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Trace element analysis provides insight into the diets of early Late Miocene ungulates from the Rudabánya II locality (Hungary)

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ABSTRACT

The early Late Miocene vertebrate locality of Rudabánya II (R. II) in northeastern Hungary preserves an abundance of forest-adapted ungulate species. To better understand the ecological relationships within this ancient ecosystem, we used analysis of enamel strontium/calcium (Sr/Ca) ratios to infer dietary preferences. The goals of the analysis were to: i) determine whether these ungulate species specialized in specific plants or plant parts; ii) discern whether the Sr/Ca ratios support what was previously suggested about the ecology of these species and iii) evaluate the factors that may have acted to promote coexistence within this diverse community of predominantly browsing herbivores. Results show significant differences in the diets of the sampled species. The highest Sr/Ca ratios were displayed by the suids *Parachleuastochoerus kretzoi* (FORTELIUS *et al.*, 2005) and *Propotamochoerus palaeochoerus* (PILGRIM, 1926) implying a preference for Sr-rich underground plant parts. Elevated Sr/Ca ratios yielded by the cervid *Lucentia* aff. *pierensis* (THOMAS, 1951) and equid *Hippotherium intrans* (KRETZOI, 1983) are indicative of intermediate feeding. The bovid *Miotragocerus* sp. (STROMER, 1928) showed higher Sr/Ca ratios than the gomphothere *Tetralophodon longirostris* (KAUP, 1832), which is incongruent with morphological and stable isotope data, and suggested browsing by both taxa. This finding is likely the result of a difference in digestive physiology (ruminant vs. monogastric) rather than a difference in dietary behaviour. The lowest Sr/Ca ratios were displayed by the tragulid *Dorcatherium nauti* (KAUP AND SCHOLL, 1834) and moschid *Micromeryx flourensianus* (LARTET, 1851) suggesting a preference for Sr-poor fruits. Resource specialization and partitioning within the local environment likely acted to decrease interspecific competition and promote coexistence within the diverse ungulate community at R. II.

KEYWORDS | Paleoeecology. Sr/Ca ratios. Late Miocene. Ungulates. Hungary.

INTRODUCTION

The relative concentration of strontium to calcium (Sr/Ca) in mammalian bioapatite has proven to be an effective

indicator of trophic level, dietary behavior, and habitat use in both modern and ancient ecosystems (Elias *et al.*, 1982; Sillen, 1986; Sealy and Sillen, 1988; Sillen *et al.*, 1992; Gilbert *et al.*, 1994; Burton *et al.*, 1999; Blum *et*

et al., 2000; Balter *et al.*, 2002; 2012; Palmqvist *et al.*, 2003; Lee-Thorp *et al.*, 2003; Balter, 2004; Sponheimer *et al.*, 2005; Sponheimer and Lee-Thorp, 2006; Domingo *et al.*, 2012; Peek and Clementz, 2012; Qu *et al.*, 2013; de Winter *et al.*, 2016). Strontium is a non-essential trace element, which mammals discriminate against relative to Ca in their intestines, kidneys, sites of bioapatite formation, and across the placenta and mammary glands (Taylor *et al.*, 1962; Lengemann, 1963; Walser and Robinson, 1963; Underwood, 1977; Sasaki and Garant, 1986; Avioli, 1988; Rossipal *et al.*, 2000; Chattopadhyay *et al.*, 2007). This results in herbivore tissues having lower Sr/Ca ratios than the plants they consume and carnivores having lower Sr/Ca ratios than their prey (Elias *et al.*, 1982; Burton *et al.*, 1999; Blum *et al.*, 2000). Systematic variations in Sr/Ca ratios also occur within trophic levels and can be used to assess the relative dietary contribution of certain plants and plant parts (Rao, 1979; Runia, 1987; Burton *et al.*, 1999; Sponheimer *et al.*, 2005; Sponheimer and Lee-Thorp, 2006; Domingo *et al.*, 2012). Due to a decrease in Sr concentration that occurs during xylem transport (centripetal accumulation) plant roots and stems have higher Sr/Ca ratios than leaves and fruits (Bowen and Dymond, 1955; Runia, 1987; Sillen, 1992; Burton *et al.*, 1999; Sponheimer *et al.*, 2005; Drouet and Herbauts, 2008). Grasses have been shown to have higher concentrations of Sr than the leaves of dicotyledonous plants (Sponheimer and Lee-Thorp, 2006). By analyzing the Sr/Ca ratios of sympatric mammalian herbivores it is possible to evaluate differences in dietary resource use and gain a better understanding of the factors that act to promote species coexistence. Here we use Sr/Ca ratios of fossil tooth enamel to evaluate dietary resource use within the ungulate community at Rudabánya II (R. II), an early Late Miocene (early Vallesian; ~10Ma) vertebrate locality in northeastern Hungary. The faunal assemblage at R. II preserves an abundance of forest-adapted fauna and presents a unique opportunity to examine species coexistence during a dynamic period in the evolution of terrestrial ecosystems in Europe.

During the early Vallesian (11.2–9.7Ma), mammalian communities in central and western Europe achieved exceptionally high levels of species diversity (Agustí *et al.*, 1997, 2003, 2013; Franzen and Storch, 1999; Daxner-Höck, 2004; Bernor *et al.*, 2004; Casanovas-Vilar *et al.*, 2014, 2016). The entry of new woodland-adapted immigrant taxa (hipparione horses, giraffids, and boselaphine bovids) during this time is not associated with the local extinction of forest-adapted faunas (Agustí *et al.*, 1997; Franzen and Storch, 1999), suggesting low levels of competition. This period of optimum diversity was followed by the decline of forest-dwelling browsers and rise of woodland-adapted mixed-feeders and grazers (Fortelius *et al.*, 2002). It was traditionally hypothesized that the diversity of forest-adapted taxa decreased abruptly at the early/late Vallesian

boundary (~9.7Ma) in a faunal turnover event termed the Vallesian Crisis (Agustí and Moyà-Solà, 1990; Agustí *et al.*, 1997, 1999, 2003, 2013; Fortelius *et al.*, 1996; Fortelius and Hokkanen, 2001). However, more recent analysis suggests that the demise of forest-dwelling communities occurred gradually through a series of extinction events that began in the late Vallesian/early Turolian (Franzen *et al.*, 2013; Casanovas-Vilar *et al.*, 2014, 2016; Daxner-Höck *et al.*, 2016).

