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Orogeny forced terrestrial climate variation during the late Eocene–early Oligocene in Europe

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ABSTRACT
Terrestrial climatic data reflect variable and often conflicting responses to the global cooling event at the Eocene-Oligocene transition (ca. 34 Ma). Stable isotopic compositions of the tooth enamel of large, water-dependent, herbivorous terrestrial mammals are investigated here to better understand the European continental climate during the late Eocene–early Oligocene. High δ¹⁸Opo₄ and δ¹³C values reflect a semi-arid climate and ecosystem in the late Eocene. In the west-southwest region of Europe, these conditions prevailed until at least 33 Ma, after which it became more humid. A similar change was recorded north of the Alpine thrust, but it occurred 2 m.y. earlier. The north and west-southwest regions show a significant offset in δ¹⁸Opo₄ composition between 35 and 31 Ma, indicating the influence of different air trajectories with different moisture sources (Atlantic versus Tethys). This also marks the presence of an orographic height in central Europe from the latest Eocene. After 31 Ma, a large drop in δ¹⁸Opo₄ is registered, explained by altitude-induced fractionation on meteoric water isotopic composition. The related paleoaltitude change is estimated to be 1200 m, and the uplift could have taken place along the Alpine-Dinarid orogenic system.

INTRODUCTION
The early Cenozoic climate has been intensively studied, and compilations of paleoclimatic data have revealed that Earth’s climate changed dramatically during this era (Zachos et al., 2001). In the Paleogene, the warm greenhouse world gradually changed to icehouse conditions, with permanent ice sheets on Antarctica. The major shift between the two climate modes is placed at the Eocene-Oligocene transition (EOT, 34 Ma), when rapid step-wise shifts toward higher δ¹⁸O values occurred in the marine oxygen isotopic record (Katz et al., 2008). The terrestrial responses to this climatic change show strong spatial heterogeneity, and the implications of the reported paleoclimatic records are often debated (e.g., Grimes et al., 2005; Zanazzi et al., 2007; Hren et al., 2013). We investigated the stable isotopic compositions of tooth enamel of large ground-dwelling herbivorous mammals from Eocene and Oligocene localities. A major Eocene–Oligocene faunal turnover that corresponds to the extinction and origination event called the “Grande Coupure” is recorded in Europe (Stehlin, 1909). Many endemic European Eocene mammals became extinct (e.g., Lophiodontidae) and gave way to new Asian immigrant groups (e.g., Rhinocerotidae) (Hooker et al., 2004).

Mammalian tooth enamel is composed of bioapatite [Ca₃(PO₄)₂(CO₃)₂(OH)] with greater crystal size and lower organic and carbonate contents than bone or dentine. These characteristics render enamel the most resistant bioapatite archive to late diagenetic and bacterial alteration. It is therefore the most suitable material to obtain an in vivo isotopic signal (e.g., Kohn and Cerling, 2002). The oxygen isotopic composition of teeth and bones of water-dependent herbivorous animals strongly depends on the isotopic composition of drinking water (e.g., local meteoric water: δ¹⁸Ow and/or other water sources) (Luz et al., 1984; Kohn and Cerling, 2002) and correlates weakly with relative humidity (e.g., Kohn, 1996). The δ¹⁸Ow reflects the isotopic composition of the moisture source and alteration during transport (e.g., latitude, altitude, continental effect, amount of precipitation), but it also shows significant correlation with mean annual temperature (MAT) at middle and high latitudes (e.g., Fricke and O’Neil, 1999). The carbon isotopic composition of the teeth reflects the diet of the animals (Kohn and Cerling, 2002) and in herbivores indirectly reflects the composition of the paleoflora. In the Eocene–Oligocene, the paleoflora was dominated by C₃ plants, as the C₄ photosynthetic carbon fixation was not yet widespread (e.g., Kohn, 2010). Therefore, any variation in the δ¹³C of C₃ plants can be linked to environmental changes (e.g., water stress, aridity, canopy effect; Farquhar et al., 1989).

