

# Systematic and Biomechanical Studies On Fossil Vertebrates in Badlands NP

By William P. Wall

Beginning in 1982, students from Georgia College, a branch of the University System of Georgia, have engaged in summer field expeditions to the rich Eocene/Oligocene rocks of southwestern South Dakota – Badlands NP and the surrounding public and private lands. Since 1987, a park collecting permit has provided access to the richest deposits in the area. Georgia College's collection of Eocene/Oligocene fossil vertebrates now is approximately 8,000 specimens, representing more than 40 genera. This collection has made Georgia College a center for study on mammalian evolution approximately 37 to 25 million years ago.

Paleontologic research at Georgia College is concentrated into two major areas, systematics and biomechanical analyses. Preliminary results of several of these projects are presented here by Dr. Wall, a Georgia College professor of biology.

The Oligocene was a time of transition in North America, both climatically and faunally. The Chadronian beds at the base of the fossil bearing sequence indicate this region was an open forest environment at the end of the Eocene. Throughout the Oligocene the region became drier; the habitat probably was similar to modern African savannas. The mammalian fauna is a mixture of archaic and advanced taxa. Artiodactyls, for example, exhibit a broad spectrum from primitive leptacanthids to advanced protoceratids.

Perissodactyls, including rhinoceroses, horses, and titanotheres, make up the other major group of Badlands fauna herbivores. I chose the South Dakota Oligocene for our fossil expeditions because of one rhino in particular that comes from there. *Metamynodon* (Fig. 1) can be found in the Orellan (early Oligocene) channel sandstones of South Dakota, but is rare or absent in equivalent age deposits of adjacent states.

*Metamynodon* is a member of the extinct rhinoceros family Amynodontidae, the group on which I based my own doctoral dissertation. Amynodontids in general were regarded as semi-aquatic animals reminiscent of hippopotami. I have shown (Wall 1980, 1982, 1989) that an aquatic lifestyle probably is valid only for *Metamynodon* and its close relatives, not for the entire family. My continuing studies on amynodontid biomechanics center on locomotor mechanics and feeding and are aimed at better interpretation of this group's life habits. Post-cranial material of *Metamynodon* is rare in museums, so the Georgia College expeditions were begun with the intent of providing adequate research material. These specimens have proved useful in systematic and biostratigraphic work (Wall 1989, in press) and form the nucleus for my biomechanical studies.

Walker Hickerson undertook a project of direct interest to my work for his master's thesis. *Hyracodon* is a small rhinoceros (extinct family Hyracodontidae), common in the Badlands. This animal is typically reconstructed as a gracile animal and colloquially referred to as "the running rhino." No

one before Hickerson had ever tested the biomechanical feasibility of this mode of life. Hickerson compared *Hyracodon* to modern cursorial (running), subcursorial, and mediportal (weight bearing) mammals in the following areas: Limb bone indices, relative development of locomotor muscles, and in force/out force ratios for these muscles. Hickerson concluded that *Hyracodon* was no cursorial. This rhino exhibited locomotor adaptations more reminiscent of a feral pig or peccary than a pronghorn.

Although rhinoceroses were the initial reason for working in the Badlands, it soon became apparent that we were collecting many other fossils of potential research value. One group of artiodactyls in particular – the oreodonts – is associated with the Badlands deposits. *Merycoidodon* is the most common fossil found in this region, strongly implying that this animal was a major component of the Oligocene fauna. Agriocherids are close relatives of oreodonts, but for some reason are much rarer in the fossil record. The two animals are similar in many ways, yet the difference in their abundance suggests they were fundamentally different in a significant way.

Many paleontologists believed agriocherids were arboreal (Colbert and Morales 1991); however, except for claws these animals exhibit none of the anatomical traits typical of large tree climbers (Coombs 1983). If these animals were terrestrial, how did they minimize competition with oreodonts? Since feeding behavior is a major ecological factor, one of my graduate students, Michael Shikany, undertook a comparative analysis of dentition and jaw mechanics in *Agriocheris* and *Merycoidodon*.

Dental wear facets are distinctly different in the two animals; *Agriocheris* facets indicate primarily a tooth/food contact characteristic of a shearing mastication, while *Merycoidodon* teeth exhibit a tooth/tooth pattern characteristic of grinding. Comparison of premolar to molar surface area ratios corroborates the wear facet data in that the ore-

odont has relatively more posterior molar surface – the area where grinding takes place. Conversely, the well developed sagittal crest (site of origin for the temporalis muscle) of *Agriocheris* points to the importance of shear in this herbivore.

Shikany concluded that agriocherids probably occupied a woodland habitat, feeding on shrubbery (a declining niche during the Oligocene) and that oreodonts were adapted for feeding on the savanna grasslands. This dietary difference probably accounts for the demise of the agriocherids and the success of the oreodonts during the Miocene.

The Badlands strata also contain important evidence of the initial radiation of rodents, including the first representatives of several modern families. Sherri Ray, for her graduate work, examined the jaw mechanics of *Ischyromys*, a common protrogomorphous rodent. Protrogomorphy (all branches of the masseter muscle originate in the zygomatic arch) is the primitive jaw muscle pattern for rodents; only one animal, *Aplodontia*, the mountain beaver, retains this masseter arrangement. Ray was particularly interested in learning what advantage the sciuriformous muscle pattern provided to animals like squirrels.