To better understand how early Vallesian ecosystem functioned it is necessary to examine the complex ecological relationships that occurred within each trophic level. In this study, we use Sr/Ca ratios to evaluate the diets of early Vallesian ungulates with the aim of determining: i) whether the sampled ungulate species show specialization for specific plants or plant parts, ii) whether Sr/Ca ratios support what is known about the ecology of these particular ungulate species from other methods, and iii) what factors may have acted to maintain coexistence within this diverse community of predominantly browsing herbivores.

GEOLOGICAL SETTING

Rudabánya is an early Late Miocene (early Vallesian) vertebrate paleontological locality situated within the Pannonian Basin, on the western flank of the northern Carpathian Mountains, in northeastern Hungary (N48°22'48.13", E20°37'43.57"; Fig. 1). There are several vertebrate localities within the Rudabánya complex; the current study analyzes fauna from the R. II locality. The fossiliferous deposits at Rudabánya accumulated near the shoreline of Lake Pannon, which formed at approximately 11.6Ma (Kázmér, 1990; Rögl, 1998; Magyar *et al.*, 1999;

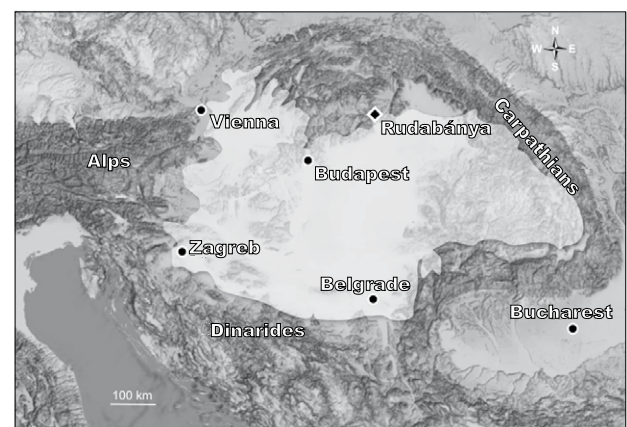


FIGURE 1. The Pannonian Basin with estimated maximum extension of Lake Pannon at ca. 10Ma indicated by white shading. Black diamond marks position of Rudabánya (N48°22'48.13", E20°37'43.57"). Black circles indicate position of Belgrade, Bucharest, Budapest, Vienna, and Zagreb for reference (modified from Rögl, 1998; Magyar *et al.*, 1999; Popov *et al.*, 2004).

Popov *et al.*, 2004). Lake Pannon reached its maximum extent (c 290,000km²) between 10.5–10Ma, during a period of high precipitation and humidity (Magyar *et al.*, 1999; Harzhauser and Mandic, 2004; Harzhauser, 2007; Harzhauser *et al.*, 2008; Utescher *et al.*, 2017). During this period coastal environments were characterized by extensive marshes grading into forested-wetlands, and mixed evergreen and deciduous forest (Kretzoi *et al.*, 1976; Erdei *et al.*, 2007; Harzhauser *et al.*, 2008; Halby and Erdei, 2013; Utescher *et al.*, 2017). Palaeobotanical remains from R. II reflect a swamp association dominated by deciduous taxa (Kretzoi *et al.*, 1976; Halby and Erdei, 2013). Stable isotope analysis of 10 species of ungulates from R. II indicates a variable forest environment, which included both open and closed canopy habitats (Eastham *et al.*, 2016).

The depositional sequence at R. II is comprised of cyclic layers of clay, mud, and lignite totaling 8–12 meters. While the sequence is too short to tie into the geomagnetic timescale, the evolutionary stage of the fauna suggests it belongs near the top of the MN9 land mammal zone (10–9.8Ma) (Kordos, 1991; Andrews *et al.*, 1996; Bernor *et al.*, 2003; Andrews and Cameron, 2010; Casanovas-Vilar *et al.*, 2011). The current study analyzes fauna from the black mud and gray marl depositional layers as one community. A lack of faunistic difference has been observed between these depositional layers suggesting that they sample overlapping communities (Kordos and Begun, 2002). Stable isotope analysis showed no significant difference in the values of fauna from the black mud and gray marl indicating little, if any, change in environmental conditions (Eastham *et al.*, 2011).

With 112 vertebrate species, including 69 species of mammals, R. II represents one of the richest early Vallesian palaeontological sites in Europe. The majority of the ungulate taxa are morphologically inferred as browsers including *Dorcatherium nauti* (Tragulidae; KAUP AND SCHOLL, 1834), *Micromeryx flourensianus* (Moschidae;

LARTET, 1851), *Miotragocerus* sp. (Bovidae; STROMER, 1928), *Tapirus* cf. *priscus* (Tapiridae; KAUP, 1833), *Chalicotherium* aff. *goldfussi* (Chaliiotheriidae; KAUP, 1833), *Hoploaceratherium belvederense* (Wang, 1929), *Aceratherium incisivum* (KAUP, 1832) and *Lartetotherium* aff. *sansaniensis* (LARTET, 1851) (Rhinocerotidae), and *Tetralophodon longirostris* (Gomphotheriidae; KAUP, 1832). Suid taxa include a suine, *Propotamochoerus palaeochoerus* (PILGRIM, 1926), first known from the Middle Miocene, and a primitive tetraconodont, *Parachleuastochoerus kretzoi* (FORTELIUS *et al.*, 2005). The equid *Hippotherium intrans* (KRETZOI, 1983), a derived member of the *Hippotherium* lineage, shows morphological adaptations suggestive of more cursorial behaviour (Bernor *et al.*, 2003, 2004; Scott *et al.*, 2005). Patterns of meso- and microwear, as well as and stable isotope values indicate that the equid was an intermediate feeder (engaged in both browsing and grazing; Merceron *et al.*, 2007; Tütken *et al.*, 2013; Eastham *et al.*, 2016). Intermediate feeding has also been interpreted for the cervid *Lucentia* aff. *pierensis* on the basis of meso- and microwear and stable isotopes (Merceron *et al.*, 2007; Eastham *et al.*, 2016). R. II is one of the very few Late Miocene sites in Eurasia that preserves extensive samples of both a hominoid and pliopithecoid (Andrews *et al.*, 1997; Harrison, 2002; Kordos and Begun, 2002; Armour-Chelu *et al.*, 2005). *Rudapithecus hungaricus* (KRETZOI, 1969) and *Anapithecus hernyaki* (KRETZOI, 1975) have been recovered from the same depositional layers supporting the assumption of sympatry in these fossil primates (Andrews *et al.*, 1997; Kordos and Begun, 2002; Armour-Chelu *et al.*, 2005).