METHODS AND RESULTS
We studied fossils from 24 localities across Europe’s middle latitudes (40º–50ºN; Fig. 1)
covering a biostratigraphic range from MP15 to MP25 (European Mammal Paleogene Reference Levels). These levels are used for our age model according to the geological time scale of Gradstein et al. (2012). Sites with well-constrained MP ages and available fauna were sampled, together with localities recording sporadic occurrences of mammals, in order to expand our data set in both time and space (Fig. 2; see the GSA Data Repository1 and Table DR1 therein). Tooth enamel was sampled along the vertical axis to average any possible seasonal variation that can be recorded in a single tooth. To trace possible taxonomical disparity, several species were chosen from Perissodactyla and Artiodactyla families (e.g., Palaeotheriidae, Lophiodontidae, Rhinocerotidae, and Anthracotheriidae; see Table DR2; Fig. 2).

From the different oxygen-bearing ions in bioapatite, the phosphate group \( \text{PO}_4^{3-} \rightarrow \delta^{18} \text{O}_{\text{PO}_4} \) is the most resistant to diagenetic alteration (e.g., Zazzo et al., 2004), and so it was separated and analyzed. Of the samples, ~75% were also analyzed for the carbon and oxygen isotopic compositions of the structural carbonate \( \text{CO}_3^{2-} \rightarrow \delta^{13} \text{C} \) and \( \delta^{13} \text{O} \). Sampling techniques, processing protocols of the teeth, and data are reported in the Data Repository, and the \( \delta^{13} \text{C} \) and \( \delta^{18} \text{O} \) values are plotted in Figure 2. The strong correlation between the two oxygen isotopic compositions (\( \text{CO}_3^{2-} \) versus \( \text{PO}_4^{3-} \); \( R^2 = 0.78; \ p < 0.05 \) supports good preservation of the tooth enamel with no considerable alteration of their isotopic compositions (see Fig. DR1).

### Testing Physiological and Habitat Effects

The physiological controls on oxygen isotopic fractionation for different mammal species are well documented (e.g., Kohn, 1996), but cannot be accurately constrained for fossil groups; this is especially difficult considering the faunal turnover in the European continental vertebrates near the EOT. Because there can be huge differences in water dependencies within the modern members of the perissodactyls and artiodactyls, statistical tests were performed on key localities where several samples were available (Monteviale, Italy; Möhren 13 and 19, Germany; Villebramar, France; see Fig. 1). These tests indicate that taxonomic differences have little role in the isotope variances, and there is no obvious pattern between the two orders (Table DR3; Fig. 2C). In contrast, few subgroups (from species to families) yielded significant offsets; however, it is difficult to resolve whether these truly reflect different water dependencies or are simply due to mixed fauna assemblages (i.e., seasonal migration). However, if the average isotopic compositions are taken for all the localities, a clear geographical variation appears (Fig. 2D). The interpretation here is that the environmental factors had more important effects on the overall \( \delta^{18} \text{O} \) values than did physiological fractionation. In addition, the \( \delta^{13} \text{C} \) data do not show any significantly different food preference between the groups (see Table DR3), with exception of the site La Débruge (France), where only two teeth were analyzed (Figs. 2A and 2B).

### DISCUSSION AND INTERPRETATIONS

#### Carbon Isotopic Composition

The site-average \( \delta^{13} \text{C} \) data reflect geographical variation (Fig. 2B); generally (1) the

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1GSA Data Repository item 2014270, Table DR1 (fossil locality information), Table DR2 (analyzed samples and their isotopic compositions), Table DR3 (statistical comparison of different taxa from the four most representative localities), method of preparation of the samples for stable isotope analyses, Figure DR1 (phosphate and carbonate oxygen isotopic compositions in biogenic apatite), Figure DR2 (detailed paleogeographic maps), and references, is available online at www.geosociety.org/pubs/ft2014.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.
west-southwest sites tend to have higher δ13C values, (2) the northern and the young eastern (younger than 31 Ma) localities have much lower δ18O, and (3) both the north and west-southwest regions recorded significant isotope shifts at different times. The first isotope shift appeared between MP19 and MP20 levels north of the Alpine thrust (~1.5‰; Student’s t-test \( t_{28} = 3.22; p \approx 0.01 \)), while a similar change occurred in the west-southwest ~2 m.y. later (MP21–MP22, ~1.6‰, \( t_{28} = 6.50; p \approx 4.8 \times 10^{-7} \)). The east-southeast and west-southwest data run similarly until ca. 31 Ma, and then the eastern sites show lower δ18O values.

