



Stable isotopes show resource partitioning among the early Late Miocene herbivore community at Rudabánya II: Palaeoenvironmental implications for the hominoid, *Rudapithecus hungaricus*



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ABSTRACT

Examining how species use and partition resources within an environment can lead to a better understanding of community assembly and diversity. The rich early Late Miocene (early Vallesian) deposits at Rudabánya II (R. II) in northern central Hungary preserve an abundance of forest dwelling taxa, including the hominoid *Rudapithecus hungaricus*. Here we use the carbon and oxygen stable isotope compositions of tooth enamel carbonate from 10 genera of medium to large-bodied mammals to evaluate resource use and partitioning among the herbivore community, and to reconstruct the palaeoenvironment of *Rudapithecus*. The range of stable carbon and oxygen isotope values ($\delta^{13}\text{C}_\text{E}$ and $\delta^{18}\text{O}_\text{E}$) displayed by the R. II fauna indicates a variable forest environment, which included both open and closed canopy habitats. The relatively low $\delta^{13}\text{C}_\text{E}$ and $\delta^{18}\text{O}_\text{E}$ values found in all sampled taxa are consistent with high levels of precipitation and humidity. Significant differences in stable isotope values were observed among the sampled fauna, supporting the interpretation of resource specialization and partitioning. Higher $\delta^{13}\text{C}_\text{E}$ values found in *Aceratherium incisivum* (Rhinocerotidae), *Lucentia* aff. *pierensis* (Cervidae), *Hippotherium intrans* (Equidae), *Tetralophodon longirostris* (Gomphotheriidae), *Propotamochoerus palaeochoerus* and *Parachleuastochoerus kretzoi* (Suidae) suggest foraging in more open canopy habitats, while lower $\delta^{13}\text{C}_\text{E}$ values found in *Miotragocerus* sp. (Bovidae), *Dorcatherium navi* (Tragulidae), and *Micromeryx flourensianus* (Moschidae) imply a preference for more densely canopied habitats. Several of the sampled taxa yielded relatively higher $\delta^{18}\text{O}_\text{E}$ and $\delta^{13}\text{C}_\text{E}$ values indicative of fruit consumption, including the small ruminants, cervid, and bovid. The analyzed isotope values reflect a moderate degree of dietary niche overlap between taxa. An abundance of plant resources likely allowed for the coexistence of this diverse community of predominantly browsing herbivores. Within the gradient of more open to closed canopy forest, it is likely that *Rudapithecus* occupied dense closed canopy habitats where access to fruit was relatively continuous. The progressive fragmentation and replacement of humid forests by more open and seasonal woodlands during the late Vallesian would have had a significant influence on the extinction of this fossil ape.

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1. Introduction

Evaluating resource use and partitioning in ancient mammal communities provides critical information for understanding patterns of species diversity and assembly through time. Interspecific competition is considered to be a major selective force encouraging the differential use of resources as well as variation in the morphology and behavior of sympatric species (Pianka, 1981; Cody, 1974; Schoener, 1974). The niche partitioning hypothesis predicts that

ecologically similar species can coexist by partitioning their resources (Schoener, 1974). Sympatric mammalian herbivores partition resources by using different habitats, selecting different plants or plant parts, and being active at different times (Gartlan and Struhsaker, 1972; Schoener, 1974; Pianka, 1981). Studies of modern herbivore communities have demonstrated increased dietary niche overlap during periods of resource abundance. The low levels of feeding competition that occur during these periods promote the coexistence of morphologically similar species (Pyke et al., 1977; Gordon and Illius, 1989; Prins et al., 2006; Storms et al., 2008; Levine and HilleRisLambers, 2009; Singh et al., 2011; Djagoun et al., 2013; Landman et al., 2013; Kartzinel et al., 2015).

