# New method to estimate paleoprecipitation using fossil amphibians and reptiles and the middle and late Miocene precipitation gradients in Europe

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## ABSTRACT

**Existing methods for determining paleoprecipitation are subject to large errors (±350–400 mm or more using mammalian proxies), or are restricted to wet climate systems due to their strong facies dependence (paleobotanical proxies). Here we describe a new paleoprecipitation tool based on an indexing of ecophysiological groups within herpetological communities. In recent communities these indices show a highly significant correlation to annual precipitation ($r^2 = 0.88$), and yield paleoprecipitation estimates with average errors of ±250–280 mm. The approach was validated by comparison with published paleoprecipitation estimates from other methods. The method expands the application of paleoprecipitation tools to dry climate systems and in this way contributes to the establishment of a more comprehensive paleoprecipitation database. This method is applied to two high-resolution time intervals from the European Neogene: the early middle Miocene (early Langhian) and the early late Miocene (early Tortonian). The results indicate that both periods show significant meridional precipitation gradients in Europe, these being stronger in the early Langhian (threefold decrease toward the south) than in the early Tortonian (twofold decrease toward the south). This pattern indicates a strengthening of climatic belts during the middle Miocene climatic optimum due to Southern Hemisphere cooling and an increased contribution of Arctic low-pressure cells to the precipitation from the late Miocene onward due to Northern Hemisphere cooling.**

**Keywords:** paleoclimate, Neogene, precipitation, herpetofauna.

## INTRODUCTION

Precipitation is one of the most important geodynamic controlling factors, but there is debate about how precipitation is coupled to deformation, erosion, and tectonics in active orogenic systems (Molnar, 2003). The development of more comprehensive paleoprecipitation databases is crucial for understanding feedback mechanisms (Hodges et al., 2004); however, high-resolution continental records of precipitation are rare. This is partly due to the facies dependence of paleobotanical methods, which are restricted by the preservation potential of pollen and leaves, which in turn is generally higher in humid areas and in nonoxygenated, nonalkaline sediments. Mammal-based methods show either large (±350–400 mm, small mammals; van Dam, *in* Bernor et al., 2004) or very large (≥1000 mm, ungulate herbivores; Damuth, *in* Bernor et al., 2004) errors.

Here we present a new method for qualitatively estimating paleoprecipitation based on fossil amphibian and reptilian communities. The distribution of amphibians and reptiles is related to global, regional, and even habitat scales of environmental conditions (Zug et al., 2001). It is further assumed that species distributions at a given spatial scale are in equilibrium with their surrounding environment (Guisan and Theurillat, 2000). Humidity plays an important role especially in the tropics to warm temperate zones (Hawkins et al., 2003). A strong positive correlation between annual precipitation and amphibian species richness has been reported from all continents (Duellman, 1999). Similar relationships are documented for several reptile groups (e.g., snakes, turtles; see Hawkins et al., 2003, and references herein), and it is obvious that climate (precipitation and temperature) more closely matches reptile distributions than do other factors such as topography (Guisan and Hofer, 2003; Owen, 1989). For herpetofaunal distributions and species richness, precipitation functions as a direct (i.e., proximal) predictor and gives robust and widely applicable modeling results (Austin, 2002). We can show that in the Holocene, ecophysiologic indices (based on types and diversity of ecophysiological groups) strongly correlate with annual precipitation. In addition, the 95% confidence interval for predictions using this method is relatively low (±250–280 mm). Consequently, we used ecophysiologic indices of fossil herpetofaunas to predict annual paleoprecipitation.

Our new paleoprecipitation tool is applicable in fossil assemblages with rich amphibian and reptile records that show relatively low taphonomical bias with respect to the herpetofauna, such as alluvial sediments, paleosols, caves, fissure fillings, pond and swamp deposits, and channel fill sediments. With the exception of swamps, these are all habitats where paleobotanical methods are usually not appropriate.

