, Mississippi, was collecting marine invertebrate fossils from Mississippi Geological Survey (MGS) locality 106 along the banks of the Big Black River (figures 1-2) near his home in west-central Mississippi, when he noticed a small, broken bone sticking out from a bluff (Figure 3). He recognized the bone as a jaw from two incomplete teeth exposed along the top edge. Realizing the find's importance, Dan's brother, Howard Davis Dear, led a party from the Mississippi Office of Geology to the site on July 18, 1988. The specimen was removed that same day, by excavating deeply into the bluff, covering the jaw in wet newspaper, and finally jacketing it in plaster. The jaw was then transported to Jackson for further work.

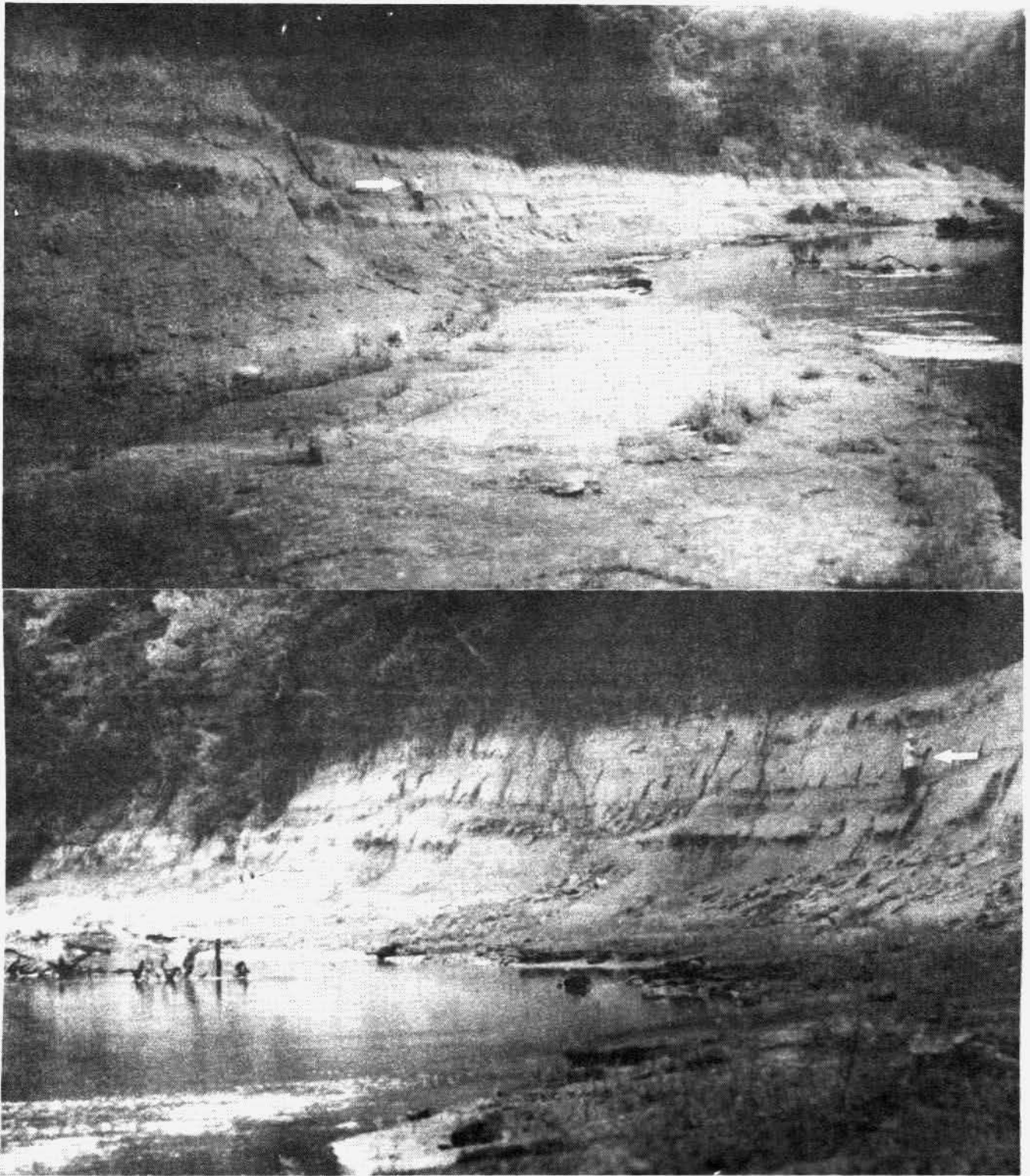


Figure 1. Top: MGS locality 106, looking downstream at the east bank of the Big Black River near Edwards in western Hinds County, west-central Mississippi. The cut bank exposes the early Oligocene Byram Formation, upper Vicksburg Group. The location of the rhinoceros jaw reported here is shown by an arrow. Bottom: Looking upstream, the arrow at upper right shows the *Subhyracodon* excavation; the arrow at left center shows the location of the *Metamynodon* find.

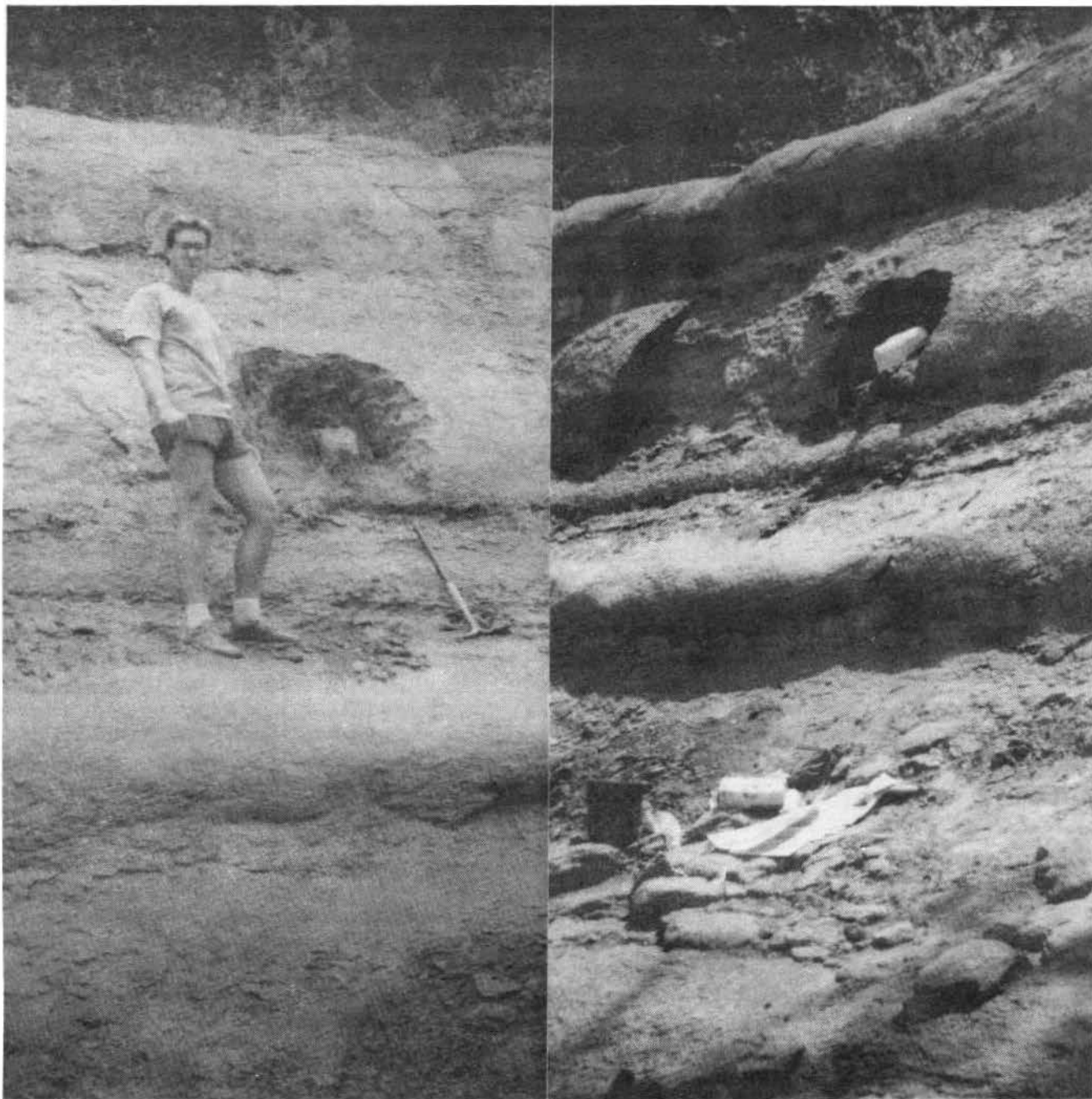


Figure 2. Left: Howard Davis Dear III of Jackson, Mississippi, next to the partially excavated rhinoceros jaw. Right: the jaw in its plaster jacket. Photos taken on July 18, 1988. The jaw is in bed K of the Byram Formation.