Stable isotope analysis of modern and fossil tooth enamel has proven to be a useful method for evaluating dietary preference, habitat use, and

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resource partitioning (Ambrose and DeNiro, 1986; Quade et al., 1995; Feranec and MacFadden, 2000; Sponheimer et al., 2005; Urton and Hobson, 2005; Feranec, 2007; Feranec et al., 2009; Tütken and Vennemann, 2009). Over the past two decades there has been an increased focus on the study of isotope ecology in ancient C₃ ecosystems (Bocherens et al., 1994a, 1994b, 1995; Quade et al., 1995; Bocherens, 2000; MacFadden and Higgins, 2004; Feranec and MacFadden, 2006; Hernández Fernández et al., 2006; Tütken et al., 2006, 2013; DeSantis and Wallace, 2008; Domingo et al., 2009; Tütken and Vennemann, 2009; Zin-Maung-Maung-Thein et al., 2011; Rey et al., 2013; Aiglstorfer et al., 2014). Globally, plants utilizing the C₄ photosynthetic pathway were only abundant from the Late Miocene (Cerling et al., 1997; Ehleringer et al., 1997; Kohn and Cerling, 2002). However, C₄ plants never became widespread in Europe (Quade et al., 1995; Cerling et al., 1997; van Dam and Reichart, 2009; Domingo et al., 2009; Tütken et al., 2013) and today make up only 5% of species (Collins and Jones, 1986). The isotopic values of herbivorous mammals from Late Miocene Europe indicate a diet of pure C₃ vegetation (Bocherens et al., 1994b; Hernández Fernández et al., 2006; Merceron et al., 2006, 2013; Tütken et al., 2006, 2013; Domingo et al., 2009, 2012; Tütken and Vennemann, 2009; Rey et al., 2013; Aiglstorfer et al., 2014). While it is not easy to distinguish C₃ grazers from browsers within a C₃-dominated ecosystem, variations in $\delta^{13}\text{C}$ enamel values ($\delta^{13}\text{C}_\text{E}$) can be used to examine resource partitioning and habitat differences (Drucker et al., 2003; Cerling et al., 2004; Feranec and MacFadden, 2006; Feranec, 2007; Tütken and Vennemann, 2009; Domingo et al., 2009, 2013; Tütken et al., 2013; Aiglstorfer et al., 2014). In this study we use stable carbon and oxygen isotope ratios of tooth enamel carbonate to evaluate patterns of resource use and partitioning at Rudabánya II (R. II), an early Late Miocene (early Vallesian) (~10 Ma) hominoid locality in northern central Hungary.

Forest-adapted mammalian communities in Central and Western Europe reached high levels of species richness during the early Vallesian (~11.2–9.7 Ma) (Agustí et al., 1997, 2003, 2013; Franzen and Storch, 1999; Daxner-Höck, 2004; Casanovas-Vilar et al., in press). More than 60 species of mammals have been recorded at the localities of Can Llobateres 1, Can Ponsic, and Rudabánya II. This period of optimum diversity was followed by the gradual decline of forest dwelling browsers and rise of woodland adapted mixed feeders and grazers, characteristic of the later Neogene (Fortelius et al., 2002). An important phase in this faunal transition was the Vallesian Crisis (~9.7 Ma), which saw the abrupt decline of many humid forest-adapted faunal elements, including the hominoids (Agustí and Moyà-Solà, 1990; Agustí et al., 2003, 2013; Fortelius and Hokkanen, 2001; Fortelius et al., 2002; Begun, 2007). The Vallesian Crisis has been linked to increasing seasonality and the replacement of subtropical evergreen forests with deciduous woodlands (Agustí et al., 2003; van Dam, 2006). However, several recent studies indicate that the decline of forest dwelling taxa did not occur in an abrupt turnover event, but instead took place gradually through a series of extinction events that began in the late Vallesian/early Turolian (Franzen et al., 2013; Casanovas-Vilar et al., 2014, in press; Daxner-Höck et al., in press). The faunal assemblage at R. II preserves an abundance of forest-dwelling taxa, including the hominoid *Rudapithecus hungaricus*. *Rudapithecus* is an extinct member of the great ape and human clade, on the basis of numerous cranial and postcranial features (Begun, 1992, 2009; Kordos and Begun, 2002; Deane and Begun, 2008; Kivell and Begun, 2009). Both the morphology and life history pattern of this fossil ape suggest that it was a large-bodied, suspensory frugivore, which would have been highly dependent on forested conditions and year-round access to fruit resources (Begun, 1992, Ungar and Kay, 1995; Ungar, 1996, 2005; Kordos and Begun, 2002; Kivell and Begun, 2009; Smith et al., 2010; Deane et al., 2013; DeMiguel et al., 2014). Because of the high faunal diversity

and unique paleoenvironmental and paleoclimatic situation, the paleoecosystem at R. II is an ideal site to examine questions related to mammalian resource use and partitioning. Here we aim to: (1) evaluate resource use and partitioning among mammal species in an evaluation of the niche partitioning hypothesis and (2) to better understand the paleoecological setting in which *Rudapithecus* lived.

