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Enamel microstructure in the fossil bovid *Myotragus balearicus* (Majorca, Spain): Implications for life-history evolution of dwarf mammals in insular ecosystems

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ABSTRACT

The causes underlying the evolution of insular dwarfs and giants are a matter of ongoing debate. Because body size is among the principle life history traits, recent works aim to understand the evolution of insular dwarfs in the framework of life history theory. However, the hypotheses put forward so far are conflicting. Early studies, suggested that dwarfing is a consequence of selection for an increased reproduction associated to an accelerated life history (formerly *r*-selection). Recent work, however, based on the analysis of bone histology of the fossil insular dwarf bovid *Myotragus balearicus* (Balearic Islands, Spain), concluded that dwarfing on islands results from a decrease in growth rate associated to a slow life history (formerly *K*-selection) in response to selective forces peculiar to insular conditions. In the present work, we reconstruct the schedule of certain life history traits by estimating the rate of dental development and eruption times in *M. balearicus* and, for comparisons, in an extant caprine (*Ovis aries*). We used histological techniques to calculate crown formation time, daily secretion rate and crown extension rate, in the lower molars. Eruption pattern in *M. balearicus* was analysed through the radiological images of an ontogenetic series of mandibles. Our results show that dental crowns grew at slower rates and the period of crown formation was more extended in the dwarfed fossil bovid than in other extant caprines, resulting in dental development and eruption time that doubles that of extant bovids of similar body size. This suggests an important delay in life history schedules. Concordant with the delayed dental development, the striking hypsodonty of *Myotragus* is indicative of an extended lifespan. These results, together with previous findings from long bone histology, provide empirical evidence for a shift towards a slow life history in this insular dwarfed mammal. Density-dependent resource limitation is hypothesized as the main trigger of the life history and body size evolution of *Myotragus*.

1. Introduction

The evolution of body size on islands is a controversial issue, as shown in the various hypotheses proposed hitherto (Bromage et al., 2002; Heaney, 1978; Köhler and Moyà-Solà, 2009, 2010; Lomolino, 2005; Meiri and Raia, 2010; Meiri et al., 2006; Palkovacs, 2003; Palombo et al., 2008; *see revision in* Köhler, 2010). On islands, large mammals evolve into dwarfs and small mammals evolve into giants over short evolutionary times (the Island Rule; Foster, 1964; Van Valen, 1973). The hypotheses aimed to explain this phenomenon focus on three ecological factors, competition, predation, and resource availability, which are expected to differ between mainland and island environments. Limited food resources, low interspecific competition and lack of predation pressure characterize insular ecosystems (Grant, 1998; Lomolino, 1985; McNab, 1994, 2002a,b; Raia and Meiri, 2006; Palkovacs, 2003; Van Valen, 1973).

Though these selective forces might act directly on body size (Burness et al., 2001; Heaney, 1978; McNab, 2010; Sinclair et al., 2003; Sondaar, 1977), an alternative explanation is based on the covariation of life history traits with body size (Brown and Sibly, 2006; Köhler and Moyà-Solà, 2009; Raia and Meiri, 2006; Palkovacs, 2003).

Life history traits, such as gestation length, size at birth, size and age at maturity, size and number of offspring, length of the reproductive span, and longevity, describe the life cycle of an organism. They are organized along a "fast–slow continuum", with small size, early age at maturity, high reproductive rates, and a short lifespan at the fast end and the opposed traits at the slow end of the continuum. Life history traits are shaped by environmental conditions, specifically by extrinsic mortality and resource availability, and may shift in one or the other direction when these conditions change, leading to a complex adaptation of an organism's life cycle termed its "life history strategy" (Brown and Sibly, 2006; Ricklefs, 2001; Roff, 2002; Stearns, 1992).