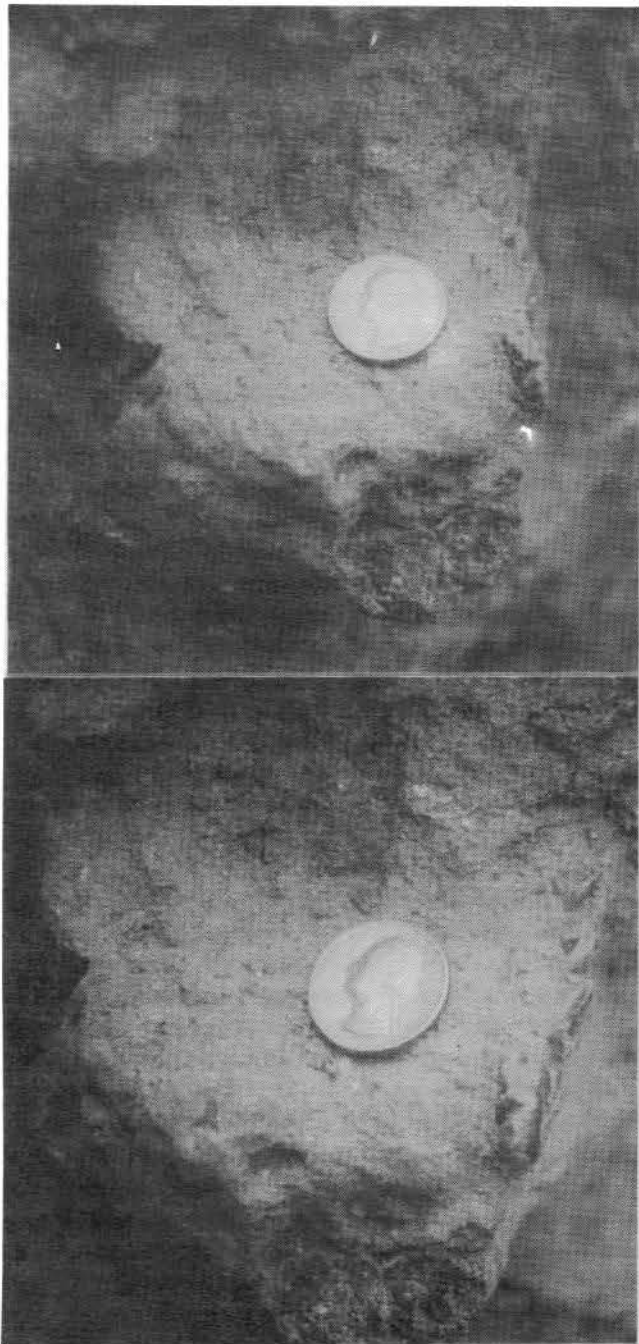


Figure 3. Two views of the partially excavated rhinoceros jaw, as it lay in the glauconitic marine sand of the Byram Formation, with a quarter for scale. When it was discovered, the only parts exposed were the broken front of the fused mandibular symphysis, the anterior part of the right P_2 , and the broken left P_2 . A hard carbonate concretion lies between the two rami of the mandible (below the quarter). The jaw lies upright in the bed, dipping slightly downward at the anterior end, with the anterior end pointing out of the bluff (west).

MGS locality 106 is a steep bluff on the east bank of the Big Black River in western Hinds County (NE/4, Section 29, T. 6 N., R. 4 W.), west-central Mississippi. It is near Edwards, about halfway between Vicksburg and Jackson, south of the Interstate 20 bridge over the Big Black River. Locality 106 was well known before Daniel Dear's discovery. Its well-preserved Oligocene molluscan fauna from the Byram Formation was illustrated, the site was figured and given its locality number six years earlier, in a publication on Mississippi's Oligocene bivalves from the Vicksburg Group (Dockery, 1982, p. 253, fig. 22-24). Marine gastropods from the site were later published in MacNeil and Dockery (1984).

Locality 106 received the attention of vertebrate paleontologists when a beautifully-preserved skull of the amynodont *Metamynodon* was published by Manning et al. (1986). The discovery of a second land mammal, a jaw of the rhinocerotid *Subhyracodon*, gave the locality even more importance. When the site was threatened by public access from a proposed casino/super-speedway complex, the Mississippi Gaming Commission received letters of protest from scientists from Washington State to Washington, D.C., and from Germany to New Zealand (Dockery, 1996). The proposed site was deemed unsuitable (Allmon, 1997).

When called to the site about the new vertebrate fossil, the Mississippi Office of Geology excavation team, under David T. Dockery, expected Daniel Dear's find to occur in the same bed of the Byram Formation that had produced the earlier *Metamynodon* discovery. To their surprise, though the new specimen was only about 150 feet downstream from the previous find, it was a vertical distance of about eleven feet higher in the section than the first find (Figure 4).

Although the front end of the *Subhyracodon* jaw had been broken off and washed away by the river prior to its discovery, the rest of the jaw is remarkably complete (figures 5-6). Of the twelve cheek-teeth present on the two sides, only the left front tooth is incomplete. The sides and top of the jaw were prepared at the Office of Geology. The harder, concretionary material between the jaws was removed, and the jaw impregnated with a hardener, at the Louisiana State University Museum of Geoscience (now part of the LSU Museum of Natural Science) in Baton Rouge.

STRATIGRAPHY AND MARINE CORRELATION

Horizon. The measured section in Figure 4 shows the exposure along the Big Black River at MGS locality 106. Beds are labeled A through Q from the river level at low water to the highest level exposed along the bluff. Two formations of the Vicksburg Group are present, the bulk of the section (beds A-P) in the Byram Formation, and the uppermost bed (Q) in the Bucatunna Formation. The *Subhyracodon* jaw was recovered from bed K in the upper Byram, about eleven feet above the level of the *Metamynodon* skull, from the lower part of bed F in the middle

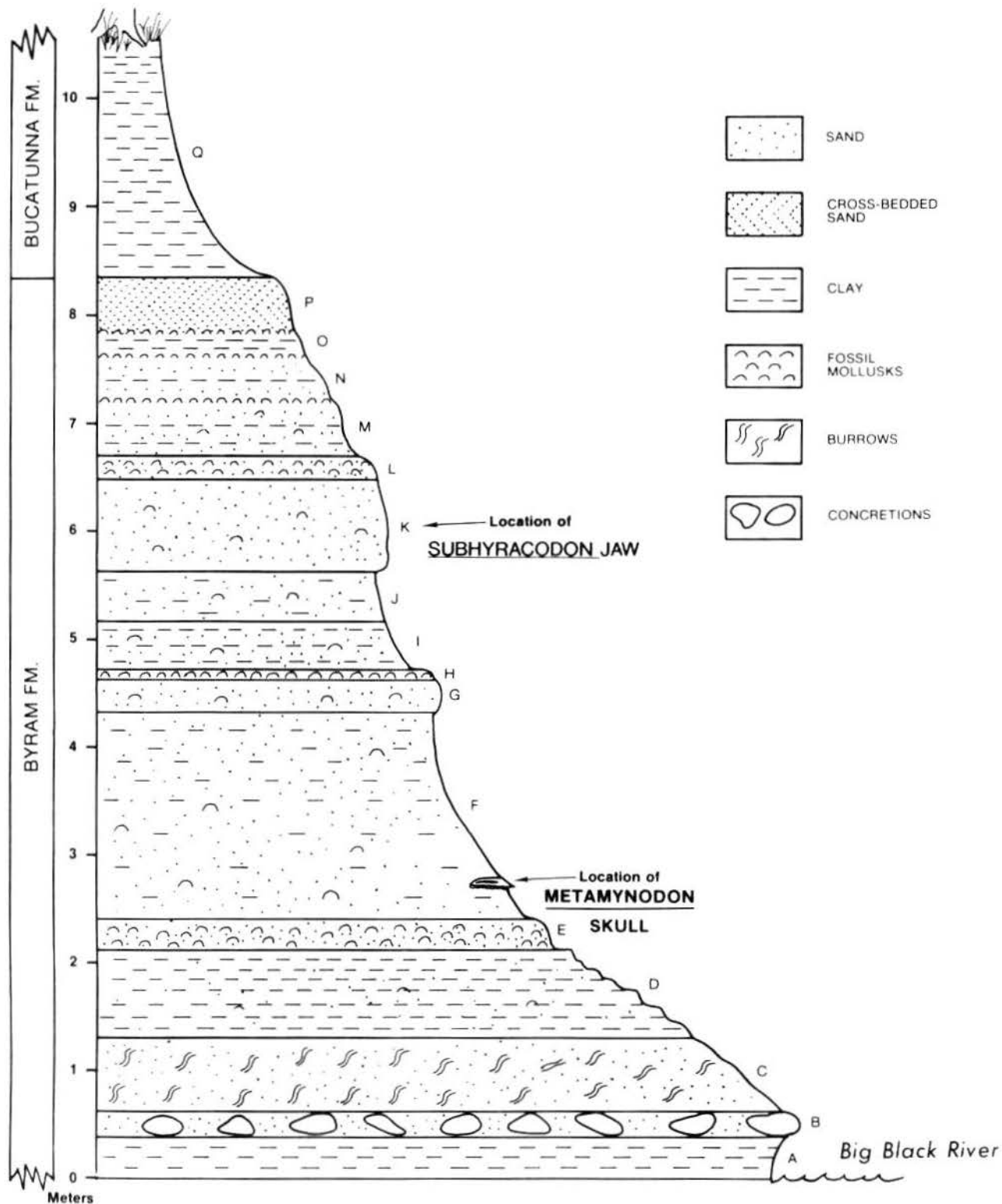


Figure 4. Measured section of the Byram-Bucatunna beds along the bluffs of the Big Black River at MGS locality 106. The location of the two terrestrial mammals within the Byram is shown, the *Metamynodon* in bed F in the middle Byram, and the *Subhyracodon* in bed K in the upper Byram. Bed H is particularly rich in mollusks. The upper Vicksburg Group Byram and Bucatunna formations form the regressive portion of the sequence begun with the lower Vicksburg Group Mint Spring Formation. After Manning et al., 1986.