MATERIALS AND METHODS

All of the faunas sampled in the current study were recovered from the R. II locality within the Rudabánya complex. A total of 45 enamel samples from eight genera of medium to large-bodied mammals were analyzed

TABLE 1. Descriptive statistics for the R. II ungulate species analyzed in this study. SD indicates the standard deviation

Taxon	Family	N	Sr/Ca x 1000				
			Mean	SD	Range		
<i>Dorcatherium nauti</i>	Tragulidae	4	0.52	0.13	0.45	To	0.70
<i>Hippotherium intrans</i>	Equidae	8	0.89	0.23	0.62	To	1.21
<i>Lucentia</i> aff. <i>pierensis</i>	Cervidae	9	0.92	0.27	0.60	To	1.26
<i>Micromeryx flourensianus</i>	Moschidae	6	0.57	0.16	0.31	To	0.73
<i>Miotragocerus</i> sp.	Bovidae	8	0.82	0.22	0.58	To	1.20
<i>Parachleuastochoerus kretzoi</i>	Suidae	4	1.54	0.38	1.25	To	2.08
<i>Propotamochoerus palaeochoerus</i>	Suidae	4	1.22	0.19	0.98	To	1.42
<i>Tetralophodon longirostris</i>	Gomphotheriidae	2	0.77	0.05	0.73	To	0.80

(Table 1). Bedrock geology controls groundwater and soil trace element concentrations, making the direct comparison of trace element ratios from plants and animals living in different regions quite difficult (Sillen and Kavanagh, 1982; Sealy and Sillen, 1988; Sponheimer and Lee-Thorp, 2006; Kohn *et al.*, 2013). There has been extensive work examining the *post mortem* incorporation of trace elements into mammalian bones and teeth (Kyle, 1986; Price *et al.*, 1992; Trueman and Tuross, 2002). In fact, trace element ratios of fossil bone have been proposed as a proxy for fossil provenance based upon the presumed prominent incorporation of trace elements through diagenesis (Trueman and Benton, 1997; Ségalen *et al.*, 2008; Tutken *et al.*, 2011; Herwartz *et al.*, 2013; Kohn and Moses, 2013). Enamel was chosen for analysis over bone or dentine in this study because of its resistance to diagenetic alteration, due in part to its greater mineral content and lack of natural pores, and because it repeatedly has been shown to reliably reflect originally incorporated geochemical values (Lee-Thorp and van der Merwe, 1987, 1991; Wang and Cerling, 1994; Kohn *et al.*, 1999; Sponheimer and Lee-Thorp, 1999, 2006; Fourie *et al.*, 2008; Tutken *et al.*, 2008; Domingo *et al.*, 2009, 2012; Brüggmann *et al.*, 2012). The exact mechanisms controlling trace element uptake in mammalian bioapatites are not completely understood and are thought to vary per element (Burton and Price, 2002; Kohn *et al.*, 2013). However, the uptake of trace elements through drinking water is generally thought to be too low to account for the concentrations found in teeth and bone, and instead it is suggested that diet and the ingestion of soil and dust account for *in vivo* trace element incorporation (Underwood, 1977; Sillen, 1992; Sponheimer *et al.*, 2005; Sponheimer and Lee-Thorp, 2006; Kohn *et al.*, 2013). While the majority of previous trace element studies have focused on Plio-Pleistocene and Holocene fossil material, works by Domingo *et al.* (2009, 2012) and Eberle *et al.* (2009) have shown the preservation of biogenic signals in Middle Miocene and Early Oligocene mammalian tooth enamel. Because the goal of our analysis was to examine variation in the feeding behaviour of adult animals, we preferentially sampled teeth that are among the last to develop, mineralize, and erupt (Hillson, 2005). Enamel (~10mg) was removed using a low speed FOREDOM™ drill and carbide dental burs. 2–3mm wide samples were taken along the non-occlusal surface parallel to the growth axis across the entire length of the tooth, which provides average values of resource use during tooth development, typically representing many months to a few years.

Samples were chemically pretreated with hydrogen peroxide (30%, H₂O₂) to remove organics and weak acetic acid (0.1N, CH₃CO₂H) to remove secondary carbonates (Koch *et al.*, 1997). Samples were centrifuged at a high speed and rinsed in distilled water to neutral pH before proceeding with the next solution. The remaining sample

(~5mg) was then dissolved in 1ml of HNO₃ in closed teflon beakers. After complete dissolution the beakers were opened and the samples evaporated to dryness on a hotplate. The residue was then dissolved in 0.5ml of 6N HNO₃ and evaporated to dryness, then dissolved again 0.5ml of 2.5N HNO₃ and evaporated to dryness. Prior to analysis the samples were dissolved in 1ml of 2% HNO₃ solution. Sr and Ca concentrations were analyzed by using an Element XR™ inductively coupled plasma-mass spectrometer (ICP-MS) at the University of California, Santa Cruz. The precision of the ICP-MS is better than +/-2–4%. Sr and Ca data are presented here as ratios multiplied by 1000 (*e.g.* Sr/Ca x 1000) (Sillen 1992; Balter *et al.*, 2002; Palmqvist *et al.*, 2003; Lee-Thorp *et al.*, 2003; Sponheimer *et al.*, 2005; Sponheimer and Lee-Thorp, 2006; Domingo *et al.*, 2009, 2012). Sr/Ca ratios were compared among taxa using both parametric (ANOVA, Fisher's LSD) and non-parametric (Kruskal-Wallis) tests where appropriate. Statistical analyses were run on SPSS 22.0, with significance set at *p*<0.05.

