

DIETS OF NOTOUNGULATES FROM THE SANTA CRUZ FORMATION, ARGENTINA: NEW EVIDENCE FROM ENAMEL MICROWEAR

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ABSTRACT—The late early Miocene Santa Cruz Formation of Patagonian Argentina is remarkable for its well-preserved and diverse mammalian fauna. This study evaluates the feeding preferences of three notoungulates from Santa Cruz (*Nesodon imbricatus*, *Adinotherium ovinum* and *Protypotherium*), typically reconstructed as open habitat grazers. Diets are inferred from enamel microwear features using a low-magnification microscopy technique. Analysis indicates that these notoungulates were primarily feeding on browse, a result that contrasts sharply with previous interpretations based on their hypsodont dentitions. All three notoungulates exhibit a low average number of scratches per taxon, indicative of browsing; high scratch averages are characteristic of grazers. Furthermore, these notoungulates were not primarily feeding on either hard objects (e.g., fruits with seeds) or abrasives (e.g., grasses). *Nesodon imbricatus*, however, exhibits microwear, suggesting it infrequently fed on hard objects such as bark. The association of tall tooth crowns with browsing diets as demonstrated by the Santa Cruz notoungulates is evidence that hypsodonty does not necessarily indicate open habitat feeding or grazing and that the diets of hypsodont herbivores should be evaluated on a case-by-case basis.

INTRODUCTION

During the early and middle Tertiary, notoungulates dominated South American mammalian faunas in terms of numbers of individuals and taxonomic diversity; more than 160 genera in approximately 13 families are currently recognized (Simpson, 1948; Cifelli, 1985, 1993; Marshall and Cifelli, 1989; McKenna and Bell, 1997; Croft, 1999). The group's taxonomic diversity is paralleled by striking morphological diversity (Simpson, 1980; Cifelli, 1985, 1993; McKenna and Bell, 1997; Croft, 1999), and the two main subclades represent divergent radiations: Toxodontia includes relatively large rhino- or horse-like animals whereas Typotheria includes small to medium-sized, mostly rodent- or rabbit-like forms (Patterson and Pascual, 1968; Cifelli, 1985; Bond, 1986; Croft, 1999; Croft et al., 2004).

Hypsodonty (tall tooth crowns) is one of the most conspicuous morphological trends evident in the South American mammal fossil record and is particularly common among notoungulates; during the late Eocene and early Oligocene, hypsodonty apparently evolved in parallel in at least four lineages of notoungulates: Archaeohyracidae/Hegetotheriidae (Hegetotheria), Interatheriidae, Mesotheriidae, and Notohippidae/Toxodontidae (Patterson and Pascual, 1968; Simpson, 1980; Marshall and Cifelli, 1990; Croft, 1999; Flynn et al., 2003; Croft et al., in press). Because the relationship between crown height and diet is well established among modern ungulates, crown height or the degree of hypsodonty has been used as a proxy for diet in notoungulates (Patterson and Pascual, 1968; Janis, 1988; Kay and Madden, 1997; MacFadden, 1999; Fortelius and Solounias, 2000). Thus, brachydont notoungulates have been considered browsers (i.e., eating soft leaves, stems, and fruits) and notoungulates with hypsodont or hypselodont (ever-growing) dentitions have been

considered grazers (i.e., eating mostly grasses and other open habitat vegetation) (Patterson and Pascual, 1968; Bond, 1986; Cifelli, 1985; Marshall and Cifelli, 1990; Croft et al., 2004).

Nevertheless, the reasons behind the parallel development of hypsodonty in numerous notoungulate lineages remain elusive, resulting in a variety of hypotheses regarding the origin of this trend. Initially, the advent of hypsodonty in notoungulates was thought to be a response to the early formation of grasslands in South America (Patterson and Pascual, 1968). Simpson (1980) suggested that notoungulates were genetically predisposed for hypsodonty. Others have proposed that hypsodonty was a response to abrasive volcanic dust on plants eaten by ungulates and other South American herbivores (Pascual and Ortiz-Jaureguizar, 1990; Flynn et al., 2003; Croft et al., in press).

As has been shown in some North American faunas, it is unclear whether the advent of hypsodonty in numerous notoungulate lineages is indicative of a comprehensive shift toward eating abrasive foods (i.e., grazing) and if this trend is correlated with environmental change (Feranec, 2003). To begin to answer these questions it is necessary to fully understand the dietary role of hypsodonty in notoungulates. Here we use low-magnification enamel microwear analysis to evaluate the diets of three contemporaneous hypsodont notoungulates from the Santa Cruz Formation (Santa Cruz Province, Argentina). This method allows us to assess the wear features left on teeth by the food these notoungulates ate during the last few days of their life (Walker et al., 1978; Solounias and Semprebon, 2002; Semprebon et al., 2004a, b). We chose to analyze mammals from the Santa Cruz Formation because specimens are abundant and well preserved and therefore highly amenable to microwear analysis. We examined two toxodonts (*Nesodon imbricatus* and *Adinotherium ovinum*) and one typotherid (*Protypotherium*) from Santa Cruz. Because the low-magnification method is relatively new, we also evaluated scorer reliability by conducting an "observer consistency test" to evaluate uniformity in scoring modern ungulate microwear.

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