We applied our method to two Neogene time slices (early middle and early late Miocene) in Europe. The resulting individual paleoprecipitation estimates are in good accord with results from other methods and show that the meridional precipitation gradient in the early middle Miocene was stronger than in the early late Miocene. This is supposed to have been due to an increase in evergreen forestation, which in turn was likely a major influence on hominoid evolution in Eurasia.

## MATERIALS AND METHODS

### Definition of Herpetological Ecophysiologic Groups

The most important environmental factors for amphibian and reptilian distributions are the availability of sunlight as the ultimate energy source, and the availability of water as a buffering medium against thermal extremes. Several different ecophysiological strategies and adaptations are involved in maintaining thermoregulation, water balance, and gas exchange. Here we used some main strategies to perform an ecophysiological grouping of amphibians and reptiles (excluding nonfossorial snakes; for source references of distributional and ecophysiologic data see Data Repository Appendix DR1[1]).

Group 1 (heliophile group) comprises taxa that rely on behavioral mechanisms to thermoregulate (e.g., basking) and cutaneous control of evaporative water loss (e.g., osteoscu-

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[1] GSA Data Repository item 2006083, distribution data and ecophysiologic data; climate data; stratigraphic, chronologic and fossil data; and regression analysis (Figures DR1–DR2, Tables DR1–DR10, and Appendices DR1–DR8), is available online at www.geosociety.org/pubs/ft2006.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

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TABLE 1. SUMMARY DATA FOR PREDICTOR SAMPLES

| Cell no. | Taxa count | MAP (mm) | Group 1 (Fr) | Group 2 (Fr) | Group 3 (Fr) | Group 4 (Fr) | Group 5 (Fr) | Group 6 (Fr) |
|---|---|---|---|---|---|---|---|---|
| 9 | 32 | 32 | 0.78 | 0.09 | 0.09 | 0.03 | 0 | 0 |
| 16 | 44 | 52 | 0.75 | 0.18 | 0.05 | 0.02 | 0 | 0 |
| 10 | 26 | 54 | 0.88 | 0.04 | 0.04 | 0 | 0 | 0.04 |
| 14 | 78 | 72 | 0.90 | 0.06 | 0.01 | 0.03 | 0 | 0 |
| 15 | 89 | 88 | 0.81 | 0.13 | 0.03 | 0.02 | 0 | 0 |
| 13 | 47 | 95 | 0.87 | 0.04 | 0.02 | 0.02 | 0 | 0.04 |
| 27 | 18 | 255 | 0.72 | 0.11 | 0.06 | 0.06 | 0 | 0.06 |
| 8 | 69 | 289 | 0.78 | 0.10 | 0.06 | 0.01 | 0 | 0.04 |
| 28 | 25 | 289 | 0.64 | 0 | 0.20 | 0.08 | 0.04 | 0.04 |
| 26 | 22 | 324 | 0.68 | 0.05 | 0.14 | 0.05 | 0 | 0.09 |
| 23 | 20 | 482 | 0.35 | 0.15 | 0.30 | 0.15 | 0 | 0.05 |
| 7 | 61 | 505 | 0.64 | 0.11 | 0.15 | 0.05 | 0 | 0.05 |
| 22 | 20 | 506 | 0.30 | 0.15 | 0.35 | 0.15 | 0 | 0.05 |
| 25 | 19 | 517 | 0.32 | 0.16 | 0.42 | 0.05 | 0 | 0.05 |
| 32 | 23 | 565 | 0.26 | 0.17 | 0.26 | 0.17 | 0.04 | 0.09 |
| 31 | 13 | 591 | 0.31 | 0.15 | 0.31 | 0.15 | 0 | 0.08 |
| 24 | 26 | 615 | 0.35 | 0.12 | 0.38 | 0.12 | 0 | 0.04 |
| 21 | 21 | 617 | 0.19 | 0.14 | 0.48 | 0.14 | 0 | 0.05 |
| 20 | 23 | 634 | 0.22 | 0.13 | 0.43 | 0.17 | 0 | 0.04 |
| 18 | 22 | 636 | 0.23 | 0.14 | 0.41 | 0.18 | 0 | 0.05 |
| 19 | 24 | 649 | 0.25 | 0.13 | 0.42 | 0.17 | 0 | 0.04 |
| 34 | 12 | 673 | 0.17 | 0.17 | 0.25 | 0.25 | 0.08 | 0.08 |
| 2 | 8 | 692 | 0.25 | 0.13 | 0.50 | 0.13 | 0 | 0 |
| 17 | 23 | 701 | 0.22 | 0.13 | 0.43 | 0.17 | 0 | 0.04 |
| 4 | 23 | 732 | 0.17 | 0.13 | 0.48 | 0.17 | 0 | 0.04 |
| 3 | 15 | 751 | 0.20 | 0.20 | 0.47 | 0.13 | 0 | 0 |
| 5 | 26 | 776 | 0.19 | 0.12 | 0.46 | 0.19 | 0 | 0.04 |
| 12 | 24 | 787 | 0.38 | 0 | 0.46 | 0.17 | 0 | 0 |
| 6 | 43 | 802 | 0.33 | 0.12 | 0.35 | 0.12 | 0.02 | 0.07 |
| 1 | 6 | 896 | 0.17 | 0 | 0.67 | 0.17 | 0 | 0 |
| 11 | 65 | 934 | 0.25 | 0.11 | 0.40 | 0.14 | 0 | 0.11 |
| 29 | 29 | 997 | 0.28 | 0.17 | 0.14 | 0.24 | 0 | 0.17 |
| 30 | 53 | 1.043 | 0.11 | 0.09 | 0.19 | 0.36 | 0.15 | 0.09 |
| 33 | 52 | 1.162 | 0.12 | 0.12 | 0.25 | 0.23 | 0.23 | 0.06 |
| 36 | 64 | 1.203 | 0.06 | 0.28 | 0.09 | 0.36 | 0.08 | 0.13 |
| 35 | 133 | 1.476 | 0.07 | 0.14 | 0.21 | 0.28 | 0.22 | 0.08 |