RESULTS

The Sr/Ca ratios of the R. II fauna (Table 1; Fig. 1; Table I in the Appendix) are comparable with those reported for both modern (Elias *et al.*, 1982; Gilbert *et al.*, 1994; Burton *et al.*, 1999; Peek and Clementz, 2012; Martin *et al.*, 2015) and fossil mammals (Balter *et al.*, 2002, 2012; Lee-Thorp *et al.*, 2003; Palmqvist *et al.*, 2003; Sponheimer *et al.*, 2005; Sponheimer and Lee-Thorp, 2006; Domingo *et al.*, 2012). Statistically significant differences in Sr/Ca ratios among taxa (Table 2) indicates that diagenesis has not obscured the original ecological signal. Sympatric suids, *Parachleuastochoerus kretzoi* ($\bar{x}$ =0.54±0.38, *n*=4) and *Propotamochoerus palaeochoerus* ($\bar{x}$ =1.22±0.19, *n*=4), displayed the highest Sr/Ca ratios of the sampled fauna. The Sr/Ca ratios of the smaller tetraconodont suid *P. kretzoi* were higher than those

TABLE 2. Significant differences in Sr/Ca ratios among the sampled R. II ungulate species. Values shown with asterisks indicate significance for $\alpha \leq 0.05$ using Fisher's least significant difference test

Taxon	<i>P. kretzoi</i>	<i>P. palaeochoerus</i>	<i>L. aff. pierensis</i>	<i>Miotragocerus</i> sp.	<i>H. intrans</i>	<i>T. longirostris</i>	<i>M. flourensianus</i>
<i>P. kretzoi</i>	-						
<i>P. palaeochoerus</i>	0.06						
<i>L. aff. pierensis</i>	0.00*	0.04*					
<i>Miotragocerus</i> sp.	0.00*	0.01*	0.32				
<i>H. intrans</i>	0.00*	0.03*	0.81	0.46			
<i>T. longirostris</i>	0.00*	0.03*	0.40	0.83	0.50		
<i>M. flourensianus</i>	0.00*	0.00*	0.00*	0.03*	0.01*	0.21	
<i>D. naui</i>	0.00*	0.00*	0.02*	0.11	0.03*	0.34	0.74

of the larger suine *P. palaeochoerus*, but not significantly different ($p=0.06$, Fisher's LSD). The cervid *Lucentia* aff. *pierensis* ($\bar{x}=0.92\pm0.27$, $n=9$), bovid *Miotragocerus* sp. ($\bar{x}=0.82\pm0.22$, $n=8$), equid *Hippotherium intrans* ($\bar{x}=0.89\pm0.23$, $n=8$), and gomphothere *Tetralophodon longirostris* ($\bar{x}=0.77\pm0.05$, $n=2$), showed intermediate Sr/Ca ratios. Large-bodied ruminants *L. aff. pierensis* and *Miotragocerus* sp. yielded higher, but not significantly different ($p=0.989$, Fisher's LSD), Sr/Ca ratios than monogastric *H. intrans* and *T. longirostris*. The tragulid *Dorcatherium naui* ($\bar{x}=0.52\pm0.13$, $n=4$) and moschid *Micromeryx flourensianus* ($\bar{x}=0.57\pm0.16$, $n=6$) displayed the lowest Sr/Ca ratios of the sampled fauna. The Sr/Ca ratios of the small-bodied ruminant *M. flourensianus* were significantly lower than those of the large-bodied ruminant *Miotragocerus* sp. ($p=0.03$, Fisher's LSD).

DISCUSSION

We found significant differences in the Sr/Ca ratios of the R. II fauna indicative of differential dietary resource use (Fig. 2; Table 2). Taxonomic differences in Sr/Ca ratios are generally concordant with those previously inferred on the basis of enamel oxygen and carbon stable isotope ratios (Eastham *et al.*, 2016; Fig. 3 of this paper). Both the heterogeneous taxonomic

correlations between the patterning of Sr/Ca and stable isotope ratios (Eastham *et al.*, 2016) indicate that original biogenic signals are reflected in the enamel. To stress, we are not arguing that the enamel of the R. II fauna has not undergone any *post mortem* alteration, but rather that the ecological patterning of concern to this study has not been obscured by diagenesis.

Plant roots, rhizomes, and stems preferentially accumulate heavier alkaline-earth elements resulting in higher Sr concentrations than leaves, flowers, and fruits (Runia, 1987; Sillen *et al.*, 1995; Burton *et al.*, 1999). Several authors have linked elevated Sr/Ca ratios in modern and fossil mammals with the consumption of Sr-rich underground plant parts (Sealy and Sillen, 1988; Sillen *et al.*, 1995; Burton *et al.*, 1999; Lee-Thorp *et al.*, 2003; Sponheimer *et al.*, 2005; Sponheimer and Lee-Thorp, 2006; Fourie *et al.*, 2008). The suids showed the highest Sr/Ca ratios of the sampled fauna (Fig. 2) suggesting diets rich in roots and rhizomes, which would have been abundant in the soft substrates along the margin of Lake Pannon. This interpretation is concordant with the higher carbon and lower oxygen isotope values reported for the R. II suids (Eastham *et al.*, 2016; Fig. 3). However, an omnivorous diet similar to that of the modern bush pig (*Potamochoerus porcus*) could also account for elevated Sr/Ca ratios (Balter *et al.*, 2002; Sponheimer *et al.*, 2005; Domingo *et*