Byram. Bed K is a glauconitic sand, with less clay than most other Byram beds at the site, including bed F. The lettered beds in the Byram section are laterally continuous, traceable for about a quarter mile along the outcrop (Dockery, in Manning et al., 1986, p. 2). The jaw was oriented upright in the bed, with the front slanting slightly downward and its anterior end pointing westward, out of the bank (Figure 3).

Sequence stratigraphy. In sequence stratigraphic terms, the Byram and Bucatunna make up the regressive highstand systems tract of a Vicksburg Group sequence which began with a basal Mint Spring Formation transgression and culminated in a maximum flooding surface at the top of the Glendon Formation (Dockery, 1986, p. 587).

Correlation. The rich molluscan fauna of the Byram Formation can be correlated to that of the Stampian (Rupelian—the early Oligocene in a two-part division) of the Aquitaine Basin of southwestern France (Dockery, 1982; MacNeil and Dockery, 1984). The calcareous nannoplankton flora of the Byram places it in marine Zone NP22 (Siesser, 1983). In recent correlations (Berggren et al., 1995, fig. 3), this zone has been placed in the early to middle part of the Rupelian, at about 31 to 33 Ma (million years ago).

SYSTEMATICS

In the perissodactyl classification of Prothero and Schoch (1989), the Byram jaw would be placed as follows:

- Class Mammalia Linnaeus, 1758
- Subclass Theria Parker and Haswell, 1897 -- marsupial and placental mammals
- Infraclass Eutheria Gill, 1872 -- placental mammals
- Superorder Ungulata Linnaeus, 1766 -- hoofed mammals and their kin
- Grandorder Altungulata Prothero and Schoch, 1989 -- higher ungulates, Pantomesaxonia of Prothero, Manning, and Fischer, 1988
- Order Perissodactyla Owen, 1848 -- hyraxes, horses, tapirs, rhinos, and kin
- Suborder Mesaxonia Marsh, 1884 -- the above, save hyraxes
- Parvorder Ceratomorpha Wood, 1937 -- tapirs, rhinos, and extinct kin
- Superfamily Rhinoceroidea Owen, 1845 -- amynodonts, hyracodonts, and rhinocerotids
- Grandfamily Rhinocerotida Owen, 1845 -- hyracodonts and rhinocerotids, node 13 of Prothero, Manning, and Hanson, 1986, fig. 4
- Family Rhinocerotidae Owen, 1845 -- true rhinos
- Subfamily Diceratheriinae Dollo, 1885 -- *Subhyracodon* and *Diceratherium*
- Genus *Subhyracodon* Brandt, 1878 (including as synonyms *Caenopus* Cope, 1880, and *Leptaceratherium* Osborn, 1898)

Subhyracodon occidentalis (Leidy, 1854)

Figures 5-6

Rhinoceros occidentalis Leidy, 1850, p. 119 (*nomen nudum*); Leidy, 1851a, p. 276 (*nomen nudum*); Leidy, 1854, p. 81, pl. 12-13.

Rhinoceros (Acerotherium) [sic] occidentalis Leidy. Leidy, 1851b, p. 331 (*nomen nudum*).

Aceratherium occidentale (Leidy). Leidy, 1869, p. 220-228, pl. 21, fig. 34, pl. 22, pl. 23, fig. 1-3.

Aceratherium (Subhyracodon) occidentale (Leidy). Brandt, 1878, p. 30.

Caenopus occidentalis (Leidy). Osborn, 1900, p. 238.

Subhyracodon occidentalis (Leidy). Wood, 1927, p. 63.

Range: early Oligocene Orellan Land Mammal "Age" of southwestern Montana, southwestern North Dakota, northwestern and southwestern South Dakota, western Nebraska, eastern Wyoming, northeastern Colorado, and west-central Mississippi.

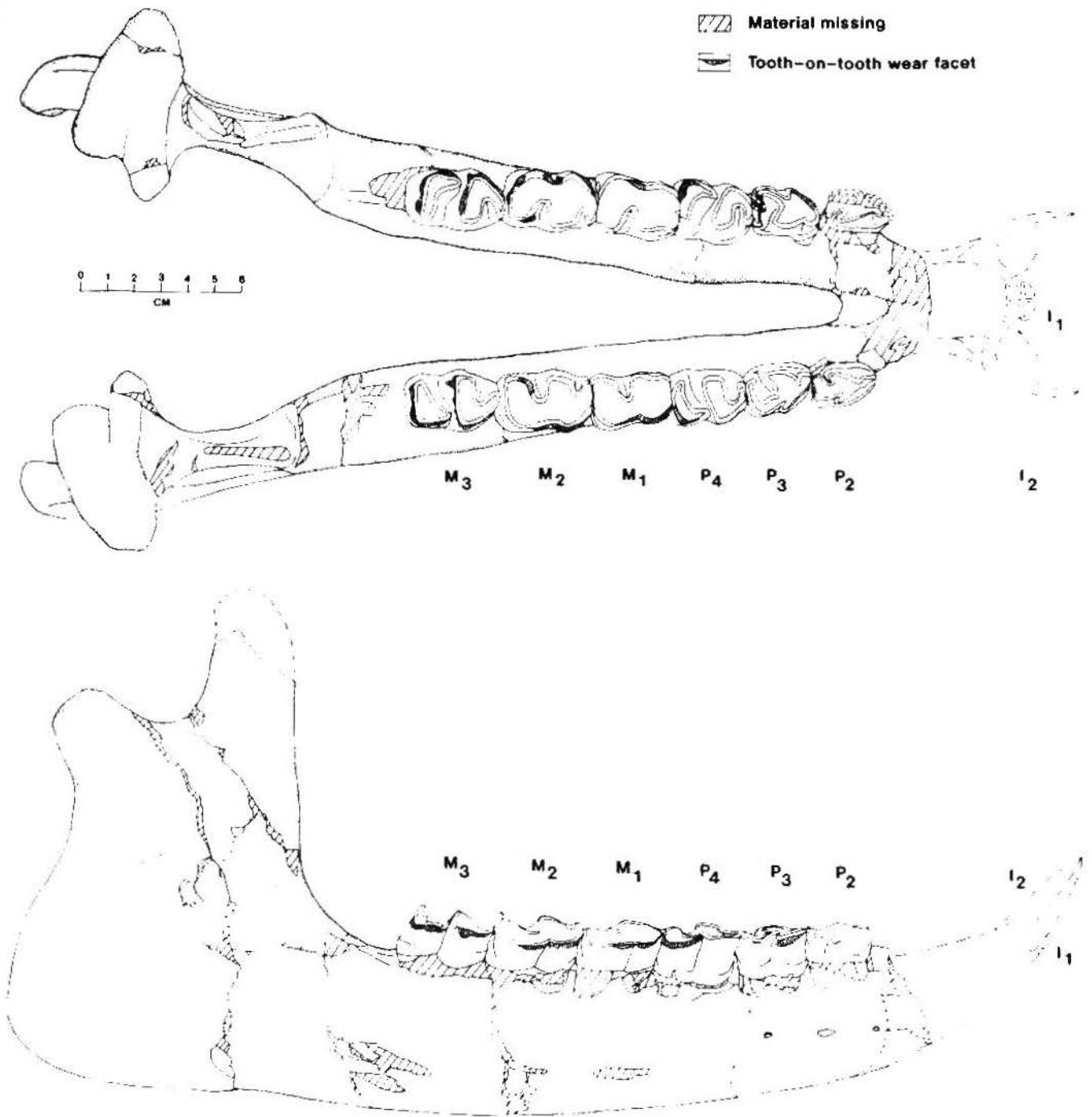
Discussion. The Byram jaw (MGS figured specimen 1794) can be placed in the higher ungulates by its fused symphysis, relatively large third lower molar (M_3), and by the lack of an adult replacement premolar for the first lower milk premolar (dP_1).

The characteristic "double L" pattern of the lower molars is typical of all primitive perissodactyls, and of most rhinos. It differs from the bilophodont pattern of tapirs in emphasizing the two anteriorly-directed lateral (labial) crests. The absence of an M_3 hypoconulid places it in the Rhinoceroidea.

The jaw differs from that of the most primitive rhinocerotid, *Teletaceras* (see Hanson, 1989), in being far larger (molar series length 93 mm, versus 65 mm), in having proportionately larger premolars, in having strong labial and lingual basal ridges (cingula) on P_2 and P_3 , and in having a more complex (more molariform) P_2 . It resembles *Teletaceras* and other primitive rhinocerotids in the general shape of the lower jaw -- with an only slightly enlarged mandibular angle (giving the lower lateral outline of the jaw a notch at the back and a gently rounded form below the cheek-teeth, more primitive than the straight ventral outline of more derived rhinos) and a slender ascending ramus with a small, high masseteric fossa. In these features, the Byram jaw shows that it had not evolved the enlarged jaw muscles used in side-to-side chewing in most rhinos (including most *Subhyracodons*).

The Byram jaw is more derived than another primitive rhino, *Trigonias*, in its molariform P_2 (with a strong ridge extending posterolabially from the posterior paralophid) and in having nearly complete labial cingula on P_2 and P_3 . In these ways, the Byram jaw more closely matches *Subhyracodon*. The Byram jaw outline, however, again more closely resembles the more primitive *Trigonias* than most *Subhyracodon* jaws.