The enamel δ13C can be used to determine plant-food carbon isotopic composition using a fractionation factor of 1.0141 between the enamel and diet (Kohn and Cerling, 2002; Fig. 2D); this yields a range of δ13Cplant from −20.8‰ to −27.8‰. Taking into account an average of 2.5‰ higher atmospheric δ13C for the Eocene–Oligocene than today (Tippelle et al., 2010), the obtained values correspond to the middle-high range of the overall modern C3 flora (from −20‰ to −37‰; Kohn, 2010). Based on the relation between mean annual precipitation (MAP) and the δ13C values of C3 plants (Kohn, 2010), the high isotopic values in our late Eocene–earliest Oligocene record indicate a dry ecosystem (<500 mm MAP). The decreasing δ13C values suggest that the climate became more humid in the north at the EOT (ΔMAP ~480 mm, calculated at 300 m and 50°N), while the west-southwest received more precipitation by 32 Ma (ΔMAP ~330 mm, calculated at 300 m and 45°N). This suggests that moisture-rich air masses gradually extended to more southern regions (Fig. 3). After 31 Ma, the eastern region became even more humid, with MAP as much as 2000 mm, which agrees with paleoflora studies (Mosbrugger et al., 2005; Erdei et al., 2012).

Oxygen Isotopic Composition [δ18OPO4]

The overall negative trend in this record (Fig. 2C) generally indicates that the drinking-water isotopic composition (e.g., δ18Owater) decreased and/or relative humidity may have increased with time in the region (e.g., Kohn, 1996). The lower δ18Owater can reflect cooler temperatures (Fricke and O’Neil, 1999), but also can reflect changes in the isotopic composition of moisture sources (e.g., alteration in air-mass trajectories, and continental and/or altitude effects). The average δ18Owater values of the localities demonstrate geographic heterogeneities that indicate complex interaction among these possible causes for the observed trend (Fig. 2D). (1) The relatively southern, maritime localities show very similar, high δ18Owater values until ca. 31 Ma. (2) Localities north of the Alpine thrust, between 35 and 31 Ma, have significantly lower isotopic values (Δδ18Owater of ~2.4‰, \( t_{28} = 8.33; p = 1.7 \times 10^{-4} \)). (3) From 31 Ma, 1%–1.5‰ isotopic offset is apparent between the west-southwest and eastern areas.

The west-southwest and southeastern localities were probably dominated by warm Tethyan moisture sources (i.e., high δ18Owater) and/or evaporative conditions until at least 33 Ma. This concurs with the time-equivalent high δ13C values. In contrast, the north received more precipitation (i.e., low δ18Owater with low δ18OPO4, mostly from the North Atlantic. The significant division in the data between the north and west-southwest regions between 35 and 31 Ma points to the existence of a potential orographic barrier for these air masses; otherwise, more mixed isotopic values would be expected. From the late Eocene, the collision between Europe and Africa triggered the emergence of the Alpine-Dinaridic system (Schmid et al., 2008), causing isotopic readjustments that formed a mainland barrier. Therefore, certain parts could already have reached elevations that had acted as an obstacle for atmospheric circulation.

