



The first application of the mesowear method to endemic South American ungulates (Notoungulata)

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ABSTRACT

Notoungulates were the most diverse and abundant clade of endemic South American ungulates, present in nearly all Tertiary faunas. Hypsodont dentitions evolved in several notoungulate lineages by the early Oligocene, and by the middle Miocene, four families were characterized by hypselodont (ever-growing) cheek teeth. The presence of hypsodont and hypselodont dentitions in notoungulates has generally been interpreted as indicating grazing and/or open habitat feeding, but few studies have attempted to test this assumption using other methods of dietary inference. The present study uses mesowear analysis to explore the correlation between crown height and diet in the three most common notoungulates of the late Oligocene (Deseadan SALMA) fauna of Salla, Bolivia: a mesotheriid (*Trachytherus alloxus*), an 'archaeohyracid' (*Archaeohyrax* sp. nov.), and an intertheriid (*Federicoanaya sallaensis*).

Mesowear analysis followed standard protocols. Specimens were digitally photographed in labial view so that cusp shape and occlusal relief could be scored. Cusp shape was scored subjectively as sharp, round, or blunt. Occlusal relief (measured digitally) was calculated as cusp height divided by intercusp distance and was categorized as 'high' or 'low' using three scenarios. The percentage of individuals of each species displaying sharp, blunt, and high cusps was calculated, normalized using the arcsine transformation, and used as variables in subsequent analyses to infer dietary preference. Statistical analyses included discriminant function (DFA) and hierarchical cluster (HCA). Mesowear scores were also explored. Analyses were executed using a comparative mesowear dataset of 64 modern ungulates of known diet (classified as browsers, grazers, or mixed feeders) as well as a subset of 27 'typical' ungulates.

Trachytherus was classified as a grazer in most (5/6) DFAs; it primarily grouped with grazing ungulates (e.g., *Alcelaphus*, *Connochaetes*, *Damaliscus*, *Equus*) in both HCAs. *Archaeohyrax* was classified as a grazer in the DFA of 'typical' ungulates and as a mixed feeder or grazer in the expanded dataset DFA; it mostly clustered with grazers in the 'typical' HCA and with grazers (*Alcelaphus buselaphus*, *Connochaetes*, *Hippotragus equinus*) and mixed feeders (*Axis* spp., *Rucervus*) in equal proportions in the expanded HCA. *Federicoanaya* was classified as a mixed feeder in all DFAs; it grouped with grazers and mixed feeders in the 'typical' DFA and with all dietary types in the expanded HCA including two grazers (*Hippotragus equinus* and *Ourebia*), a mixed feeder (*Tetracerus*), and a browser, (*Litocranius*). Mesowear scores for the three species generally overlapped those for extant grazers, extending into the upper range of mixed feeders.

These analyses suggest: (1) all three notoungulates included some grass in their diet and/or fed at least part of the time in open habitats; (2) these notoungulates were partitioning available dietary resources by foraging in different areas and/or varying the composition of their diets; and (3) *Trachytherus* had the most abrasive diet of the three notoungulates, and *Federicoanaya* had the least abrasive. Based on these analyses and the diversity of other mammals present at Salla, the fauna probably represents a semi-open woodland community.

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1. Introduction

Notoungulates may be the most diverse mammalian clade devoid of living representatives. They ranged in size from less than 1 kg (e.g., the

intertheriid *Punapithecus*; López and Bond, 1995; Hitz et al., 2006) to more than 1,000 kg (e.g., *Toxodon*; Fariña et al., 1998); their dentitions varied from brachyodont and complete (e.g., *Homalodotherium*) to extremely hypsodont and highly reduced (e.g., *Mesotherium*); and their postcrania suggest diverse forms of terrestrial locomotion ranging from cursoriality (e.g., some intertheriids; Stirton, 1953; Cifelli, 1985; Croft and Anderson, 2008) to fossoriality (e.g., mesotheriids; Shockey et al., 2007). They occurred throughout South America from the Paleocene to

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