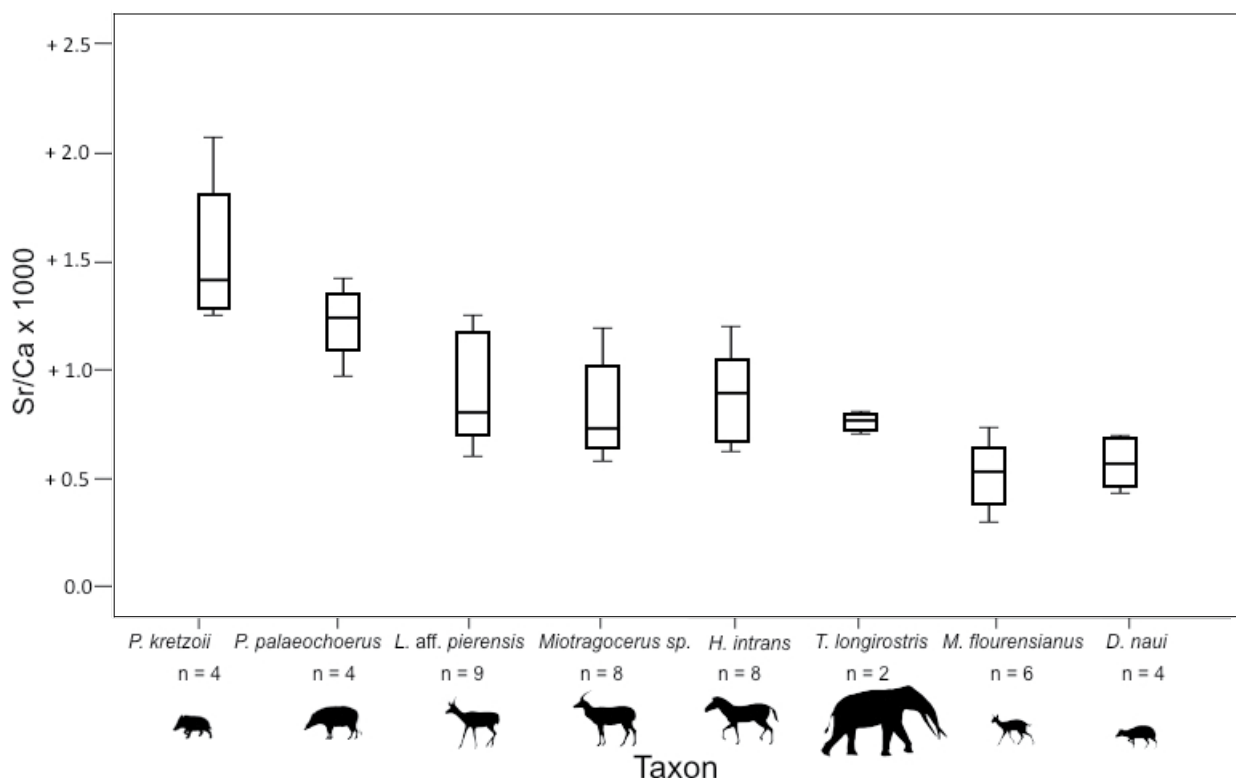


FIGURE 2. Mean value ± 1 standard deviation plots of Sr/Ca enamel ratios of the R. II ungulates. Mammal reconstructions are not to scale.

al., 2012). Patterns of molar emergence and wear indicate that the R. II suids had similar diets, with some degree of niche separation (Bernor *et al.*, 2003). Bernor *et al.* (2003) suggested that the R. II locality was situated within the core habitat of the larger suine *Propotamochoerus palaeochoerus* and marginal to the preferred habitat of the smaller tetraconodont suid *Parachleuastochoerus kretzoi*. Stable isotope analysis also indicates differential dietary resource use, with *P. palaeochoerus* displaying significantly higher carbon isotope values than *Parachleuastochoerus kretzoi* (Eastham *et al.*, 2016; Fig. 3). Sr/Ca ratios support the interpretation of niche separation with *P. kretzoi* ($\bar{x}=1.54\pm0.38$) showing comparatively higher Sr/Ca ratios than *P. palaeochoerus* ($\bar{x}=1.22\pm0.19$). While it is likely that both of the R. II suids were engaged in rooting the lower Sr/Ca ratios of *P. palaeochoerus* could indicate an increased dependence on Sr-poor resources, such as fruit. The higher and more varied Sr/Ca ratios of *P. kretzoi* could suggest a more omnivorous diet and/or an increased dependence on underground plant parts. An omnivorous diet has been interpreted for the Middle Miocene tetraconodont suid *Conohyus simorreensis* (LARTET, 1851) on the basis of heterogeneous Sr/Ca ratios (Domingo *et al.*, 2012).

The cervid *Lucentia* aff. *pierensis* ($\bar{x}=0.92\pm0.27$) and equid *Hippotherium intrans* ($\bar{x}=0.89\pm0.23$) share relatively higher Sr/Ca ratios, which could indicate

intermediate feeding including some intake of C_3 graminoids. Grazing herbivores have been shown to reflect higher Sr/Ca ratios than coexisting browsers (Sponheimer *et al.*, 2005; Sponheimer and Lee-Thorp, 2006), as grasses are more enriched in Sr than dicotyledonous plants (Runia, 1987; Burton *et al.*, 1999). A flexible feeding strategy that included the consumption of grasses, leaves, and possibly fruits has been interpreted for Late Miocene *Hippotherium* on the basis of stable isotope and meso- and microwear data (Merceron *et al.*, 2007; Merceron, 2009; Tütken *et al.*, 2013; Eastham *et al.*, 2016). Meso- and microwear and stable isotope analysis of *L. aff. pierensis* also indicates intermediate feeding (Merceron *et al.*, 2007; Eastham *et al.*, 2016; Fig. 3). Domingo *et al.* (2009, 2012) analyzed the stable isotope, Sr/Ca, and barium/calcium (Ba/Ca) ratios of the Middle Miocene equid *Anchitherium* cf. *A. cursor* (SÁNCHEZ *et al.*, 1998) from the Somosaguas site in Spain, and interpreted that equinid population as being intermediate feeding. Here, the Sr/Ca ratios of *Anchitherium* were higher than those of the coexisting gomphothere, but slightly lower than those of the large-bodied ruminants (Domingo *et al.*, 2012). At R. II, the Sr/Ca ratios of *H. intrans* are higher than those of the gomphothere *Tetralophodon longirostris* ($\bar{x}=0.77\pm0.05$), and fall between those of the two large-bodied ruminants (*L. aff. pierensis* and *Miotragocerus* sp.).