Today, a debate focuses on whether insular dwarfs shifted towards the fast or the slow end of the life history continuum. Because insular endemic mammals are predicted to follow similar evolutionary

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trends, which has been confirmed for a series of shared peculiar traits (reduced limb length, reduced size of brain and sense organs, increase in hypsodonty, low metabolic rates, etc.), a similar common trend should be expected for life history traits (*see discussion in* Grant, 1998; Köhler, 2010; Köhler and Moyà-Solà, 2003; MacArthur and Wilson, 1967; McNab, 2002a).

Based on the scaling of body size with life history traits, some authors proposed that the life history traits of insular dwarfs accelerate (fast end) to increase reproductive investment, i.e. fast growth rate, early age at maturity, and increase in production rate (Bromage et al., 2002; Brown and Sibly, 2006; Brown, et al., 1993; Meiri and Raia, 2006, 2010; Raia et al., 2003). Conversely, some authors (Köhler and Moyà-Solà, 2009, 2010; Palkovacs, 2003) suggested that the trend for insular dwarfs is to shift resource allocation from reproduction to growth and maintenance, thus moving toward the "slow" end of the life history continuum.

Fossil faunas from Mediterranean Islands provide many examples of body size evolution, such as dwarf elephants, hippos, deer, etc. (Bover et al., 2008; Hooijer, 1951; Lister, 1993; Palombo, 2001; Raia et al., 2003). An ideal case for studying the evolution of life history traits under insularity is the fossil bovid *Myotragus* (Bate, 1909) (Artiodactyla, Bovidae, Caprinae), an endemic taxon from the Gymnesics or eastern Balearic Islands (Majorca and Minorca, Fig. 1). The genus *Myotragus* underwent significant changes in body design after geographic isolation at the end of the Messinian Salinity Crisis (5.2 mya) under the special ecological conditions that characterised the Balearic Islands from Pliocene through Holocene (limited food resources, absence of predation, increase in intraspecific competition, and times of mass starvation) (Köhler and Moyà-Solà, 2004, 2009).

The genus *Myotragus* comprises a group of six fossil endemic chronospecies from Pliocene through Holocene (Fig. 2). Because of the numerous apomorphies of *Myotragus* that obscure phyletic relationships, the Miocene mainland ancestor is so far unknown. *Myotragus* became extinct coinciding with the first human arrival some 3000 years ago. In addition to an important size decrease, *Myotragus* underwent changes that affected the locomotor, the visual and the digestive (dentition) system (Alcover et al., 1981; Ramis and Bover, 2001; Köhler and Moyà-Solà, 2004, 2009; Moyà-Solà and Pons-Moyà, 1982; Moyà-Solà et al., 1999; Palombo et al., 2008;). Changes in dentition are characterized by the progressive reduction of the number of incisors and premolars, the increase in the degree of hypsondonty of all teeth, and the acquisition of evergrowing incisors (Bover and Alcover, 1999; Alcover et al., 1981; Bover et al., 2008; Moyà-Solà, et al., 2007). *M. balearicus*, the terminal species of the lineage, presents an extremely modified dentition that is not shared by any other known Caprinae. This species displays a single evergrowing incisor in each jaw, a single premolar in the lower dentition (P4), two in the upper dentition (P3 and P4), and three highly hypsodont molars; the dental formula for an adult is I 0/1, C 0/0, P 2/1, M 3/3. It has been suggested that this type of dentition is related to an increased feeding efficiency on abrasive vegetation (Alcover et al., 1998; Bover and Alcover, 1999).

A recent work (Köhler and Moyà-Solà, 2009) showed that the peculiar bone histology of *Myotragus* provides a direct evidence of the developmental and growth pattern and a indirect evidence regarding its physiology. The histological pattern indicates that this dwarf bovid grew at slow and variable rates and ceased growth cyclically, which was associated with an important delay in the attainment of skeletal maturity, suggesting that *Myotragus* shifted towards the slow end of the life history continuum.