After 31 Ma, the δ18Owater values of both the west-southwest and eastern sites (Fig. 3) record a negative shift of 4.3‰ relative to the corresponding older sites, and 2.2‰ compared to the northern ones. It is important that other oxygen isotope data (reported from southern German rodent teeth), also reveal a large negative δ18Owater shift (~2.2‰) at 31–30 Ma (Hérán et al., 2010; see Fig. 3). This shift further supports the sudden, wider presence of light δ18Owater in the region, even if the physiology of small mammals is quite different from the large herbivores. The isotope offset between the west-southwest and eastern regions (Fig. 2D) suggests fractionation in δ18Owater due to longer moisture transport from the Atlantic across the continent (i.e., a continental effect). This may also exclude long-term dominance of possible eastern air trajectories with moisture having low isotopic composition; otherwise, the direction of the west-east isotopic offset should be reversed. Therefore, the major air trajectories are assumed to be Westerlies from the Atlantic. However, in the eastern region, a large surface area was covered by an epicontinental sea (i.e., Central Paratethys; Fig. 3). Evaporation from this water body could have added moisture to the western air trajectories, increasing precipitation inland (i.e., low δ18O in the east; see Fig. 2B). Nevertheless, changes in any of these moisture sources could not have resulted in such a widespread negative isotope shift, especially when the global sea-water δ18O composition increased during the EOT and was rather stable in the early Oligocene (e.g., Katz et al., 2008).

An increase in relative humidity can also be a factor for the negative δ18Owater shift (Kohn, 1996), but the sensitivity of water-dependent animals to relative humidity is also very low, plus the paleoflora already indicates an overall high humidity (75%–80%; Erdei et al., 2012) with no major changes at the time (Mosbrugger et al., 2005). Moreover, the δ18O values of the teeth are compatible with an already humid environment.

Considering only a minimum drop of ~2.2‰ in δ18Owater, it can be translated to ~2.8‰ ± 0.5‰ changes in δ18Owater compositions (0.7‰–0.9‰PO4/‰MW; see Luz et al., 1984; Kohn and Cerling, 2002). From this, ΔMAT can be calculated, −7.0 ± 2.9 °C (from 0.3‰ to 0.6‰MW/°C, representing modern and past mid-latitude end members, respectively; Fricke and O’Neil, 1999). Such a temperature shift is not currently supported by any records. In addition, the global marine climate record is rather stable (Zachos et al., 2001), and the paleoflora record does not indicate any temperature change in the late Rupelian (Mosbrugger et al., 2005).

Paloaltitude

The wide appearance of low δ18Owater values from 31 Ma is best explained by topography-induced fractionation of the drinking water and/or redistribution of this water due to modificat-
tion of drainage patterns; the latter process can be responsible for about half of the overall 4.3‰ negative shift, given that in the north such low values already existed earlier (Fig. 2D). If the residual ∼2.2‰ δ18OCH3 shift is only due to altitude, then relative elevation change can be estimated from the derived Δδ18Osw using global average and modern Central Alps lapse rates as two end members (0.28‰/100 m and 0.2‰/100 m, respectively; Poage and Chamberlain, 2001; Campani et al., 2012). The calculated relative paleo-elevation change is 1200 ± 340 m. An ancient warmer climate regime, however, would lead to even more reduced lapse rates, meaning that the obtained altitude change is a minimum estimate. This sudden uplift agrees well with other reported data, such as intensified sediment accumulation (e.g., Kuhlemann and Kempf, 2002) and comparable cooling and exhumation ages (e.g., Steck and Hunziker, 1994; Jourdan et al., 2013) which all support the enhanced emergence of the Alpine-Dinaric orogenic belt.

**Eocene-Oligocene Transition Temperature Drop?**

Oxygen and carbon isotope data show that the south-western European climate was semi-arid during the EOT. The moisture source was controlled by the warm Tethys Ocean, which buffered any global signal related to the EOT cooling event. In contrast, the sites north of the Alpine thrust (Fig. 3) had more precipitation, and the data also reveal a significant δ18OCH3 shift of −1.6‰ exactly at the EOT (Fig. 2D; MP20 → pair-wise t-tests; MP19–20, t(16) = 3.87, p = 0.001, and MP20–21, t(15) = 2.64, p = 0.02). If this shift was only caused by MAT, a temperature drop of −5.1 ± 2.1 °C can be determined. However, at the same time more humid conditions arose (see the δ13C data in Fig. 2B); this complicates any certain interpretation here. For example, an increase of 10% in relative humidity (RH) would reduce the MAT to only −1.9 ± 0.8 °C (−0.1%εCH3/εH2O; see Kohn, 1996). Therefore, the quantitative MAT must be estimated with caution. Moreover, after MP20, the δ18OCH3 returned to previous MP19 values, indicating strengthened local conditions in this region.

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