*Note*: Cell no. refers to Data Repository, Figure DR1; MAP = mean annual precipitation (references for climate data see Appendix DR 2); Fr = Frequency of an ecophysiologic group; group number refers to the ecophysiologic groups in the text.

tes). These species exploit more open and drier environments where sunlight reaches the ground. The preferred respiration surface is the lung. Heliophile species favor habitats with large diurnal amplitude both in atmospheric water vapor content (which is low on average) and in air temperature (high on average). Their body size is small to medium, enabling these taxa to use shadowed places under stones or in fissures for cooling. Nearly all such species are largely independent of the existence of water bodies (most scincomorph reptiles, some gekkonids, some monitor lizards and turtles, green toads).

Group 2 (subterranean and arboreal group) comprises taxa that live mainly on trees and shrubs (chamaeleonids, some long-tailed lizards, agamids, monitor lizards, and gekkonids), and fossorial taxa that spend most of their life cycle in the soil or in organic matter. The latter prefer soft, well-oxygenated and well-drained soils (worm lizards, blind snakes, some skinks, some anguids, dibamids, spadefoots, some toads).

Group 3 (periaquatic group) comprises taxa that live in the water only during reproduction and spend the remainder of their life cycle near (perennial or periodic) water bodies (some salamanders, most frogs, some turtles).

Group 4 (semiaquatic and woodland group) comprises semiaquatic taxa of smaller body size that spend a significant part of their life cycle in the water and, if the water body dries out, are able to survive within the mud or on land. These taxa are small enough (in contrast to the aquatic group) to aestivate during the dry season under stones or in small fissures (many salamanders and newts, water frogs, water dragons, water skinks, some turtles). This group contains also woodland taxa, e.g., heliophile taxa with large body size. For cooling their body temperature they need vegetation cover (large and giant turtles).