Here we aim to draw inferences about the evolution of the life history traits of *Myotragus,* as an example of a typical insular dwarf, through the study of the enamel microstructure in *M. balearicus*, the terminal species of this genus. It is well known that the study of the incremental structures of dental tissues permits determination of the rate and duration of dental growth and development, so providing insight into developmental pathways and into life history traits of mammals (Bromage et al., 2002, 2009; Dean, 2006; Dean et al., 2001; Schwartz et al., 2002; Smith et al., 2007). Thus, these results will allow us to go deeper into the debate on the direction in which insular dwarf mammals shifted along the 'slow–fast continuum'. Specifically, our study focuses on the estimation of the rate of dental development and eruption times of lower cheek teeth in *M. balearicus* and its comparison with extant caprines.

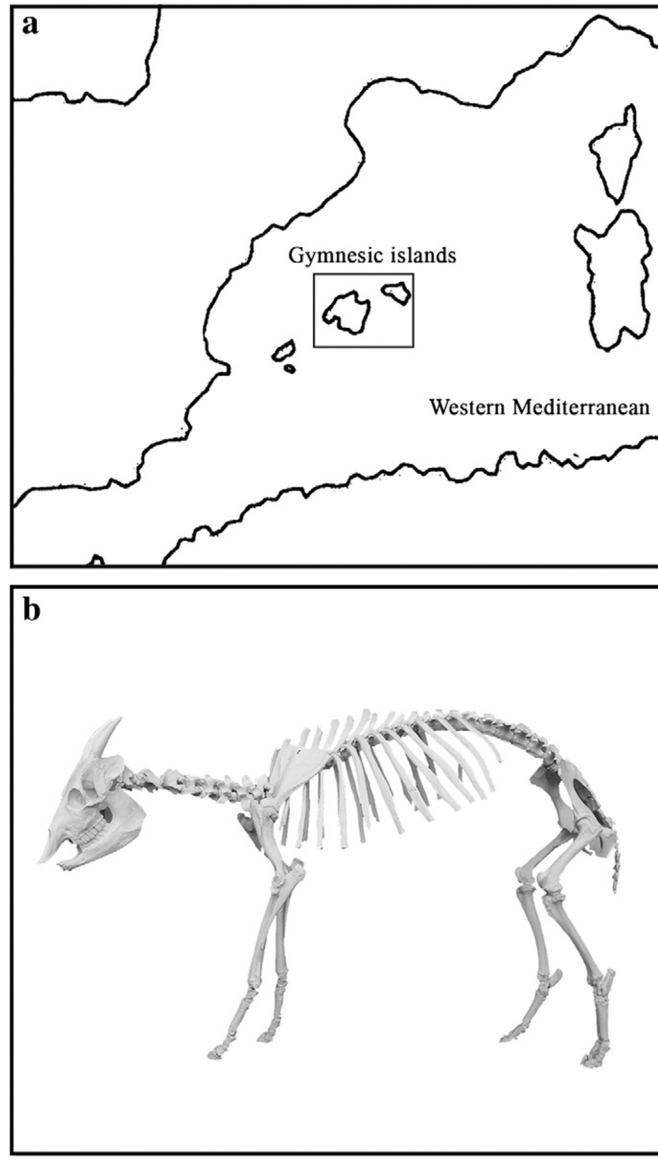

Fig. 1. (a) Map of Western Mediterranean with the position of the Gymnesic islands. (b) Reconstructed skeleton of *Myotragus balearicus.*

2. Methods

The study was based on the analysis of enamel incremental structures observed in ground sections with polarized light microscopy. The sample (Table 1) comprises five lower molars of *M. balearicus* from the Pleistocene sites of Majorca. Additionally, for the comparisons, we analysed three lower molars of an extant caprine (*O. aries*). The latter were also used to assess whether our histological results are compatible with biological observations on lower molar emergence times (Hillson, 2005; Pérez-Barbería and Mutuberría, 1996).

Histological slices were made using standard procedures in our laboratory of thin sections: teeth were embedded in epoxy resin