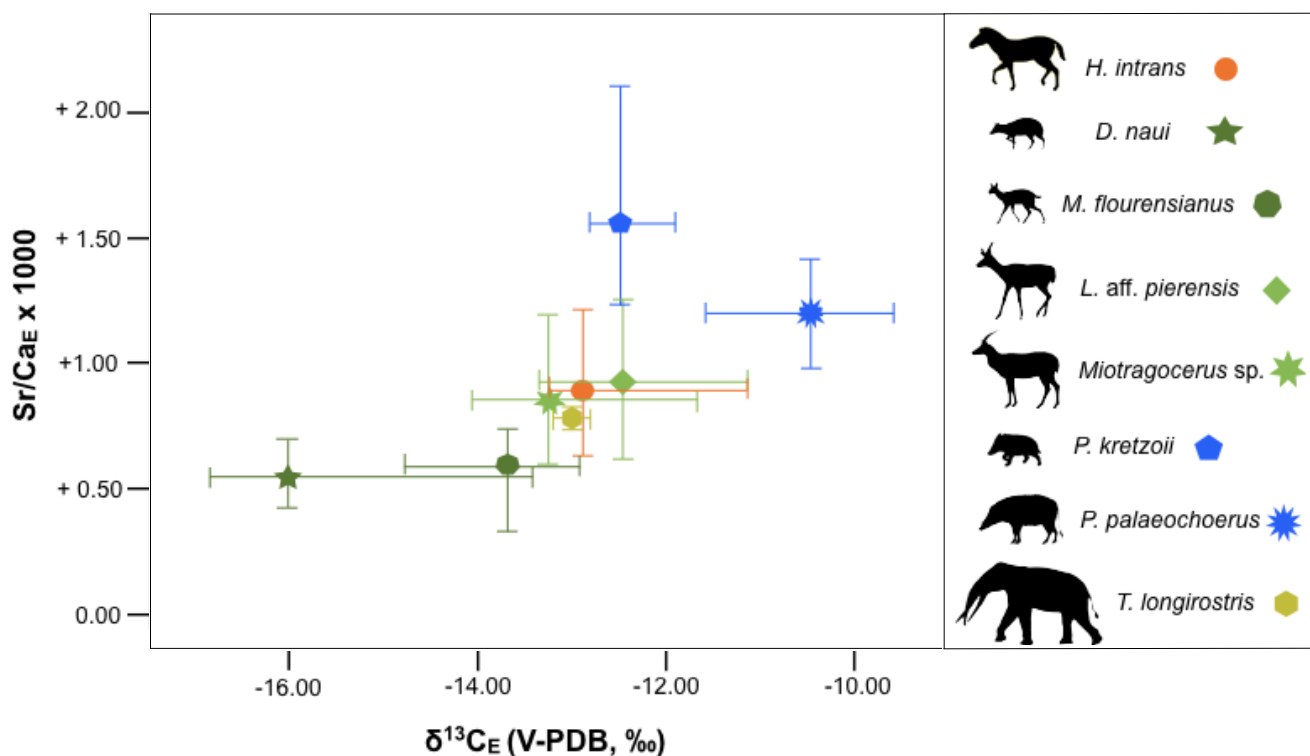


FIGURE 3. Scatter plot of mean values and total ranges of enamel Sr/Ca ratios and carbon stable isotope ($\delta^{13}C$) values of the R. II fauna. $\delta^{13}C$ enamel values are taken from Eastham *et al.*, 2016.

Unlike the cervid (*Lucentia* aff. *piernes*) and equid (*Hippotherium intrans*), the elevated Sr/Ca ratios of the bovid *Miotragocerus* sp. are incongruent with morphological and stable isotope data, which suggest a diet dominated by leaves with a small fruit component (Solounias and Dawson-Saunders, 1988; Spassov and Geraads, 2004; Merceron *et al.*, 2007; Merceron, 2009; Eastham *et al.*, 2016). This type of diet would typically be associated with relatively low Sr/Ca ratios (Burton *et al.*, 1999; Lee-Thorp *et al.*, 2003; Sponheimer *et al.*, 2005; Drouet and Herbauts, 2008). The discrepancy between morphological and trace element data could be accounted for by differences in the gastrointestinal tract of ruminant vs. monogastric ungulates. Balter *et al.* (2002) found that ruminants were enriched in Ba compared to contemporaneous monogastric mammoths, rhinoceroses, and equids. Barium is chemically very similar to strontium and shows a comparable metabolic behavior (Burton, 2008). In fact, several studies have shown that Ba/Ca and Sr/Ca ratios reflect similar dietary information (Burton and Wright, 1995; Burton *et al.*, 1999; Burton, 2008). These authors suggest that the prolonged retention of digesta in ruminant bodies, in addition to more efficient cellulose digestion, results in a greater concentration of non-essential trace elements in the bones and teeth. Deer and antelope have been shown to yield significantly higher Ba/Ca ratios than other non-ruminant herbivores (Gilbert *et al.*, 1994; Burton *et al.*, 1999). Domingo *et al.* (2009, 2012) found the highest Sr/Ca and Ba/Ca ratios in the large-bodied ruminants at the Somosaguas site. At R. II, the Sr/Ca ratios of *Miotragocerus* sp. are higher than those of the gomphothere *T. longirostris* ($\bar{x} = 0.77 \pm 0.05$) and comparable with those of the cervid and equid. While limited by sample size ($n = 2$), the Sr/Ca ratios of *T. longirostris* are congruent with morphological and stable isotope data indicating a browsing diet (Agustí and Antón, 2002; Domingo *et al.*, 2013; Eastham *et al.*, 2016). It is likely that the comparatively higher Sr/Ca ratios of the bovid reflect a different digestive physiology (ruminant vs. monogastric) rather than a significant difference in diet.