The status of the many described species of *Subhyracodon* (including some of those usually placed in *Caenopus*, a junior synonym) is unclear. A major revision of the American rhinos,



Figures 5 (top) and 6 (bottom). *Subhyracodon occidentalis* mandible (MGS figured specimen 1794) from MGS locality 106. Anterior is toward the right. The missing anterior part (lost to surface erosion) is here shown restored as a male (with large I_1 tusks). For clarity, stippling and cracks have not been included on the teeth. Theogosis (tooth-on-tooth wear) facets are shown at the tops of the teeth in fine parallel lines. Cheek-teeth present are left and right P_2 to M_1 , with some damage to the labial side of the left P_2 . There is no evidence of a dP_1 , and only the far posterior tips of the I_2 tusk roots appear on the broken surface of the fused symphysis. The tip of the right coronoid process was lost, and the cracks in the jaw were formed during preparation and removal of the concretion from the inside of the jaw. See centimeter bar for scale. Figure 5- right lateral view of the right ramus of the mandible. Figure 6- occlusal view of the mandible.

including *Subhyracodon*, is under way by Donald Prothero, but until the detailed comparisons are done, it can't be said with certainty how many *Subhyracodon* species are valid. My research on the genus suggests that all species may intergrade. They might better be treated as a series of subspecies within a single species, with only chosen statistical boundaries between them. This situation is not unusual for any group with a rich fossil record, and *Subhyracodon* is represented by a great deal of excellent material from the High Plains. Often, the more complete the fossil record of a group, the fewer discrete species are represented. *S. occidentalis*, the type and first-named species of *Subhyracodon*, will certainly survive the winnowing of species that will inevitably come.

Where the Byram jaw fits within *Subhyraco* 'on. Of the various named species of *Subhyracodon*, the Byram jaw is on the primitive (though not the most primitive) end. As already noted, the general lateral outline of the jaw is more slender and less robust than most described material. It is also smaller than most (see Table 1). In a general way, the *Subhyracodon* species *S. mitis* (type species of "*Caenopus*"), *S. copei*, *S. occidentalis*, and *S. tridactylus*, ranging from the late middle Eocene Duchesnean Land Mammal "Age" through the middle early Oligocene Whitneyan Land Mammal "Age," are successively larger and more derived. The Byram jaw (M_1 - M_3 length of 93 mm) is larger than *S. mitis* (M_1 - M_3 length of 77 mm - Osborn, 1898, p. 140) and appears to have proportionately larger premolars than *S. copei* (when roughly compared to the upper cheek-teeth - Osborn, 1898, pl. 13, fig. 3). It appears to fit the size range (Figure 7) of a small individual of the Orellan *S. occidentalis* (M_1 - M_3 length of 93 mm), rather than of a large individual (M_1 - M_3 length of 103 mm - both measurements from Scott, 1941, p. 811); and when roughly compared to the upper cheek-teeth (Osborn, 1898, pl. 13, fig. 5, rather than the larger fig. 7). It is far smaller than the middle early Oligocene Whitneyan Land Mammal "Age" species *S. tridactylus* (M_1 - M_3 length of 122 mm in the type specimen, versus 93 mm in the Byram jaw - Wood, 1927, Table 6). Besides the jaw outline and small size, the Byram jaw also suggests a relatively primitive *S. occidentalis* in the rather weak development of the labial cingula of the cheek-teeth. They are strongly developed on P_2 and P_3 , weakly on P_4 , and barely present on the molars. In more derived individuals of *S. occidentalis* (e.g. Scott, 1941, pl. 84, fig. 1), the labial cingula are strongly developed on P_2 to M_1 , and weakly developed on M_2 and M_3 .

It seems likely that, with a detailed comparison of tooth size and cingular development, the Byram jaw could be placed fairly precisely within the continuum of *S. occidentalis* individuals. For now, it can be said that the Byram jaw fits the smaller, more primitive, end of that continuum (Figure 7).

Table 1. Measurements (in mm) of the Byram Formation *Subhyracodon occidentalis* lower cheek-teeth.

Teeth	left		right	
	length	width	length	width
P_2	21.8*	13.3'	22.2*	14.5
P_3	23.0*	16.5	23.4*	16.7
P_4	25.6*	19.6	27.7*	19.2
M_1	28.8*	19.9	29.5*	19.9
M_2	32.2*	21.0	31.9*	20.9
M_3	30.7	21.4	32.0	21.4
P_2 - P_4	69.9		70.8	
M_1 - M_3	93.0		93.5	
P_2 - M_3	162.9		164.9	

* Tooth lengths slightly shortened by interstitial wear

' Measurement approximate, labial side broken

Jaw measurements:

Length from rear of symphysis to back of right ramus: 298

Depth of horizontal ramus below posterior M_1 : left 46.4, right 46.0

Length of the narrowest part of the ascending ramus: left 81.8, right 78.5

Height of the left ramus to the top of the coronoid process: 174

Width of the mandibular condyle: left 63.2 mm, right 62.7

Remaining portion of the partial symphysis: 30

DESCRIPTION

Why the original shape of the jaw was maintained. The Byram *Subhyracodon* jaw (figures 5-6) is very well preserved, with no noticeable deformation due to compression from overlying sediment (as is often the case with Badlands material). Likely, the reason it escaped the slight compression seen in the *Metamynodon* skull (Manning et al., 1986, p. 8) is that a large carbonate concretion (or nodule) had formed between the rami of the mandible, and hard carbonate fills most of the empty cavities in the jaw. The nodule was probably at least partly lithified before the weight of the overlying sediment was placed on it. As it was buried in an upright position, had it not been supported in some way, the weight of the overlying sediment would have caused the two rami of the mandible to break apart at the symphysis and turn to lie flat on the bedding plane.

Concretions and the Byram land mammals. It is of interest that both the *Metamynodon* skull and the *Subhyracodon* jaw from MGS locality 106 had carbonate concretions formed between their jaws and nowhere else. The remains of the originally much larger carbonate concretion on the middle of the palate of the skull can be seen medial (lingual) to the right P^4 and M^1 in the photograph and drawing of it (Manning et al., 1986, fig. 8A and

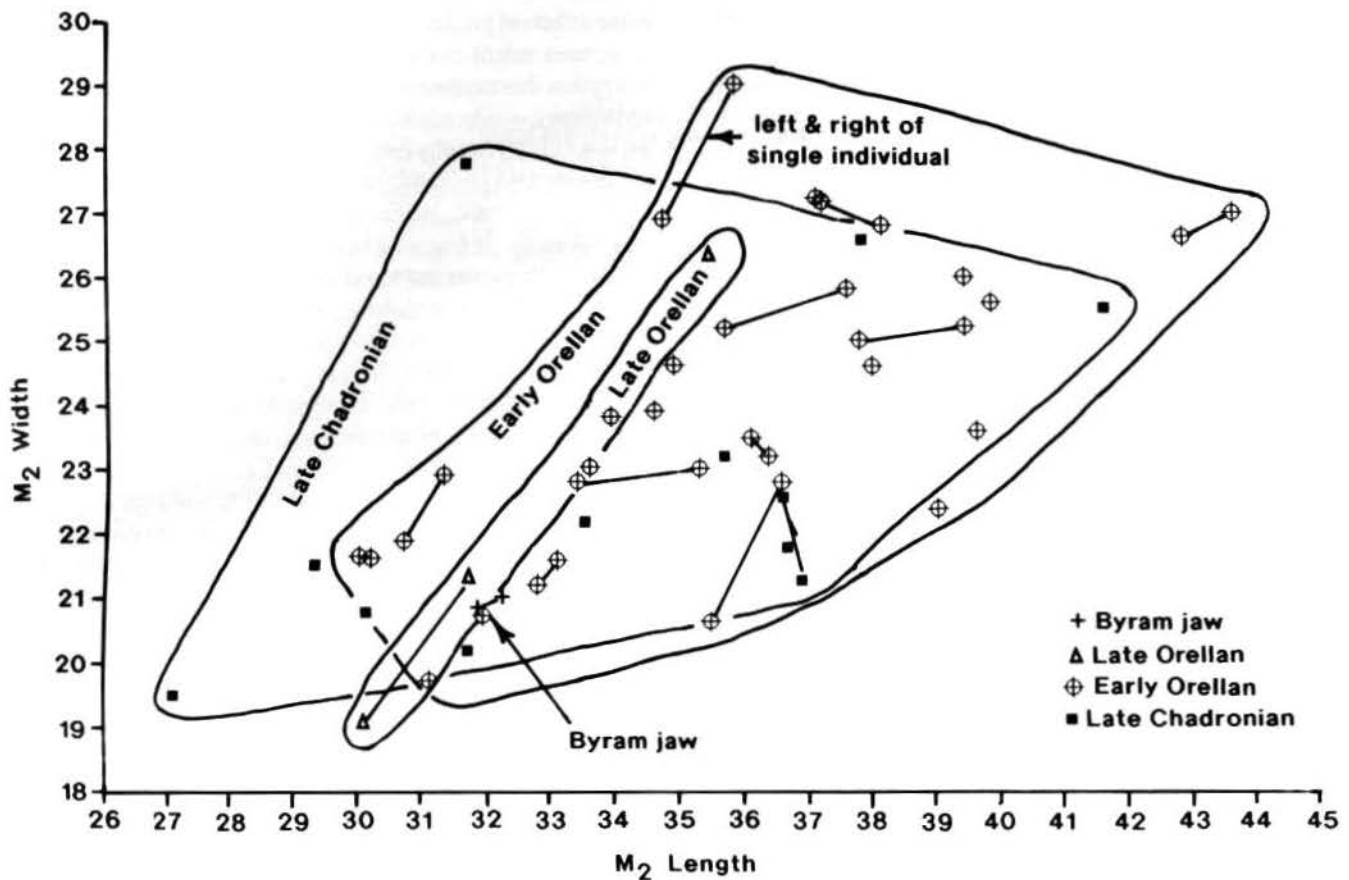


Figure 7. Plot of the relative size of the first lower molar of the Mississippi jaw in comparison with those in late Chadronian (late late Eocene) and Orellan (early early Oligocene) *Subhyracodon* jaws from the High Plains (ND, SD, NE, WY, CO) in the American Museum of Natural History, New York. The material may represent three successive subspecies of *S. occidentalis*. Measurements provided by Donald R. Prothero.