2. Background

2.1. Rudabánya: geology, paleontology, and paleoecology

Rudabánya is located within the Pannonian Basin, on the western flank of the northern Carpathian Mountains, in northern-central Hungary (N48°22'48.13", E20°37'43.57"). The fossiliferous deposits at Rudabánya accumulated in a shallow valley near the shoreline of Lake Pannon, a relict of the Paratethys Sea, which formed approximately 11.6 Ma (Kázmér, 1990, Rögl, 1998; Magyar et al., 1999; Popov et al., 2004) (Fig. 1). As lake levels gradually rose, the Rudabánya range and adjacent valleys were flooded, creating a variety of lacustrine and peri-lacustrine environments including swamp, wetland, and riparian forest. Lake Pannon reached its maximum extent (c. 290,000 km²) between 10.5 and 10 Ma, during a period of high precipitation and humidity (Magyar et al., 1999; Harzhauser and Mandic, 2004, 2008; Harzhauser et al., 2007, 2008). There are a number of fossiliferous localities within the Rudabánya complex; here we focus on fauna from the R. II locality, where the majority of primate material has been recovered. Cyclic layers of clay, mud, and lignite totaling 8–12 m characterize the depositional sequence at this locality. While the sequence is too short to tie into the geomagnetic time scale, having likely accumulated within a few thousand years or less, the evolutionary stage of the fauna suggests that it belongs near the top of the MN9 land mammal zone (10–9.8 Ma) (Kordos, 1991; Andrews et al., 1996; Bernor et al., 2003; Andrews and Cameron, 2010; Casanovas-Vilar et al., 2011a).

The faunal assemblage at R. II is extraordinarily diverse with 112 vertebrate species, including 18 species of amphibians, 13 species of reptiles, 11 species of birds, and 69 species of mammals. Ungulate taxa are dominated by morphologically inferred browsers including *Dorcatherium nauti* (Tragulidae), *Micromeryx flourensianus* (Moschidae), *Miotragocerus* sp. (Bovidae), *Tapirus* cf. *priscus* (Tapiridae), *Chalicotherium* aff. *goldfussi* (Chaliotheriidae), *Hoploaceratherium belvederense*, and *Aceratherium incisivum*, and *Lartetotherium* aff. *sansaniensis* (Rhinocerotidae) (Bernor et al., 2004). Meso and microwear data indicate intermediate feeding (i.e., both browsing and grazing), which included the intake of C₃ graminoids, in *Hippotherium intrans* (Equidae) and *Lucentia* aff. *piensis* (Cervidae) (Merceron et al., 2007). This suggests some presence of more open canopy habitats, such as forest clearings, where higher levels of light penetration promote the development of an herbaceous layer. The gomphothere *Tetralophodon longirostris* likely also inhabited more open canopy habitats distal to the lake margin. Stable isotope and microwear analysis of Late Miocene gomphotheres from Central and Western Europe generally indicate intermediate feeding in woodland environments (Calandra et al., 2008; Domingo et al., 2009, 2012; Tütken and Vennemann, 2009). The suids at R. II include a suine, *Propotamochoerus palaeochoerus*, first known from the Middle Miocene, and a primitive tetraconodont, *Parachleuastochoerus kretzoi* (Bernor et al., 2004). This locality represents one of the very few in Eurasia that preserves extensive samples of both a hominoid and pliopithecoid (Andrews et al., 1996; Harrison, 2002; Kordos and Begun, 2002; Armour-Chelu et al., 2005). *Rudapithecus* and *Anapithecus hernyaki* have been recovered from the same depositional layers although, interestingly, their frequency differs between layers (Andrews et al., 1996; Kordos and Begun, 2002; Armour-Chelu et al., 2005). The majority of hominoid

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