

# THE FEEDING MECHANICS OF *LEPTAUCHENIA DECORA* BASED ON SPECIMENS FROM THE WHITNEYAN (OLIGOCENE) OF BADLANDS NATIONAL PARK, SOUTH DAKOTA

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**Abstract**—*Leptauchenia* is a common fossil mammal found in late Oligocene strata exposed in Badlands National Park, South Dakota. The life habits of this small ungulate have been the subject of much speculation. Proposed life histories have ranged from a semi-aquatic beaver like existence to a semi arid lifestyle similar to African rock hyraxes. In this study we apply biomechanical analyses to interpret the cranial and dental specializations of *Leptauchenia* compared to the basal morphotype, *Prodesmatochoerus*. The results from distortion grid, quadrant analysis, dental indices and vector analysis of reconstructed adductor musculature indicate that *Leptauchenia* was adapted to a more abrasive diet than normal for oreodonts. The vector for the masseter/pterygoideus complex is shifted anteriorly and is increased in magnitude relative to the temporalis compared to basal oreodonts. Dental characters of *Leptauchenia* compare most closely with modern selenodont artiodactyls that are mixed feeders in closed habitats. We believe the cranial morphology of *Leptauchenia* is the result of a selective shift in the feeding niche of this oreodont from browsing on succulent vegetation to mixed feeding on more fibrous plants in response to climatic shifts that resulted in more xeric vegetation.

## INTRODUCTION

Merycoidodontids were a common part of the North American paleofauna during the transitional period between the decline of primitive mammalian herbivores (e.g., phenacodontids) in the Eocene and the rise of modern pecoran groups in the Miocene. Merycoidodontids and the less diverse and more primitive Agriocheridae, make up the Oreodontoidea, commonly referred to as “oreodonts.” Oreodonts are small to medium sized selenodont artiodactyls that are endemic to North America with a stratigraphic range from the early Uintan to late Hemphillian NALMA (46.7-5.2 Ma). Oreodonts exhibit a unique combination of suiform and ruminant features. They are distinguished from other selenodont artiodactyls by the absence of a diastema, a primitive pig-like tarsus and a derived dental condition in which p1 is enlarged and caniform while the lower canine is reduced and incisiform. The basic oreodont body plan is pig-like in form having a dense robust cranium, short neck, and short limbs.

The subfamily Leptaucheniiinae, an enigmatic group with unusual facial features and an early trend toward hypsodonty, are among the most common Whitneyan and early Arikarean mammals found in the White River sediments exposed in Badlands National Park (BADL), South Dakota. Opinions on the life habits of leptaucheniians have ranged from semi-aquatic beaver-like animals (Scott, 1929) to inhabitants of rocky habitats where they may have formed social groups similar to hyraxes (Lander, 1998). Joeckel (1992) examined the auditory bullae of *Leptauchenia* using CAT scans and concluded that the enlarged bullae were an adaptation for increased low frequency hearing. Most opinions about the possible life habits of leptaucheniians are based on either comparative anatomy or depositional geology. The purpose of this paper is to present a biomechanical analysis of feeding adaptations in *Leptauchenia decora* from the Poleslide Member of the Brule Formation (Whitneyan NALMA) in BADL.

## MATERIALS AND METHODS

### Specimens

The classification scheme and phylogenetic interpretation for *Leptauchenia* used in this paper is that of Cobabe (1996) for genus and species level taxonomy and Lander (1998) for higher level taxonomy. All

of the *Leptauchenia* specimens utilized in this study were collected in BADL in Whitneyan aged exposures that are referred to in the geologic literature as “the *Leptauchenia* Beds.” We used specimens of *Prodesmatochoerus periculatorum* (= *Merycoidodon culbertsoni*) from the Orellan beds in BADL as a functional out group for our biomechanical analysis of the feeding apparatus in *Leptauchenia decora*. All the specimens used in this study are housed in the Georgia College & State University Vertebrate Paleontology collection (GCVP). Of the 104 catalogued specimens of *Leptauchenia* in the collection, we only used specimens identified as young adults (m3 fully erupted but relatively little wear on the molars).