Group 5 (heliophobe group) comprises taxa without cutaneous control of evaporative water loss (thermoregulation by evaporative cooling). They exploit shadowed and moist environments covered by dense vegetation usually near forest streams. Due to high values of cutaneous respiration, they prefer habitats with small diurnal amplitude in both atmospheric water vapor content (high on average) and air temperature (low on average) (some salamanders, some ranid and megophryid frogs).

Group 6 (aquatic group) comprises taxa of mostly larger body size that spend their whole life cycle very near or in the water. They need water as a buffering medium against temperature extremes. If the water body dries out, it is difficult for these species to find protected environments for aestivation due to their large body size (giant salamanders, proteid salamanders, soft-shell and water turtles, some monitor lizards, crocodiles).

### Climate Data

To analyze the statistical relationship between the distribution of ecophysiologic groups and the annual precipitation, we compiled a data set with 469 data points covering boreal to tropic climates (Appendices DR2 and DR3; see footnote 1). We choose the Palearctic realm to avoid errors and inconsistencies in application to Eurasian fossil communities.

We grouped the data of 185 weather stations from the European and African Atlantic margin from 70°–20°N in cells of 5° latitude and ~15° longitude, and 21 weather stations from the Arabian peninsula in cells spanning 5° of latitude (Data Repository; see footnote 1). In order to include tropical humid stations, we added two cells covering Gambia (13–14°N) and Ghana (5–6°N). For high continental climates we chose 163 stations from 8°–52°E grouped in steps of 4° longitude spanning the mid-latitudes at 44°–52°N. From East Asia we selected 96 stations from 8 Chinese provinces and northern Laos and grouped them according to the province boundaries. Islands and stations above 800 m altitude were excluded in all cells. For each of the 36 resulting cells (Fig. DR1), we calculated the mean annual precipitation.

### Modeling the Relationship Between Herpetological Ecophysiologic Groups and Annual Precipitation

We performed a regression analysis with the annual precipitation (mean annual precipitation, MAP) as the dependent variable and the relative frequencies (Fr) of the ecophysiological groups (Table 1) as explanatory variables. Because the relative frequencies of each cell add up to 1, we used group 1 as the reference group ($b_1 = 0$). The following regression is fitted:

$$\begin{aligned} \mathrm{MAP} = {} & b_0 + b_1 \cdot \mathrm{Fr(group\ 1)} \\ & + b_2 \cdot \mathrm{Fr(group\ 2)} + b_3 \cdot \mathrm{Fr(group\ 3)} \\ & + b_4 \cdot \mathrm{Fr(group\ 4)} + b_5 \cdot \mathrm{Fr(group\ 5)} \\ & + b_6 \cdot \mathrm{Fr(group\ 6)}. \end{aligned} \tag{1}$$

The regression coefficients $b_k$ are a quantitative measure for the relationship between annual precipitation and abundance of species of group k, which are estimated from the recent amphibian and reptilian communities of the 36 cells (Table 1; Tables DR1–DR5 [see footnote 1]). We constructed an index that is supposed to range from 0 to 1. If all species are from group 6, the index is defined to be

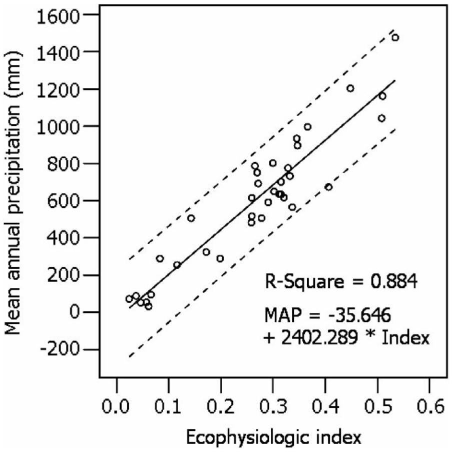

**Figure 1. Relationship between mean annual precipitation (MAP) and ecophysiologic index in recent herpetological communities. Dashed lines represent 95% confidence interval for predicted values.**