Dorcatherium navi ($\bar{x} = 0.52 \pm 0.13$; Tragulidae) and *Micromeryx ourensianus* ($\bar{x} = 0.57 \pm 0.16$; Moschidae) displayed the lowest Sr/Ca ratios of the sampled fauna (Table 2; Fig. 2) indicating a preference for Sr-poor plants or plant parts. Trace element concentrations are unevenly distributed in plants, with the highest concentrations in the roots and lowest concentrations in the fruits (Rao, 1979; Runia, 1987; Burton *et al.*, 1999; Drouet and Herbauts, 2008). For example, an early study of chicku (*Achras sapota*) and mango (*Mangifera indica*) trees revealed lower Sr concentrations in fruits as compared to leaves (Rao, 1979). The low Sr/Ca ratios of *D. navi* and *M. ourensianus* are in accordance with morphological and stable isotope data indicating a dietary preference for fruit

(Tütken *et al.*, 2006; Merceron *et al.*, 2007; Merceron, 2009; Aiglstorfer *et al.*, 2014; Eastham *et al.*, 2016; Fig 3.). The presence of species dependent on fruit is consistent with the abundance of endocarps recovered from R. II (Kordos and Begun, 2002; Hably and Erdei, 2013). *D. navi* and *M. flourensianus* are suggested to have occupied a similar niche to extant duikers (*Cephalophus* sp.; SMITH, 1827) and water chevrotains (*Hyemoschus aquaticus*; OGILBY, 1841), which inhabit the forest floors of tropical Africa and selectively feed on fruits and seeds fallen from the canopy (Nowak, 1991; Cerling *et al.*, 2004; Merceron *et al.*, 2007; 2009; Rössner, 2007; Alba *et al.*, 2011).

Interestingly, the Sr/Ca ratios of *M. flourensianus* were significantly lower ($p = 0.03$, Fisher's LSD) than those of the bovid *Miotragocerus* sp. (Fig. 2; Table 2). The results are unexpected given that both species were ruminants thought to have browsed on leaves and fruits (Tütken *et al.*, 2006; Merceron *et al.*, 2007; Merceron, 2009; Aiglstorfer *et al.*, 2014; Eastham *et al.*, 2016), which are Sr-poor plant resources. As far as we know, the behavior of Sr in the gastrointestinal tracts of small vs. large-bodied ruminants has not yet been studied, so no conclusive remarks can be made. However, it is possible that the unique digestive adaptations of extant small-bodied ruminant frugivores could help to clarify this finding. Rumination is a relatively inefficient way to obtain energy from low fiber foods, like most fruits (Cork, 1996). Despite this, many small-bodied ruminants living in tropical forests throughout the world depend on fruit for energy and nutrients. The success of small-bodied ruminant frugivores has been related to several adaptations in their digestive process. Their small rumen and fermentation capacity relative to energy requirements requires that they eat more readily fermentable carbohydrates and subsequently pass plant fiber more rapidly through the digestive tract (Demment and Van Soest, 1985). They also tend to have a larger reticulo-omasal orifice, which allows some digesta to escape rumen fermentation (Hofmann, 1973). If the prolonged retention of digesta by large-bodied ruminants is associated with an increase in the uptake of non-essential trace elements, it seems plausible that the rapid passage of digesta by small-bodied ruminant frugivores could result in a decrease in trace element uptake. Testing this hypothesis, however, requires further baseline work with modern ruminants examining the behaviour of Sr under different digestive strategies.

Determining ecological relationships within trophic levels is important for understanding how ecosystems function. The niche partitioning hypothesis predicts that ecologically similar species can coexist by partitioning their resources in one or more of the three primary niche dimensions (diet, habitat and time; Hardin, 1960; Schoener, 1974; DiBitetti *et al.*, 2009), with diet being the most commonly segregated axis

among herbivores (Stewart *et al.*, 2002). The trace element analysis shows significant differences in dietary resource use within the early Late Miocene ungulate community at R. II, implying that the different analyzed ungulate species did partition resources by selecting different plants and/or plant parts, which would diminish competition. However, the overlapping ranges of Sr/Ca values displayed by the two suids, the cervid and equid, and the tragulid and moschid indicate some degree of dietary niche overlap. 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 ecologically similar species (Pyke *et al.*, 1977; Gordon and Illius, 1989; Stevenson *et al.*, 2000; Levine and Hille Ris Lambers, 2009; Singh *et al.*, 2011; Djagoun *et al.*, 2013; Landman *et al.*, 2013; Kartzinel *et al.*, 2015). A local abundance of plant resources in addition to dietary resource partitioning likely acted as the primary factors promoting species coexistence within the ungulate community at R. II.

While the fossil record at R. II provides important information for understanding the factors that acted to promote the assembly and coexistence of early Vallesian mammalian communities, it lacks the depth of time required to evaluate changes in faunal diversity through time. Recent analysis of small mammal diversity in the Vallès-Penedès Basin in Spain indicates a slow decline in taxonomic richness occurring since the late Vallesian (Casanovas-Vilar *et al.*, 2014, 2016). These findings are contrary to previous studies, which reported an abrupt extinction event at the early/late Vallesian boundary (the Vallesian Crisis; Agustí and Moyà-Solà, 1990; Agustí *et al.*, 1997, 1999, 2003, 2013). Casanovas-Vilar *et al.* (2014, 2016) suggested that the decline of forest-dwelling taxa occurred gradually through a series of extinction events beginning in the late Vallesian. These authors asserted that the abrupt pattern of extinctions interpreted as the “Vallesian Crisis” resulted from uneven sampling. In central Europe, studies by Franzen *et al.* (2013) and Daxner-Höck *et al.* (2016) have demonstrated the persistence of some forest-adapted fauna (chalicotheres, moschids, and certain rodents) well into the early Turolian. Environmental changes associated with the Late Miocene cooling are not well expressed in the Pannonian Basin (Ivanov *et al.*, 2011; Hably, 2013; Utescher *et al.*, 2017), due to the buffering effect of Lake Pannon. A recent palaeoclimatic study utilizing Plant Functional Types (PFTs) indicated constantly humid conditions along the northern margin of the lake throughout the early and middle Turolian (9–6.5Ma; Utescher *et al.*, 2017).