9). The concretion on the jaw has been almost entirely removed (to reveal the medial jaw morphology) but can be seen in medial openings of the jaw and between some of the cheek-tooth roots on the lingual side.

The carbonate needed to form such concretions could have been placed into solution in the interstitial pore space of the sediment by dissolving the aragonite from some of the mollusk shells in the bed. Carbonate concretions form when carbonate ions in the interstitial water are drawn to a localized reducing environment. This can be created by the decay of organic material, as oxygen is depleted in the decay process. This is why Pennsylvanian leaves at some sites are found exactly in the center of small, flat concretions. One might speculate that the carbonate concretions formed between the jaws of the two Byram land mammals because part (or all) of the tongue (or other soft tissue) was still present for a time after burial, and that carbonate was drawn preferentially to the area

with the most decaying flesh.

In order for a floating carcass to reach so far out into the Gulf, most of the skin would have to remain intact (see Taphonomy section). One might speculate that the reason the incisors and anterior premolars of the *Metamynodon* skull became loosened and fell out of their sockets prior to burial (while the remaining teeth are all well preserved and firmly rooted in the skull) is that the skin and connective tissue over the nose and anterior palate had been nibbled away by scavenging fish, etc., as the bloated carcass floated out to sea, and had fallen off the carcass before the skull did. There is no way of knowing if the same thing happened to the *Subhyracodon* jaw, as its anterior end had broken off and was lost prior to its discovery.

Condition of the jaw. The surface condition of the jaw is very good and shows no indication of either erosion or scavenger bite marks. The muscle (attachment) scars on the bone still

show clearly. The tooth enamel is shiny and still shows clear thegosis facets, resulting from wear of the enamel of the lower teeth against the enamel of the upper teeth; (these beveled surfaces have been shown on the drawings in figures 5 and 6).

Posterior to the broken symphysis, very little of the jaw has been lost. The top of the right coronoid process was lost in preparation, and some bone was lost to breakage when the hard concretion was chipped away from the jaw.

Of the cheek-teeth, only the labial surface of the left P_2 was lost to surface erosion prior to discovery. The left P_1 to M_1 and right P_2 to M_3 are well preserved. There is no evidence of a retained dP_1 , as occurs in some *Subhyracodon* individuals.

Sex of the Byram rhino. There are small remnants of the far posterior part of the I_2 tusk (an enlarged second lower incisor) roots present in the broken surface of the symphysis (Figure 6), but not enough to say much about the lower tusks. It's unfortunate that the anterior symphysis and anterior teeth (a small I_1 and large I_2 tusk in *Subhyracodon*) were lost on the Byram jaw, as the size and shape of the I_2 tusk reveal the gender of the individual. As in the more primitive three of the five living rhinoceroses (the Sumatran, Javan, and Indian rhinos), the male lower tusks are large, and have an acute-triangle shape to the tusk crown in dorsal view; in contrast, the females have small tusk crowns, with an equilateral-triangle shape. The larger male tusks are used in competition with other males, as well as for defense. Without the lower tusks, it will not be possible to determine the sex of the Byram rhino. In figures 5 and 6, it has arbitrarily been restored as a male.

Age of the Byram rhino at death. The age of the Byram rhino at the time of its death can be determined. There are no milk teeth; M_1 is fully erupted, and there is at least moderate wear on all six cheek-teeth. There is heavy wear on M_1 because it erupts into occlusal position (from a crypt within the jaw) first of the three molars, and prior to the loss of the milk premolars, which protect their underlying adult premolar replacements. Thus, M_1 has been in wear for the longest time of the cheek-teeth present. In addition to occlusal wear (resulting from food abrasion and tooth-on-tooth wear), there is also a fair amount of interstitial wear between the cheek-teeth, notably on the anterior ends of M_1 and M_2 . This occurs as adjoining teeth grind against each other in vigorous chewing, and is not unusual in rhinos with low-crowned teeth. The fully erupted adult premolars and moderately worn M_1 (about to the same extent as in the Byram *Metamynodon* M^1) show that the Byram rhino was a young adult, in the prime of life, at its death.

It is surprising that both the Byram *Metamynodon* and *Subhyracodon* (and, parenthetically, the middle Eocene titanotheres *Notiottitanops* from the marine Cook Mountain Formation of eastern Mississippi -Gazin and Sullivan, 1942) were adults in their prime, rather than juveniles or aged individuals. Many terrestrial animal fossils found in marine beds (particularly among dinosaurs) are juveniles, possibly due to inexperience foraging along a coast. Weak older individuals might be more likely to be lost to infirmity. There is no evidence

of the effects of predation (although carnivore tooth punctures or scrapes might not appear on the head) or of any bone resorption due to disease. In normal population attrition in a community, young adults rarely die. How it happened that two such seemingly healthy individuals came to be swept out to sea is unclear. One possibility might be that both were caught in the fast-rising water of a spring flood.

Jaw features. It might be noted that there are three mental foramina (for nerves and blood vessels entering the jaw) on the right ramus (below anterior P_2 , posterior P_2 , and middle P_3), while only two on the left ramus (below anterior P_2 and posterior P_2). The only notable difference between the left and right cheek-teeth (which sometimes vary in the degree of molarization of the premolars) is an unusual thegosis facet on the posterolabial occlusal surface of the left P_1 . It is triangular, with the pointed end directed anterolingually toward the center of the talonid basin. Its lateral edge deeply notches the hypolophid just behind the hypocone. Wear from the upper third premolar would normally only bevel the posterolabial corner of the top of the tooth enamel at a steep angle. The anomalous facet cuts almost horizontally across the talonid, not vertically. This anomaly is probably due to a maloccluded left P^1 . Should the skull, left maxilla, or even just the left P^1 of the Byram individual ever be found, it would be easy to identify as the counterpart of the jaw.

The coronoid process is short (about 50 mm above the saddle between the coronoid and condyle) and nearly vertical. The mandibular condyle surface is still somewhat rounded, rather than being strongly flattened, as in most *Subhyracodon* jaws. The condyle slopes medially rather than being horizontal. The postcotyloid process is heavy and slopes medioventrally from the lateral edge of the condyle. The rim of the mandibular angle is strongly in-turned posteriorly and out-turned ventrally. There appear to be heavy ridges on both rims for strong jaw muscle attachments. The relatively small, primitive mandibular angle of the Byram rhino suggests that it still hadn't developed the broadened jaw muscle sheets present in most *Subhyracodons* with an expanded mandibular angle. The condyle, as typical of most rhinos, is high above the occlusal surface of the cheek-teeth (about 8 cm), indicating that the jaws didn't open widely. Large mandibular foramina open posteriorly for Meckel's cartilage on the posteromedial surface of the jaws, directly below the anterior edge of the ascending ramus and just below the level of the upper edge of the bone of the horizontal rami.

SUBHYRACODON

Among the most interesting and unexpected paleontological discoveries in America is that of the former existence of the Rhinoceros family upon this continent. (Leidy, 1869, p. 219)

Subhyracodon occidentalis was the first rhinoceros to be reported from the New World (Leidy, 1850). Along with the

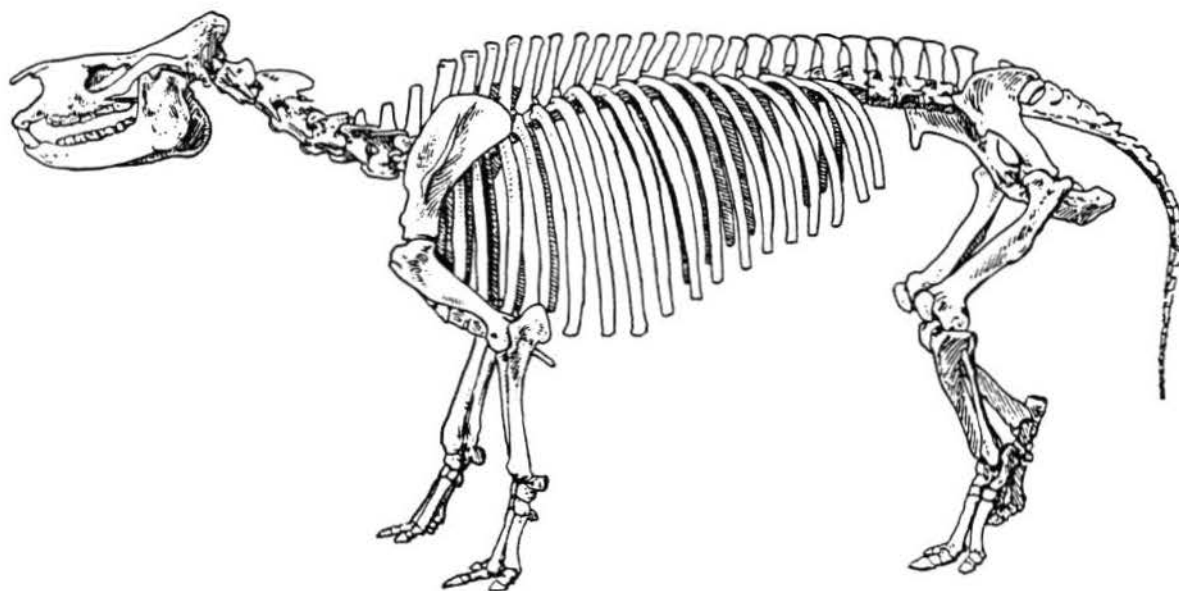


Figure 8. The skeleton of the hornless early Oligocene rhinoceros *Subhyracodon occidentalis*. It can be identified as a male from its large I₂ tusk. *S. occidentalis* was a common large mammal in the Orellan fauna of the American High Plains. The Byram individual would have been about the size of a pony. From a skeleton at the American Museum of Natural History, New York. From Scott, 1941.

earlier discovery of the elephant-like mastodon in America, the occurrence of what was then an entirely Old World group was a considerable surprise. Likewise, the discovery of a well-known High Plains species on the Gulf Coastal Plain in Mississippi—its first record east of the Mississippi River—was also a surprise.