### Biomechanical Analysis

#### Skeletal Analysis

Distortion grids (Thompson, 1961) of lateral and ventral views of *Leptauchenia* were performed using *Prodesmatochoerus* (the likely primitive morphotype for merycoidodontids, Wall and Shikany, 1995) as a template. A quadrant analysis was performed on mandibles of *L. decora* and *P. periculatorum* (see Mead and Wall, 1998 for a similar study).

#### Dentition

Hypsodonty Index (HI) is the height of m3 divided by its width. Molar height was measured from the tip of the protoconid to the crown/root interface directly below it on the labial side. Molar width was the maximum distance between the protoconid and the entoconid. Lengths of the lower molar and premolar series were measured at bone height to produce a premolar/molar ratio. Average values for all ratios were obtained from ten specimens of *L. decora* and ten of *P. periculatorum*. Wear facets of *L. decora* were examined and compared to those described by Greaves (1973). All linear measurements were taken with Mitutoyo digital calipers, accurate to within 0.01 mm. A two factor analysis of variance (ANOVA) was performed using the SAS® program on the quantitative measurements to determine statistical significance of differences between the two taxa. Comparative data on modern herbivores is from Wall and Collins (1998).

## Adductor Musculature

Our estimates for vector direction and magnitude for the temporalis and masseter/pterygoideus complex are based on reconstruction of the jaw adductor musculature in ten *Leptauchenia* specimens and then averaging the results. Modeling clay was used to estimate the muscle mass for each of the jaw adductor muscles (see technique in Turnbull, 1970). Six muscles were evaluated in this study, the dorsal Temporalis (Td), ventral Temporalis (Tv), Zygomaticomandibularis (Zm), Masseter (M), internal Pterygoideus (Pi) and the external Pterygoideus (Pe). Dissections of heads of *Sus scrofa* and *Odocoileus virginianus* were made to familiarize the authors with this musculature in modern artiodactyls. Muscle descriptions provided by Greaves (1972) also influenced our reconstruction of *Leptauchenia* adductor musculature.

## RESULTS

### Skeletal Analysis

The *Leptauchenia* skull is highly modified from the primitive oreodont morphotype (Fig. 1). *Leptauchenia* has a shortened rostral portion of the skull, enlarged dorsally displaced orbit and a dorsoventrally expanded temporal and mandibular angle region. With respect to skull width versus length, *Leptauchenia* is clearly more brachycephalic than *Prodesmatochoerus*. *Leptauchenia* also has a more slender muzzle relative to palatal width than *Prodesmatochoerus*.

*Leptauchenia* is different from *Prodesmatochoerus* with respect to the distribution of bone in the region of the mandible sculpted by the insertion of the adductor musculature (Fig. 2). In *Leptauchenia* the percentage of bone falling within each quadrant is: I 17.4%; II 16.1%; III 31.7%; and IV 34.8%. The distribution of bone in the four quadrants for *Prodesmatochoerus* is: I 18.8%; II 6.8%; III 14.5%; and IV 59.8%. Seventy-four percent of the mandibular angle lies beneath the occlusal

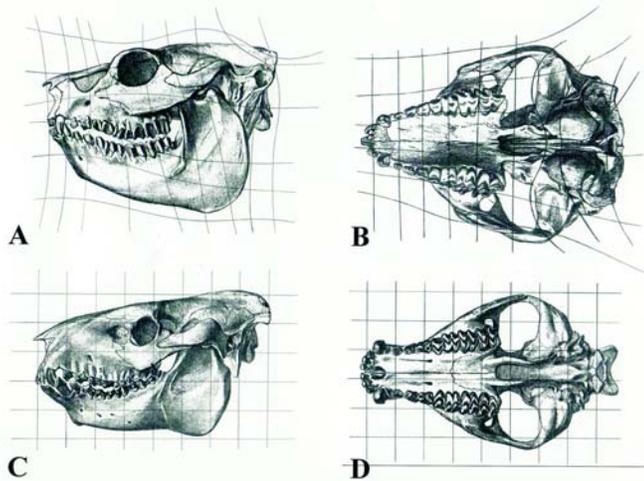


FIGURE 1. Distortion grid analysis of the A, lateral and B, ventral view of *Leptauchenia decora* using *Prodesmatochoerus pericolorum* (C and D) as the template. Modified from Scott (1940).