Sciuromorphy, one of the three jaw muscle patterns in advanced rodents, is characterized by having the lateral branch of the masseter expand its origin onto the rostrum of the skull via a zygomatic plate. *Protosciurus*, the first true squirrel, is a rare component of Badlands fauna. Since this animal was protrogomorphous, substitution of the more common *Ischyromys* in a jaw mechanics comparison with modern squirrels is valid. Ray dissected recent squirrels to produce a vector analysis for the temporalis and the three heads of the masseter (lateralis, medialis, and superficialis). The relative size and orientation for the same muscles were determined from study of several fine *Ischyromys* skulls in our collection.

Results show that modern squirrels have exag-

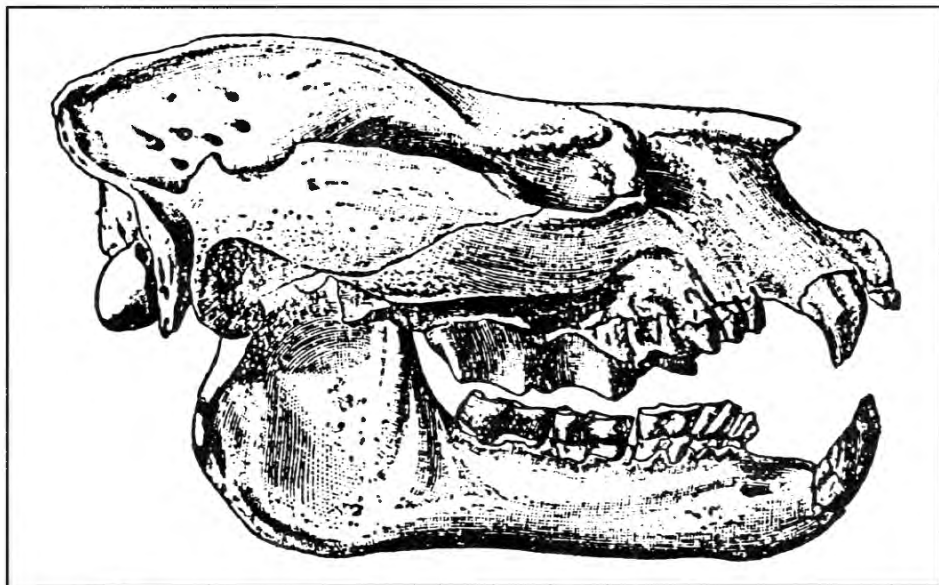


Figure 1. Lateral view of a skull and jaws of *Metamynodon*, a semi-aquatic rhinocerotoid from the Oligocene of North America (from Osborn, 1898).

generated the anterior and posterior components of these muscles when compared to *Ischyromys* (Fig. 2). The vector directions for *Ischyromys* indicate this animal, and probably most protrogomorphs, could not have split the masticatory cycle into separate incisor and cheek teeth phases as efficiently as modern rodents. Evergrowing, chisel-like incisors are the hallmark of rodent success; hence it is not surprising that rodents that could not take optimal advantage of this tool lost out to rodents that could.

Through concerted effort we have built an impressive Oligocene microvertebrate collection. Our four skulls of the burrowing lizard, *Rhineura*, give us one of the largest samples of this intriguing animal. Our collection also contains complete or nearly complete skulls of *Protosciurus*, *Agnotocaster*, *Paleocaster*, *Eumys*, eomyids, several as yet unidentified genera of rodents, the insectivore *Cenitetodon*, and the marsupial *Peratherium*. These, along with several hundred jaws and maxillae, will form the nucleus of a graduate thesis project by Murali Thirumal, our best microvertebrate collector.

A separate but related thesis project involves a microvertebrate accumulation from a stream channel deposit from the Chadronian in the Badlands NP's Southern Unit. This isolated riparian sandstone is important for its early age and rarity of fossils from a river environment (most of the beds in the badlands preferentially preserve members of the terrestrial ecosystem). Due to the nature of the soil however, it will take several more years of collecting to obtain sufficient specimens to characterize this fauna adequately.

These projects provide an indication of the abundance of paleontologic work still to be done on Badlands fossils. Fieldwork and research by faculty and students at Georgia College should continue to contribute to our knowledge of vertebrate evolution in North America during the Oligocene.

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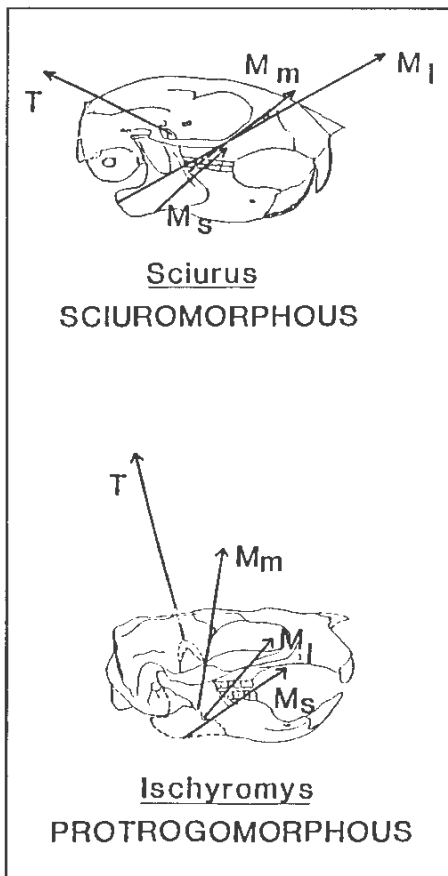


**Figure 2.** Vector analysis of the major jaw muscles in a modern squirrel, *Sciurus*, and the Oligocene rodent, *Ischyromys*. Abbreviations: Ml, lateral masseter; Mm, medial masseter; Ms, superficial masseter; T, temporalis.