Discovery of the Badlands fauna. *S. occidentalis* was one of the first fossils collected and reported from the newly discovered fossil beds of the White River Badlands (“mauvaises terres a traverser” to the early French-Canadian trappers of the region—“bad lands to travel across,” due to their lack of water and vegetation as much as their rough terrain) of what is now southwestern South Dakota. The first report of a fossil from these beds (Prout, 1846) related to the upper jaw of a huge extinct perissodactyl, now known as a titanotherium. Joseph Leidy—medical doctor, anatomist, parasitologist, and Father of American Vertebrate Paleontology (1823-1891)—soon after Prout’s report began describing material shipped East from these beds, the beginning of his long and illustrious career. The first *Subhyracodon* specimens were collected by Thaddeus Culbertson for the Smithsonian Institution in May of 1850 (Emry and Purdy, 1984) and were reported at the Academy of Natural Sciences of Philadelphia by Leidy later that year.

Rhinos in America. Years of collection have revealed that

rhinocerotids had a long and successful history in North America. They probably arose in the middle Eocene of Eurasia, quickly migrated across the Bering land bridge from eastern Asia to North America (about 40 Ma), broadly diversified into several lineages, and became extinct in North America only relatively recently, in the earliest Pliocene, about five million years ago (Prothero et al., 1989). *Subhyracodon* lived in North America for about ten million years, from the late middle Eocene (Duchesnean Land Mammal “Age” [LMA], about 40 Ma) to the middle early Oligocene (late Whitneyan LMA, about 30 Ma). Rather than becoming extinct, it evolved into *Diceratherium*, the first horned rhinoceros, in the late early Oligocene (see Relationship to *Diceratherium* section).

Coastal Plain endemism? Although endemic rhinos (those which become specialized by evolving in isolation), such as the two dwarf middle Miocene rhinos of Texas (Prothero and Manning, 1987), do occur on the Gulf Coastal Plain, most coastal rhinos appear to be just the same as those that occur on the High Plains (as is the Mississippi *Metamynodon*). Coastal vertebrate paleontologists constantly look for signs of endemism (e.g. Schiebout, 1979), but more often than not the evidence favors free cross-country emigration, not endemism.

Nature of the Byram rhino. *Subhyracodon occidentalis* (Figure 8) looked rather different from the large modern African

rhinos most people think of as typical (though not as different from the smallest and most primitive of the five living rhinos—the Sumatran rhino *Dicerorhinus*). Compared to the modern African black or white rhino, *S. occidentalis* (and especially the Byram individual) was far smaller and more lightly built (the Byram rhino was about the size of a pony). It was hornless and had a long, narrow skull—quite unlike the heavy-horned, broad-skulled African rhinos. Also unlike the African rhinos, it had front tusks. It didn't have the huge barreled chest or the short heavy legs of the big modern forms, but a horse-like chest and relatively long, slender legs. Overall, it would have looked more like a horse than a black or white rhino, except for having somewhat shorter legs and browsing on leaves and twigs (as revealed by the low-crowned teeth) rather than grazing grass. Unlike the browsing black rhino today, *Subhyracodon* may have fed in small groups rather than alone.

***Subhyracodon* and *Metamynodon*.** Although both *Metamynodon* and *Subhyracodon* were browsers (one large, the other medium), unlike the hippo-like *Metamynodon*, *Subhyracodon* is not closely associated with the river deposits of the Badlands beds (most are terrestrial sheet flows of volcanic ash mixed with water), and is not thought to have been semi-aquatic like *Metamynodon*. It was a fully terrestrial rhinoceros. While both Byram land mammals are rhinocerotoids, amynodonts like *Metamynodon* are only cousins to the true rhinos like *Subhyracodon*. Both families were not equally successful in America. The amynodonts died out in North America with the last of the *Metamynodons* at the end of the early Oligocene Orellan Land Mammal "Age" (32 Ma), while the rhinos survived and prospered for another 27 million years.

Relationship to *Diceratherium*. It has long been known that *Subhyracodon* is closely related to the first horned rhinoceros, *Diceratherium*. They are linked in recent rhino classifications within the Subfamily Diceratheriinae (Prothero et al., 1986, fig. 4; Prothero and Schoch, 1989, p. 535). Although the more primitive *Subhyracodon* (including the Byram rhino) were all hornless, a middle early Oligocene (Whitneyan LMA) species called *S. tridactylus* had paired, elongate rugosities near the front of its greatly thickened nasals in large old males (Osborn, 1898). It's clear that from these roughened areas the peculiar paired, low, anteroposteriorly-oriented ridge-like nasal horns of *Diceratherium* evolved (the generic name means "two-horned beast").

Osborn and Wortman (1895, p. 373) reported with confidence that, "As regards specific succession, it is now certain that *A. occidentale* was directly ancestral to *A. tridactylum*," That confidence came from having a long series of intergrading specimens which, in itself, is a systematic problem as well as an advantage. Just as the primitive species of *Subhyracodon* may intergrade and lose validity, the genus itself, if the record is complete enough, may intergrade with *Diceratherium*. As more skulls of the primitive late early Oligocene (early Arikarean LMA) *Diceratherium* are found, the slight differences between

the genera may disappear. In that case, *Subhyracodon* Brandt, 1878, would become a junior synonym of *Diceratherium* Marsh, 1875.

As matters stand, the genus *Subhyracodon* is already a paraphyletic assemblage (one based on shared primitive features) of species, each in turn more closely related to *Diceratherium*. *S. tridactylus* is more closely related to *Diceratherium* than it is to *S. occidentalis*. Removing *S. tridactylus* from *Subhyracodon* and placing it in *Diceratherium* (as done by Scott, 1941) is also unsatisfactory, as *S. occidentalis* certainly intergrades with *S. tridactylus*. As suggested earlier, the best solution may be to treat all the intergradational taxa as subspecies (which don't require discrete boundaries, as species do) of the same variable and long-ranging species, probably of *Diceratherium* rather than of *Subhyracodon*.

Taphonomy Land mammals in marine beds. How do terrestrial mammals end up buried in oceanic sediments? It probably happens in one of two ways, either as floating carcasses carried out to sea or as animals buried first in river deposits, then later dug up by ocean currents and reburied in marine sediments.

In the first process, a large coastal land animal (it appears to occur rarely with small forms) either gets swept into a large, fast-flowing coastal river by falling into it as a live animal (which then drowns) during spring flood, or as a dead carcass picked up along the floodplain of a river in flood stage and swept into it. In either case, the dead animal is kept afloat by gases built up mostly in the abdominal cavity by internal decay. The bloated carcass, probably floating belly up, with limbs and head hanging down, can then be carried out the river delta and into the open sea. A bloated fossil rhinoceros carcass of this type has, surprisingly, been described (Chappell et al., 1951). There, a late Tertiary rhinoceros carcass (probably a middle Miocene *Teleoceras*) was surrounded by partially hardened pillow lava as it floated near the shore of a lake in Washington state. Molten lava flowing into the lake at the time created the pillows. When the pillows finally hardened around the carcass, it decomposed, leaving a remarkable cave in the form of a dead rhinoceros with head drawn back, legs extended, and gut distended. Bones of the rhino were found both on the floor of the cave and embedded in its basalt walls (Chappell et al., 1951).

When a carcass floating in the ocean decomposes and is nibbled on by marine scavengers, its bones (probably with some flesh attached) fall off the carcass and drop to the sea floor. In this way, exceptionally well preserved complete individual bones are delivered to the marine sediment. Such bones are associated with other skeletal elements only if the carcass becomes waterlogged and drops to the sea floor. This process would be expected during the high sea level period at the middle of a sedimentary sequence, rather than at the initial marine transgression of a sequence.

In the second process, a land mammal (or its individual bones) is first buried in river channel deposits on land, often after tumbling along the river bed for some time. At the start of a marine transgression, the coast is drowned by rising sea level. Next, coastal currents dig up the old fluvial deposits, winnow out the finer sediment, and concentrate the more durable material (pebbles, petrified wood, teeth, bones, etc.). These fluvial materials are mixed with shark teeth, phosphatic nodules, worn bone fragments, and other durable marine objects to create a transgressive lag bed often found at the base of a shallow water sequence. By this process, terrestrial fossils are secondarily mixed with marine fossils (Manning and Dockery, 1992, p. 15). Unlike the first method, the terrestrial fossils here are generally incomplete and badly worn by mechanical erosion. On the positive side, terrestrial material in marine beds resulting from this process is far more common than in the floating carcass process (the lag concentrate often extends for miles, and is extremely rich in poorly preserved material) and normally includes small animal remains not found the other way.

The floating Byram carcasses. The excellent preservation and isolated nature of the Byram *Metamynodon* skull and *Subhyracodon* jaw leave no doubt that both were deposited onto the sea floor by the floating carcass process. That these Byram fossils occur in the middle of a regression, rather than at the start of a transgression, also supports this hypothesis.