plane in *Prodesmatochoerus*. Only 66.5% of the mandibular angle lies below the occlusal plane in *Leptauchenia*.

### Dentition

The ratio of unworn height to width of m3, the hypsodonty index, revealed significant differences between *L. decora* and *P. pericolorum*. The average hypsodonty of *Leptauchenia* was 2.01 while *Prodesmatochoerus* averaged 1.40 (the statistical difference between the two samples has a P value of 0.0001). Measurements of molar and premolar series revealed a higher premolar ratio in *P. pericolorum* (0.87) than *L. decora* (0.74) (with a P value of 0.0075).

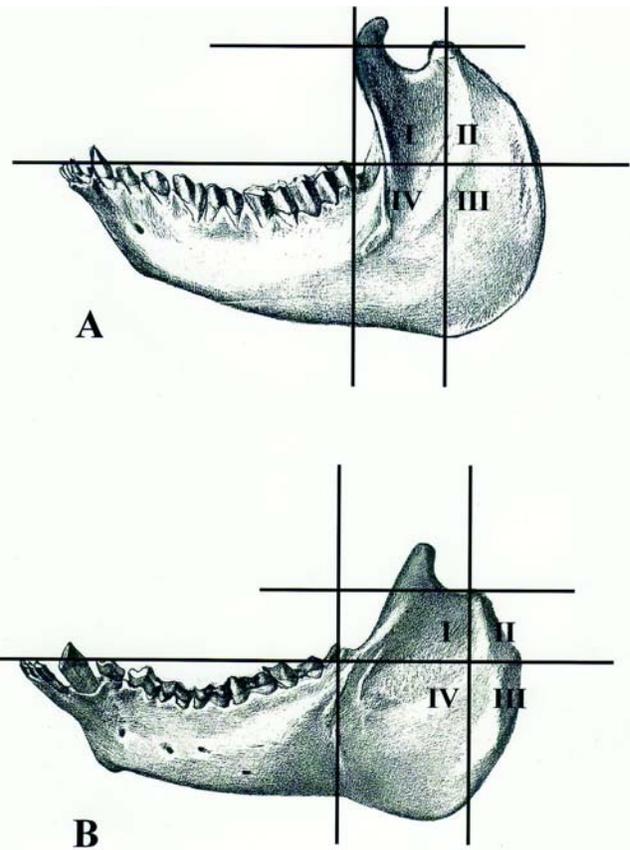


FIGURE 2. Lateral view of the mandibles of A, *Leptauchenia decora* and B, *Prodesmatochoerus pericolorum* illustrating quadrant analysis of the mandibular adductor region. Modified from Scott (1940).

### Adductor Musculature

A vector diagram of the major jaw adductor musculature is provided in Figure 3. The jaw musculature of oreodonts is peculiar among ungulates due to the well-defined separation of the dorsal and lateral temporalis and the presence of a distinct zygomaticomandibularis. The temporalis group originates on the braincase bordered by the sagittal and nuchal crests. The dorsal and lateral temporalis are separated by a large diagonal ridge that tends to follow the parietosquamosal suture from the middle of the braincase to the pterygoid crest in *Prodesmatochoerus* and to a protuberance at the level of the posterior root of the zygomatic arch in *Leptauchenia*. *Leptauchenia* also exhibits one or two smaller, more anterior ridges that run parallel to the main ridge. The lateral temporalis inserts on the coronoid process and likely functioned in a similar manner to the standard artiodactyl temporalis. The dorsal temporalis inserts on a boss found just posterior to m3 on the lingual side of the dentary. The diagonal groove in the temporal region of the skull keeps the dorsal temporalis isolated from the lateral temporalis.