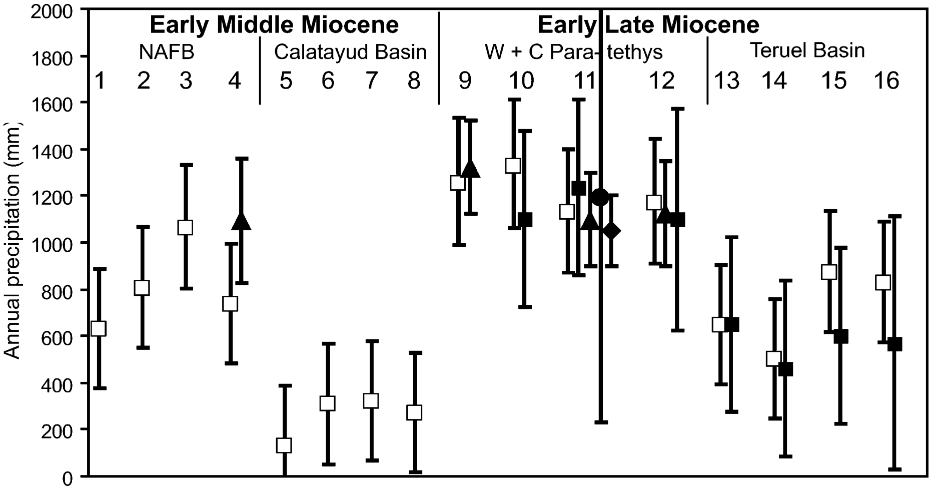

**Figure 2. Paleoprecipitation estimates for early middle and early late Miocene of Spain (Calatayud-Daroca and Teruel Basins) and central Europe (North Alpine foreland basin [NAFB] and western and central [W + C] Paratethys), compared to estimates resulting from other methods. 1—Sandelzhausen; 2—Walda 1; 3—Walda 2; 4—North Alpine foreland basin, 15.7–15.3 Ma; 5—La Col C; 6—Moratilla 2; 7—Villafeliche 4A; 8—Calatayud-Daroca Basin, 15.89–15.51 Ma; 9—Hammerschmiede; 10—Götzendorf; 11—Rudabanya; 12—western and central Paratethys, 10.3–9.8 Ma; 13—Cascante 4; 14—Masia de la Roma 3; 15—Masia de la Roma 4B; 16—Teruel Basin, 10.1–9.7 Ma; open squares—estimates from this paper; black squares—estimates based on small-mammal community structure (van Dam, 2003; van Dam, *in* Bernor et al., 2004); triangles—coexistence approach (Utescher, *in* Bernor et al., 2004; Bruch et al., 2006; Böhme et al., 2006; Bruch, 2004, personal commun. for locality 9); circle—ungulate hypsodonty (Damuth, *in* Bernor et al., 2004); diamond—mammalian dental morphology and local species richness (Damuth, *in* Bernor et al., 2004).**

1, and if all species are from group 1, the index is defined to be 0. Dividing all $b_k$ by $b_6$ gives us this normalized index:

$$\begin{aligned}\text{Index} = {} & 0\cdot\text{Fr(group 1)} + (b_2/b_6)\cdot\text{Fr(group 2)} \\ & + (b_3/b_6)\cdot\text{Fr(group 3)} \\ & + (b_4/b_6)\cdot\text{Fr(group 4)} \\ & + (b_5/b_6)\cdot\text{Fr(group 5)} \\ & + (b_6/b_6)\cdot\text{Fr(group 6)}. \qquad (2)\end{aligned}$$

The relationship between the index of a cell and MAP can be described as a simple linear regression, which yields a prediction for fossil data points (localities):

$$\text{MAP} = a + b \cdot \text{index}. \qquad (3)$$

The prediction error is estimated by the last regression equation with a correction on the degrees of freedom from equation 1.