Whether there is any significance to the orientation of both specimens in an upright position (the skull with the teeth down and the jaw with the teeth up) is hard to assess. Their broad bases and lack of mechanical wear make it unlikely that either specimen moved far once it dropped to the sea floor. It is likely that the jaw might drop through the water column most easily with the rounded ventral edges of the jaw (assuming that the throat skin had been mostly lost) at the bottom, and with the fin-like coronoid processes at the top. The same could not be said of the skull, whose concave (or flat, if the tongue were still attached) ventral surface would seem unstable dropping through the water. It may have stayed upright because the large molar teeth made it bottom-heavy.

Even more speculative is the question of how both specimens came to be aligned with the anterior ends pointed west. It is unlikely that any current direction (applied to either the isolated specimens or the carcasses) can be inferred from this. The orientation is probably fortuitous, especially considering that the jaw was deposited long after the skull, and both had traveled far from land (see Paleogeology section).

Burial at sea. It does not appear that the two specimens were exposed on the sea floor for an equal length of time. Based on the size and growth rate of the largest attached *Pycnodonte paroxis* oyster shell on the dorsal side of the *Metamynodon* skull, Dockery (in Manning et al., 1986, p. 6) was able to determine that the skull had lain exposed on the sea floor for at least 15 weeks. It apparently sank slowly into the muddy sediment, probably aided by burrowing crustaceans, over a

considerable time.

In contrast to the *Metamynodon* skull, which served as a substrate for many oysters and corals (Manning et al., 1986, p. 4, 6), the *Subhyracodon* jaw had no attached epifauna. Even with the likely dissolution of most of the aragonitic invertebrates in the area of the jaw (as indicated by the large carbonate nodule between the mandibular rami), calcitic species such as oysters would have survived the dissolution. Because it was buried in a clay-poor, glauconitic sand (which would have been an especially good, clear-water/low-turbidity habitat for attached, filter-feeding organisms), it seems likely that the jaw was buried far more quickly than the skull, probably in a large deposit of sand. Additional evidence for rapid deposition in bed K is the burial in life position of specimens of a burrowing clam.

PALEOECOLOGY

A number of things can be determined about sea floor conditions during the deposition of bed K, and about conditions during the deposition of the Byram Formation in general. Although bed K is not as rich in mollusk diversity as other beds in the outcrop, such as bed H, some invertebrates are known from the bed. Most striking among them is the hermatypic coral *Archohelia vicksburgensis*. Long, cylindrical, complexly-branched, and usually complete specimens of branching coral can be found in bed K (Dockery, personal communication, 1997). This branching coral suggests shallow, relatively clear, sunlit water of normal marine salinity. The preservation of the entire coral suggests rapid burial. The unusual biocoenosis (life assemblage) of the deep-burrowing geoduck clam *Panopea oblongata* consists of individuals preserved in upright living position—as if their long tube-like siphons were still raised to the overlying sediment surface. The live entombment of such able burrowers suggests that their normally clear-water marine environment experienced an event of very rapid deposition to a depth from which they could not recover (Dockery, personal communication).

The Byram mollusk fauna generally suggests a shallow water marine (inner shelf depth) habitat of relatively clear water and normal marine salinity (Dockery, personal communication, 1997). The Byram sea floor supported a diverse community of larger foraminiferans, corals, mollusks, and bryozoans. Although there is evidence for current sorting of mollusk shells in some beds (base of bed F, beds E, H, and L—Dockery in Manning et al., 1986, p. 4), there is no evidence of it in rhino-bearing bed K (Dockery, personal communication, 1997). Based on the foraminiferans of the Byram Formation slightly west of MGS locality 106, near Redwood, Fisher and Ward (1984) suggested that the Byram was deposited in shallow offshore bars, seaward of a bay environment.

Oligocene cooling. Fossil pollen data (e.g., the appearance of *Quercus* [oak] pollen) suggest that the Gulf Coast began a cooling period at the start of the Oligocene (uppermost Yazoo

Clay), in nannoplankton Zone NP21 (Frederiksen, 1988 and 1991). This may have affected the terrestrial coastal flora more than it did the marine benthic community, as it was clearly warm enough to support the symbiotic algae of the hermatypic coral in bed K. The browsing rhino and amynodont provide evidence that the coastal flora was still predominantly wooded, as no grazing (grasslands) forms (*Hyracodon*, *Mesohippus*, etc.) have yet been found.

POSITION OF THE EARLY OLIGOCENE GULF COAST SHORELINE

Due to the erosion of most of the updip nearshore sediment, it is difficult to place the early Oligocene Gulf coastline position. We know that at the northernmost Byram Formation exposure (before it is lost to surface erosion), about three miles north of Redwood in Warren County (about 15 miles north of MGS locality 106), the Byram is still of normal salinity, with no indication that the coast is near. Based on this, and the lack of any indication of a nearby coast (save for two land mammals), one is forced to conclude that MGS locality 106 was many miles offshore.

The Mississippi Embayment. In the late Eocene, the Gulf of Mexico extended as far north as northwestern Tennessee and possibly as far as the southern tip of Illinois, in a northward lobe of the Gulf Coastal Plain called the Mississippi Embayment. This embayment formed over a trench created in the lower Mississippi Valley area by a downdropped rift formed by an aulocogen (in this case a failed tectonic attempt to split North America into east and west halves). Research by the author on fossils from below the Pleistocene cover in northwestern Mississippi and southeastern Arkansas, the deepest part of the Mississippi Embayment, suggests that the Gulf did not occupy the upper Mississippi Embayment in the early Oligocene. Downwarping of the embayment by the rift may have ceased in the late Eocene. Clearly, there was still at least a short bay in the area during the early Oligocene, as shown by the orientation of the Vicksburg Group outcrop, but it may not have extended much farther north than Greenville, Mississippi. Uncertainty about the condition of the early Oligocene Mississippi Embayment adds to the problem of locating the Vicksburg-time coastline. A major sea level lowstand occurred after the Vicksburg Group was deposited, causing the middle Oligocene coastline to shift far to the south, and exposing many sea floor regions to subaerial erosion.

Turbidity from fresh-water plumes. It is noteworthy that the Byram Formation isn't equally "shelly" along its exposure in central Mississippi. It is poor in mollusk shells in its type area at Byram along the Pearl River, becomes "shellier" in the Big Black River exposure, and is most shell-rich in the Vicksburg area (Dockery, personal communication, 1997). This may suggest that the turbidity was increasing eastward toward the Pearl River area. It may also suggest that there was a river outflow into the Gulf in that area, perhaps even the early

Oligocene Pearl River itself. The Byram Formation becomes shelly again to the east in Smith County outcrops. Land-derived wood is rare in the Byram (Dockery, personal communication, 1997), so concentrations of wood in the formation cannot be used to locate deltas. An analysis of the percentage of terrigenous sediment in the Byram along strike might establish a delta outflow.

Coincidence? Because the early Oligocene coastline is so difficult to determine, it is probably impossible to locate with certainty the river delta that sent the two land mammals floating out into the Gulf of Mexico toward MGS locality 106. Westward-moving longshore currents similar to those in the Gulf today may have carried them far west of the delta from which they entered the Gulf. Still, it would be a remarkable coincidence if similar currents did not direct the carcasses of two very differently-sized animals (one pony-sized and one hippo-sized) at greatly different times (the rhino jaw is eleven feet higher in section than the amynodont skull), floating them miles out into the Gulf of Mexico, and then deposit them within 150 feet of each other. It can only be hoped that more bones were similarly deposited in the area, and are yet to be found.

CORRELATION TO THE HIGH PLAINS

The hunt for the sea-going NALMA. As interesting as the geographic range extension and odd taphonomy of the two Byram land mammals are, the most important aspect of the specimens is the correlation of the marine bed (which can be directly tied to the Oligocene type sections in Europe) to the provincial "ages" (not true chronostratigraphic ages, as they don't correlate directly to marine stages) of the North American Land Mammal "Ages" (NALMA). The NALMA series was drawn up by a committee of distinguished vertebrate paleontologists, headed by fossil rhinocerotoid specialist H. E. Wood (Wood et al., 1941). The Wood committee based their series of Tertiary "ages" (they have since been extended downward into the late Cretaceous) on the terrestrial mammal faunas of the American High Plains and Rocky Mountain intermontane basins (with a few referred faunas from the Coastal Plain) then known. Each "age" included certain mammalian index fossils and characteristic fossils. The idea was to cover all Tertiary time with a series of distinctive mammal faunas.

The NALMAs have had a mixed history. They have been extremely helpful in correlating terrestrial deposits all across the country, on both the High Plains and Coastal Plain, even to the high Canadian Arctic of Ellesmere Island. They have been instrumental in constructing a sequence of migration events into and out of North America to and from east Asia, western Europe and Scandinavia (across an only partly opened North Atlantic), the Caribbean Islands, and South America. They have been a stabilizing influence on North American Tertiary and Quaternary biostratigraphy, when concepts of epochs, glacial events, distinctive volcanic ash beds, and supposedly distinctive terrestrial magnetic anomalies have

radically changed. Still, this stability has also created a problem. The NALMAs are primarily set up for faunal analysis, not for geochronology. Problems have arisen when the approximate age assignments of the NALMAs originally assigned have been taken as gospel. The Oligocene is an excellent case in point. As originally conceived, the Oligocene included three NALMAs—Chadronian the oldest, Orellan the middle, and Whitneyan the youngest. They were thought of as early, middle, and late Oligocene, respectively. Even though correlation problems arose (they currently range from late Eocene to middle early Oligocene), the “age” assignments made by the Wood committee weren’t questioned for years. They gained a weight they were never intended to have.