Oreodonts differ from most other ungulates in having a well-defined masseteric fossa and a medial muscle attachment site on the zygomatic arch. In many pecorans, the zygomaticomandibularis is fused to the deep masseter, however, it is likely that this muscle retained its independence in oreodonts. The masseter muscle group in ungulates is commonly separated into the deep and superficial masseter muscles, however, we concur with Greaves (1972) assessment that these muscles are not separate in oreodonts.

The pterygoid group is made up of the internal and external pterygoid muscles. The origin of this group is concentrated on the pterygoid process but includes most of the pterygoid bone as well as the connecting palatal bone. The internal pterygoid is the larger of the two muscles. It inserts on the medial side of the angular process of the dentary. The

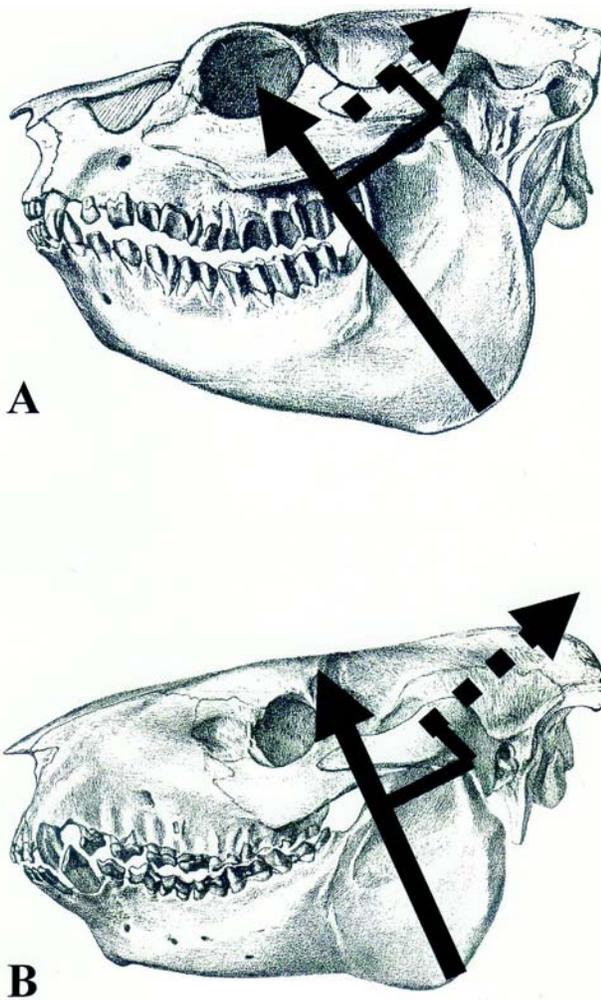


FIGURE 3. Lateral view of the skull and mandible of **A**, *Leptauchenia decora* and **B**, *Prodesmatochoerus periclorum* illustrating vector analysis of the mandibular adductor musculature. The temporalis group is represented by a dashed vector and the masseter/pterygoideus group is depicted with a solid vector. Total vector lengths are drawn to the same scale for the two taxa. Modified from Scott (1940).

external pterygoid is much smaller than the internal portion. Its origin is posterior to that of the internal pterygoid on the lateral surface of the pterygoid process. The insertion of this muscle is immediately below the mandibular condyle on the medial side of the jaw. As is common among ungulates, the pterygoid and the masseter are the largest two muscle groups. They act synergistically as the main muscles in transverse and anterior movement of the jaw.