### Fossil Data and Stratigraphy

To apply this method to the geologic past, we chose two time slices from the European Neogene; the earliest middle Miocene (early Langhian, 15.97–15.16 Ma) and the early late Miocene (early Tortonian, ca. 10.3–9.7 Ma; for more details regarding chronology see Appendix DR4). These periods were selected due to their well-known amphibian and reptile record, the high chronologic resolution, and the possibility of comparing the results with precipitation estimations from other methods. To investigate the meridional distribution of precipitation in Europe for both time slices, we used Spain and central Europe as key areas (Fig. DR2; see footnote 1). For the middle Miocene, we selected the Calatayud-Daroca Basin (localities La Col C, Moratilla 2, Villafeliche 4A) and the North Alpine foreland basin (localities Sandelzhausen, Walda 1, Walda 2). For the late Miocene, we selected the Teruel Basin (localities Cascante 4, Masia de la Roma 3, Masia de la Roma 4B) and the western and central Paratethys area (localities Hammerschmiede, Götzendorf, Rudabanya).

The selected localities show low taphonomic bias regarding their ectotherm fauna, evidenced by the good preservation of both smaller and larger species. The fossil record of amphibians and reptiles was extracted from available literature or databases (Appendix DR4 and Tables DR7–DR10) and verified by one of us (Böhme) on the original materials. The determination of the ecophysiologic group of a fossil species is based either on his functional morphology and paleoecology in regard to the nearest living relatives (in the case the fossil belong to an extinct taxon), or on the nearest living relative only (in the case that the fossil belong to an extant species group).

## RESULTS

### Estimation of Annual Precipitation

The result from the regression was (Appendix DR5; see footnote 1):

$$\begin{aligned}\text{MAP} = {} & -35.646 + 220.300\cdot\text{Fr(group 2)} \\ & + 941.288\cdot\text{Fr(group 3)} \\ & + 1232.452\cdot\text{Fr(group 4)} \\ & + 2346.574\cdot\text{Fr(group 5)} \\ & + 2402.289\cdot\text{Fr(group 6)}, \qquad (4)\end{aligned}$$

with $r^2 = 0.884$ and $p < 0.001$. The index is given by:

$$\begin{aligned}\text{Index} = {} & 0\cdot\text{Fr(group 1)} + 0.0917\cdot\text{Fr(group 2)} \\ & + 0.3918\cdot\text{Fr(group 3)} \\ & + 0.5130\cdot\text{Fr(group 4)} \\ & + 0.9768\cdot\text{Fr(group 5)} \\ & + 1\cdot\text{Fr(group 6)}. \qquad (5)\end{aligned}$$

The regression equation can be expressed by:

$$\text{MAP} = -35.646 + 2402.289 \cdot \text{index}. \quad (6)$$

The predicted values for the annual precipitation and their 95% prediction intervals (ranged between ~250 and 280 mm) are displayed in Figure 1.

### Application to the Fossil Record and Comparison with Other Methods

We use equation 6 to estimate paleoprecipitation values. The results for the early late Miocene show a high degree of correspondence between the herpetological tool and both the botanical coexistence approach and the small-mammal method (Fig. 2, 9–16; Table DR10 [see footnote 1]). The precipitation north of the alpine mountain range in the western and central Paratethys is 1129–1328 ± 270 mm (Fig. 2, 9–12), which is very high and shows excellent agreement with estimates from other methods. The precipitation estimates for the contemporaneous Teruel Basin south of the alpine mountain range give significantly lower values, between 501 and 873 ± 260 mm, in good agreement with small-mammal estimates (Fig. 2, 13–16; due to taphonomy there are no paleobotanical remains in this sequence). The results from our new method have lower errors and usually are within the upper range given by mammalian data, probably because the small-mammal data set incorporates species covering a wider spatial range.