CONCLUSIONS

Examination of tooth enamel Sr/Ca ratios in early Late Miocene ungulates from R. II showed significant

differences in dietary resource use. In general, the Sr/Ca ratios of the sampled species support previous ecological determinations made on the basis of morphological and stable isotope data. The suids *Parachleuastochoerus kretzoi* and *Propotamochoerus palaeochoerus* displayed the highest Sr/Ca ratios suggesting a preference for Sr-rich roots and rhizomes. *Parachleuastochoerus kretzoi* yielded higher and more heterogeneous Sr/Ca ratios than *Propotamochoerus palaeochoerus*, which could be indicative of a more omnivorous diet. Elevated Sr/Ca ratios exhibited by the cervid *Lucentia* aff. *pierensis* and equid *Hippotherium intrans* suggest intermediate feeding, which included the intake of C₃ graminoids. The bovid *Miotragocerus* sp. displayed higher Sr/Ca ratios, suggesting intermediate feeding, than the gomphothere *Tetralophodon longirostris*. The implication for *Miotragocerus* sp. as an intermediate feeder is incongruent with morphological and stable isotope data, which identifies it as a browser. This discrepancy likely reflects a difference in digestive physiology (ruminant vs. monogastric) as opposed to a difference in dietary behavior. The tragulid *Dorcatherium nani* and moschid *Micromeryx flourensianus* showed the lowest Sr/Ca ratios of the sampled R. II fauna suggesting a preference for Sr-poor fruit. A similar range of Sr/Ca values were found in several of the sampled species implying some degree of interspecific competition. To diminish potential competition it is likely that the different ungulate species partitioned plant resources within the local environment, which would have acted to promote coexistence within this diverse community of predominantly browsing herbivores. This study further highlights the utility of trace element ratios to discern the complex ecological relationships of species in ancient ecosystems.

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APPENDIX I

TABLE I. Sr/Ca ratios of the ungulate dental enamel samples from R. II

Specimen No.	Species	Family	Tooth position	Sr/Ca x 1000
RUD1026	<i>P. kretozii</i>	Suidae	M2	1.25
RUD1673	<i>P. kretozii</i>	Suidae	M3	1.31
RUD668	<i>P. kretozii</i>	Suidae	p4	1.52
RUD543	<i>P. kretozii</i>	Suidae	P3	2.08
RUD1355	<i>P. palaeochoerus</i>	Suidae	M2	1.42
RUD1021	<i>P. palaeochoerus</i>	Suidae	M3	1.19
RUD1331	<i>P. palaeochoerus</i>	Suidae	P3	1.28
RUD1343	<i>P. palaeochoerus</i>	Suidae	M1	0.98
RUD1851	<i>L. aff. pierensis</i>	Cervidae	P3	1.26
RUD279	<i>L. aff. pierensis</i>	Cervidae	m2	1.15
RUD486	<i>L. aff. pierensis</i>	Cervidae	m3	0.67
RUD1547	<i>L. aff. pierensis</i>	Cervidae	M1	0.7
RUD695	<i>L. aff. pierensis</i>	Cervidae	m2	0.71
RUD579	<i>L. aff. pierensis</i>	Cervidae	m1	1.21
RUD1513	<i>L. aff. pierensis</i>	Cervidae	M3	0.6
RUD1011	<i>L. aff. pierensis</i>	Cervidae	M2	1.17
RUD154	<i>L. aff. pierensis</i>	Cervidae	M2	0.8
RUD1611	<i>Miotragocerus</i> sp.	Bovidae	m2	0.77
RUD1530	<i>Miotragocerus</i> sp.	Bovidae	M3	0.68
RUD167	<i>Miotragocerus</i> sp.	Bovidae	M1	0.6
RUD176	<i>Miotragocerus</i> sp.	Bovidae	M2	0.58
RUD377	<i>Miotragocerus</i> sp.	Bovidae	m3	1.13
RUD391	<i>Miotragocerus</i> sp.	Bovidae	m2	0.69
RUD699	<i>Miotragocerus</i> sp.	Bovidae	M3	1.2
RUD693	<i>Miotragocerus</i> sp.	Bovidae	m1	0.88
RUD1014	<i>H. intrans</i>	Equidae	m3	0.63
RUD804	<i>H. intrans</i>	Equidae	M2	0.62
RUD794	<i>H. intrans</i>	Equidae	m2	1.03
RUD139	<i>H. intrans</i>	Equidae	M3	0.84
RUD429	<i>H. intrans</i>	Equidae	m3	0.7
RUD628	<i>H. intrans</i>	Equidae	m2	0.94
RUD721	<i>H. intrans</i>	Equidae	M3	1.21
RUD728	<i>H. intrans</i>	Equidae	M3	1.06
MAFI6	<i>T. longirostris</i>	Gomphotheriidae	M3	0.73
MAFI7	<i>T. longirostris</i>	Gomphotheriidae	m2	0.8
RUD181	<i>D. naui</i>	Tragulidae	p2	0.45
RUD1133	<i>D. naui</i>	Tragulidae	M3	0.38
RUD1624	<i>D. naui</i>	Tragulidae	m2	0.64
RUD1691	<i>D. naui</i>	Tragulidae	M2	0.31
RUD130	<i>M. flourensianus</i>	Moschidae	m2	0.73
RUD1844	<i>M. flourensianus</i>	Moschidae	M3	0.58
RUD692	<i>M. flourensianus</i>	Moschidae	M2	0.46
RUD1613	<i>M. flourensianus</i>	Moschidae	P3	0.7
RUD1760	<i>M. flourensianus</i>	Moschidae	m2	0.67
RUD563	<i>M. flourensianus</i>	Moschidae	M3	0.48