The Byram gets a new NALMA. The NALMA originally assigned to the Byram (Manning et al., 1986, p. 14) is an example of how complex NALMA correlation problems can become. Following the correlation of calcareous nannoplankton Zone NP22 with the Chadronian NALMA in Prothero et al. (1982), problems soon arose. First, the age of the Eocene/Oligocene boundary was raised about three million years—from 36.5 Ma (Berggren et al., 1985) to 33.7 Ma as a result of new dating of the boundary stratotype at Massignano, Italy (Montanari et al., 1988). Then new radiometric dates on volcanic ashes in the upper Eocene upper Yazoo Clay of Mississippi yielded an age of 34.3 Ma (Berggren et al., 1992, p. 37, 40; Obradovich et al., 1993). With the new stratotype boundary date of 33.7, the new upper Yazoo date confirmed that the Jackson/Vicksburg Group contact was just above the Eocene/Oligocene boundary. This made sense with the Byram as Chadronian, so long as the Chadronian was early Oligocene, as the Wood committee had said. Unfortunately, new radiometric dating on the High Plains White River Group shifted the Chadronian/Orellan boundary backward in time from 32.4 to 33.9 (Swisher and Prothero, 1990; Prothero and Swisher, 1992; Berggren and Prothero, 1992; Prothero, 1994), just below the new Eocene/Oligocene boundary at 33.7. With the Chadronian now late Eocene, and therefore equivalent to the Yazoo Clay in Mississippi, it was no longer possible for the Byram Formation, in the upper Vicksburg Group, to correlate with the Chadronian.

More recent correlations place nannoplankton Zone NP22 within the Orellan NALMA (Prothero, 1994, fig. 1), which follows the Chadronian NALMA. The Orellan is thought to have lasted only two million years, from 34 to 32 Ma (Swisher and Prothero, 1990).

The Mississippi/South Dakota connection. As originally formulated by the Wood committee (Wood et al., 1941), both *Subhyracodon occidentalis* and *Metamynodon planifrons* were considered index fossils of the Orellan NALMA. Curiously, given the age changes in the NALMAs, the Orellan was originally correctly considered correlative of the Rupelian (Wood et al., 1941, pl. 1), as it is today.

The assignment of the Byram to the Orellan, rather than the Chadronian, makes more sense for both the *Subhyracodon* and *Metamynodon*. As was noted in Manning et al. (1986, p. 14),

most specimens of *M. planifrons* in South Dakota come from the “*Metamynodon* Channels” in the Scenic Member of the Brule Formation, White River Group, in the Orellan NALMA (the Scenic Member of South Dakota is the equivalent of the Orellan Member of western Nebraska, for which the Orellan was named). *Metamynodon* specimens are rare in the Chadronian NALMA. Likewise, *Subhyracodon occidentalis* is restricted to the Orellan NALMA. Because of the primitive nature of the Byram specimen, the Byram Formation appears to correlate best with the early Orellan, though not the earliest part.

The rain on the plains. The Orellan of the High Plains is now thought to be the start of a period of cooling and drying, with the dense forests of the Chadronian undergoing a transition in the Orellan to a wooded grassland, ending in open grasslands in the late Oligocene Arikareean. *Subhyracodon* seems to have survived this environmental transition just fine (Prothero, 1994, p. 153), though its descendant, *Diceratherium*, seems to have had problems adapting to the new grasslands habitat, as it becomes very rare at the end of the Arikareean and stays rare till it becomes extinct.

Predictions. If the presence of two different-sized browsers suggests that the early Oligocene Gulf Coast was densely wooded, it is perhaps surprising that no browsing artiodactyls have yet been recovered from the Vicksburg Group. Common High Plains Orellan taxa that might be expected on the Coastal Plain include the small early camel *Poebrotherium* and the tiny deer-like *Leptomeryx*. If, as suggested earlier, only larger carcasses were able to float as far as MGS locality 106, then possibly the large, scavenging, pig-like entelodont *Archaeotherium* might be expected. As noted in the *Metamynodon* report by Manning et al. (1986, p. 14), the most likely candidate for the next Byram land mammal is still the semiaquatic associate of *Metamynodon* in the “*Metamynodon* Channels”—one of the long-snouted anthracotheres.

The importance of the Mississippi finds. The significance of land mammals in the Byram Formation seems to have been lost in some quarters. In a major review of North American Oligocene terrestrial mammal faunas, the following surprising statement was made: “To the best of our knowledge, there are no occurrences of Chadronian, Orellan, or Whitneyan land mammals in deposits that can be directly related to any marine sequence” (Emry et al., 1987, p. 128). What the statement underscores is the significance of the two Orellan mammals in the marine Byram Formation—apparently the only such records of their kind.

Unlike the Miocene, where many terrestrial mammals are known from the Gulf Coastal Plain of Texas and Florida (Tedford and Hunter, 1984), the only good Oligocene terrestrial fauna yet published from the Gulf and Atlantic coastal plains is from a terrestrial sinkhole deposit in northern Florida (Patton, 1969), not from a marine bed. Middle Oligocene terrestrial faunas are likely to be common in the limestone region of northern Florida, as sinkholes would be an inevitable result of the major sea-level lowstand of that time (equivalent to the gap in Mississippi’s

Oligocene record between the Vicksburg Group and the Chickasawhay Limestone).

Another rare Mississippi fossil further underscores the unfortunate inability of reasonable fossil correlation to budge nearly intractable NALMA age assignments. A new genus of titanotheres, *Notiotitanops*, was named in 1942, based on a well preserved skull and jaw found in a middle Eocene marine bed (what is now the Archusa Member of the Cook Mountain Formation) near Quitman, in Clarke County, Mississippi (Gazin and Sullivan, 1942). The NALMA assignment of the titanotheres was clear - although new, its affinities were with Uintan NALMA titanotheres of the intermontane basins of the Rocky Mountains (Gazin, in Gazin and Sullivan, 1942, p. 3-4). The problem was that, as originally conceived by the Wood committee (Wood et al., 1941), the Uintan NALMA was considered late Eocene. Gazin pointed out that the Mississippi titanotheres provided evidence that the Uintan might be middle rather than late Eocene, but the suggestion was ignored. In more recent correlations, the Duchesnean/Chadronian boundary has become the middle/late Eocene boundary (Prothero, 1995, fig. 3). Thus, the conflict was entirely artificial—the Uintan (which precedes the Duchesnean) is middle Eocene. It probably must be accepted that simple fossil correlations will never be given the weight of radiometric age dates; still, they deserve more credence than given in the past.

A REVIEW OF LAND MAMMALS FROM MARINE BEDS IN MISSISSIPPI

Mississippi is surprisingly rich in the generally rare occurrence of land mammals in marine beds—five different beds bear them, ranging in age from late Cretaceous to early Oligocene (excepting the late Oligocene, almost the entire range of time when Mississippi lay beneath the waters of the Gulf of Mexico). In chronologic order of bed age, the five terrestrial-in-marine mammal records are as follows:

1. A single unidentified eutherian mammal partial lower molar from the late Cretaceous (late Santonian) basal Tombigbee Sand of Vinton Bluff, Clay County (Emry et al., 1981).

2. A diverse fauna of small mammals (mostly rodent teeth) from the latest Paleocene upper Tuscaloosa Formation, middle Wilcox Group, of the Red Hot Truck Stop site in Meridian, Lauderdale County (Dockery et al., 1991; Beard et al., 1995; Dockery, 1997, p. 38, fig. 19). This important fauna, called the Red Hot local fauna, has recently been assigned an early Wasatchian NALMA (Beard et al., 1995). This is a contradiction of earlier usage, as the Wasatchian had traditionally been considered entirely early Eocene.

3. A single partial omomyid primate lower jaw fragment with a third molar was recovered ten feet above the latest Paleocene faunal level at the Red Hot Truck Stop locality, in the early Eocene Bashi Formation, upper Wilcox Group (Beard and Tabrum, 1991; Dockery et al., 1991; Dockery, 1997, p. 40). This level has also been assigned a Wasatchian NALMA. A jaw

fragment with molar and a jaw fragment with a molar and premolar from the Bashi Formation at Gallagher Creek in Meridian were identified, respectively, by Beard and Tabrum (Dockery, 1997, p. 40) as the small horse *Hyracotherium* and the creodont *Protomus deimos*, but were lost in a return shipment before they were formally described.

4. Skull, jaw, and rib fragments of the titanotheres *Notiotitanops mississippiensis* from the middle Eocene Archusa Member of the Cook Mountain Formation, Claiborne Group, from near Quitman, Clarke County (Sullivan, 1942, p. 161-162; Gazin and Sullivan, 1942; Dockery, 1997, p. 41). A Uintan NALMA has been assigned to the site.

5. Skull of *Metamynodon planifrons* from the early Oligocene Byram Formation, upper Vicksburg Group, from near Edwards, in western Hinds County (Manning et al., 1986; Dockery, 1987; Dockery, 1997, p. 47, fig. 22). Previously assigned a Chadronian NALMA, it is re-assigned an early Orellan NALMA here. The lower jaw of the rhino *Subhyracodon occidentalis* described here from the same site has previously been noted in Dockery and Manning, 1990, and Dockery, 1997, p. 47, fig. 23.

Of these five records, numbers 1-3 probably were reworked from previously buried river sediment and re-buried in a marine transgression, and numbers 4-5 were likely from floating carcasses carried out to sea (see Taphonomy section).

One further record should also be noted, for the sake of completeness: several well-preserved rib fragments from the middle Eocene Kosciusko Formation, Claiborne Group, of Clarke County, were originally reported (based on an identification by Judith Schiebout) as rhinoceros (Dockery, 1980, p. 45-46), but are actually rare records of a very early whale, as yet the oldest recorded from the state.

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