Such a detailed locality by locality comparison is not possible for the early middle Miocene, simply because botanical remains are not associated with vertebrates, due to taphonomy, and small-mammal–based estimates are not available. In the Calatayud-Daroca Basin, fossil plants (leaves and pollen) are generally absent. Only the longer-term precipitation for the North Alpine foreland basin can be compared with coexistence approach estimates based on fossil wood (4 in Fig. 2). Both results show moderately high values that overlap between 830 and 1000 mm. The higher discrepancies between both results could be related to higher fluctuations of precipitation in this basin. Wood remains are usually found in the very wet sedimentary end members (e.g., gravels; Böhme et al., 2006), whereas small vertebrates are found in finer graded sediments representing somewhat drier periods (Böhme, 2003). This explanation could be supported by the broad range of estimates, between 629 and 1043 mm, from individual localities (Fig. 2). For the early middle Miocene in general, the herpetological tool gives relatively wet conditions for localities north of the alpine mountain range (629–1043 ± 260 mm) and significantly lower, arid to semiarid values for the southern Calatayud-Daroca Basin (130–321 ± 255 mm), indicating a strong meridional precipitation gradient during that time. The arid to semiarid values during the Langhian are in accordance with very dry climatic conditions indicated by the development of extensive evaporitic playa lakes in nearly all basins in Spain (Calvo et al., 1993), leading to the precipitation of anhydrite, gypsum, glauberite, and halite in the center of the Calatayud-Daroca Basin (Sanz-Rubio et al., 2001). In addition, in both areas a significant increase in precipitation could be observed during the early Langhian, estimated north of the alpine mountain range from 630 to 1040 mm and in the Calatayud-Daroca Basin from 130 to 320 mm.

## DISCUSSION

The paleoprecipitation values given by the new method indicate the existence of a significant European meridional precipitation gradient since the early middle Miocene. This gradient was stronger during the early Langhian (15.9–15.3 Ma), leading to the development of evaporitic playa lakes and an annual precipitation between 130 and 321 ± 255 mm in Spain, and fluvial-dominated sedimentation north of the alpine mountains with a threefold increase in precipitation, between 629 and 1043 ± 260 mm. This gradient and the high precipitation north of the orogen are in accord with results from studies of the paleobiogeography of snakehead fishes (Böhme, 2004), indicating >150 mm monthly precipitation during the warm season.

During the early Tortonian (10.3–9.7 Ma) this gradient was reduced, especially due to increased precipitation (501–873 ± 260 mm) in the Calatayud-Daroca Basin (in the North Alpine Foreland Basin, 1129–1328 ± 270 mm). This is in accord with results based on the botanical coexistence approach (Bruch et al., 2006) and on small mammals (van Dam, 2003). These more or less humid to perhumid conditions all over Europe supported dense forest habitats dominated by evergreen elements—prerequisites for a major step in Miocene hominoid evolution. This episode was terminated at 9.6 Ma by a significant increase in deciduous vegetation leading to ‘‘the end of the hominoid experiment in Europe’’ (Agusti et al., 2003, p. 1).

## CONCLUSIONS

The new paleoprecipitation tool introduced here gives precipitation estimates consistent with other methods. The method yields significantly lower errors than methods based on mammals and is applicable in a broad range of sedimentary contexts, complementing existing paleobotanical approaches. This is especially true for carbonate and dry climate systems where paleobotanical remains are usually rare or not preserved.

Both time intervals analyzed here, the early middle Miocene and the early late Miocene, show significant meridional gradients in precipitation. The gradient was accentuated between 15.9 and 15.3 Ma with threefold lower precipitation in southern Europe. The gradient was significantly stronger than today. This indicates a strengthening of climatic belts causally linked to the intensification of the Southern Hemisphere glaciations. Between 10.3 and 9.7 Ma the precipitation gradient was reduced to twofold lower values in southern Europe, corresponding approximately to the strength of the gradient today. This could possibly be related to the late Miocene Northern Hemisphere cooling trend, bringing Europe under an increasing influence of Arctic low-pressure cells.

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