Our estimates for the percentage of total adductor muscle mass in *Leptauchenia* are: masseter and zygomaticomandibularis 41.5%, pterygoideus complex 29.4% and dorsal and lateral temporalis 29.1%. The corresponding percentages for *Prodesmatochoerus* are: 38%, 23.9% and 38.1%. These percentages are reflected in the lengths of the vectors illustrated in Figure 3.

## DISCUSSION

Many features of the *Leptauchenia* cranium, a typical representative of the subfamily Leptaucheniinae, are the result of a marked departure from other lineages of oreodonts with respect to the feeding component of the niche. Not only are leptaucheniinae among the smallest of oreodonts (Schultz and Falkenbach, 1968), they are also the first selenodont artiodactyl group to evolve any degree of hypsodonty. *Leptauchenia* displays the following characteristics associated with mastication that

distinguish this lineage of oreodonts: smaller and more brachycephalic skull; anteroposteriorly shortened braincase; reduced rostrum; relatively higher sagittal and nuchal crests; massive zygomatic arch; expanded mandibular angle; relatively narrow muzzle; reduced caniniform teeth; small, peg-like incisiform teeth that exhibit wear facets; relatively high hypsodonty index; significant increase in molar surface area relative to premolars; submolariform p4; anterior shift in the orientation of the masseter/pterygoideus vector; and increase in the mass of the masseter/pterygoideus relative to the temporalis.

These morphological differences correlate closely with dietary differences. The hypsodonty index and relative premolar row length for *Leptauchenia* correlate most closely with modern herbivores occupying a mixed feeding, closed habitat niche (whose HI mean equals 2.07 with a mean premolar ratio of 0.73), while *Prodesmatochoerus* compares favorably with modern selective browsers with respect to these dental parameters (mean HI of 1.5 and premolar ratio of 0.86). The anterior expansion of the zygomatic arch (Fig. 1) and the posterior expansion of the mandibular angle in *Leptauchenia* (Fig. 2) indicate a significant anterior shift in orientation of the masseter (and pterygoideus with respect to the mandibular angle) in this taxon (compare vector directions in Fig. 3). The mass of the masseter/pterygoideus has also increased relative to the temporalis (compare vector lengths in Fig. 3). The anterior shift in muscle orientation increases the horizontal vector component of these muscles. The horizontal vector is most important in the lingual phase (jaw moves forward and downward) of the chewing cycle during which the molars are used to grind food. The rearrangement of the masseter/pterygoideus musculature also results in an increase in size of the lever arm, and therefore the out force, of these muscles. Increased brachycephaly in *Leptauchenia* also correlates with greater side to side movement during mastication (a direction of movement only important during grinding activity). Mastication in *Prodesmatochoerus* reflects more of a compromise between the buccal (jaw movement is forward and upward during which shearing is emphasized) and lingual phases of mastication in this basal oreodont.

It is possible that the cranial and dental modifications evident in *Leptauchenia* reflect the small size of these oreodonts. Body size and metabolic rate are inversely related in mammals. It is therefore possible that these modifications could be due to the demands associated with quantity of food required relative to body size. Janis (1988) noted another complicating factor in that hypsodonty index may more accurately reflect feeding at ground level rather than actual dietary preference. However, we believe the totality of the cranial, dental and adductor muscle adaptations evident in *Leptauchenia* support the hypothesis of a dietary shift in this group. If an increase in the quantity of food intake was the primary selection factor in leptaucheniinae, then a behavioral response that increased foraging time is a more likely solution to the problem. The weight of evidence indicates that *Leptauchenia* fed on a diet that required more thorough mastication than typical for oreodonts. We believe *Leptauchenia* was adapted to feeding on a diet consisting of more fibrous, less succulent vegetation, possibly even some early grasses. Prothero (1994) came to a similar conclusion based on paleoclimate evidence. While our data show that the dentition of *Leptauchenia* compares most favorably with modern artiodactyls that are mixed feeders in a closed habitat, we keep open the possibility of a more open habitat niche since the auditory features of *Leptauchenia* appear to be adapted to a more open environment (Joekel, 1992).

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