

Cenozoic continental climatic evolution of Central Europe

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Continental climate evolution of Central Europe has been reconstructed quantitatively for the last 45 million years providing inferred data on mean annual temperature and precipitation, and winter and summer temperatures. Although some regional effects occur, the European Cenozoic continental climate record correlates well with the global oxygen isotope record from marine environments. During the last 45 million years, continental cooling is especially pronounced for inferred winter temperatures but hardly observable from summer temperatures. Correspondingly, Cenozoic cooling in Central Europe is directly associated with an increase of seasonality. In contrast, inferred Cenozoic mean annual precipitation remained relatively stable, indicating the importance of latent heat transport throughout the Cenozoic. Moreover, our data support the concept that changes in atmospheric CO₂ concentrations, although linked to climate changes, were not the major driving force of Cenozoic cooling.

continental climate | Neogene | Paleogene | precipitation

The Earth's Cenozoic climate history has been intensely studied during the last few decades. Based on oxygen isotope records from various deep-sea sediment cores, ocean water temperature changes have been reconstructed in detail (e.g., ref. 1). Stable isotopes have provided insight into ice volume changes and global climate fluctuations, their frequency and amplitudes (e.g., refs. 1–3), indicating an initial Antarctic glaciation during the late Eocene and a major ice volume increase in the earliest Oligocene (1).

In contrast, relatively little quantitative climate information is available for the European continental Cenozoic, and only a few correlation attempts with marine records have been made. This lack of information has severe consequences for the modeling of Cenozoic climates because the atmospheric data generated by General Circulation Models commonly cannot be validated by using proxy data. During the last two decades, considerable progress was made in applying foliar physiognomic approaches on fossil leaf floras to obtain quantitative terrestrial paleoclimate data. As a result, the evolution of mean annual temperature (MAT) and mean annual precipitation (MAP) have been documented for various intervals of the Cenozoic, predominantly for North America (e.g., refs. 4 and 5). However, previous data do not provide insight into the evolution of summer and winter temperatures and their associated seasonality. Recently, the use of new methodologies for reconstructing paleoclimate from micro- and megaflores has considerably improved our available data (e.g., refs. 6–8). Quantitative climate curves for the last 25 million years (My) (Miocene–Pliocene) have been published based on fossil floras from northwest Germany (9). The climate trends observed correspond, for the most part, to marine temperature changes.

In this study, a total of 45 well dated megaflores from different but adjacent Cenozoic basins of Central Europe have been analyzed to produce paleoclimate reconstructions from the Eocene to the Pliocene. For the Atlantic realm, a record from the northeast German Cenozoic is presented based on the analysis of 21 megaflores. When combined with the record from

the northeast German Cenozoic (9), we have obtained the first consistent, continental paleoclimate record for Central Europe from the middle Eocene to the late Pliocene. These floras cover a time span of almost 45 My. A record is also presented for the Paratethyan realm extending from the Oligocene to the middle/late Miocene transition covering a time span of ≈ 20 My. Because of the method used, data for MAT and MAP and for the warm month means (WMMs) and cold month means (CMMs) are available, providing a more precise description of paleoclimatic change. This extended data set also provides a framework for assessing the potential impact of declining atmospheric CO₂ during the Cenozoic on temperature change and thus the inferred mechanism of heat transport from the equator to the poles.

The following records, which are discussed, show a stepwise cooling that is more pronounced in the winter, and increasing seasonality from the middle Eocene onwards. Except single oscillations in the early and middle Miocene, precipitation rates remained stable and relatively high until the early Pliocene, and then decreased by >250 mm. It can also be demonstrated that the major aspects of the long-term climate variations, known from marine isotope records, are mirrored in continental climate variations. Sometimes even short-term oscillations can be correlated. Finally, the comparison of contemporaneous continental records from different regions gives an insight into spatial climate differentiation during the Cenozoic.

Study Area and Selected Floras

To study the Cenozoic climate variation of Central Europe, three basin complexes were selected based on long sedimentary records and abundant paleobotanical data (Fig. 1). The Weisselester and Lausitz Basins (both northeast Germany), and the Lower Rhine Basin (northwest Germany) are part of the Atlantic realm, bordering on the south side of the “Cenozoic North Sea” (Fig. 1). Sediments in these basins consist of shallow marine to continental deposits, with some important lignites. The South German Molasse Basin is part of a shallow marine to lacustrine strait bordering the evolving alpine fold-belt to the north, and belonging to the Western Paratethys (Fig. 1).

In this study, 45 well dated megaflores (fruits and seeds, leaves) were used to reconstruct paleoclimate history (Figs. 2 and 3). For additional information, see Table 1, which is published as supporting information on the PNAS web site and provides locality names, stratigraphical ages, and references. Fifty-three percent of the floras can be assigned to nannoplankton or mammal zones, the others are dated by paleobotanical means supported by sequence-stratigraphical concepts, as proposed for the Lausitz and the Lower Rhine Basins (10, 11).

Abbreviations: CA, coexistence approach; CMM, cold month mean; MAP, mean annual precipitation; MAT, mean annual temperature; My, million years; NLR, nearest living relatives; WMM, warm month mean.

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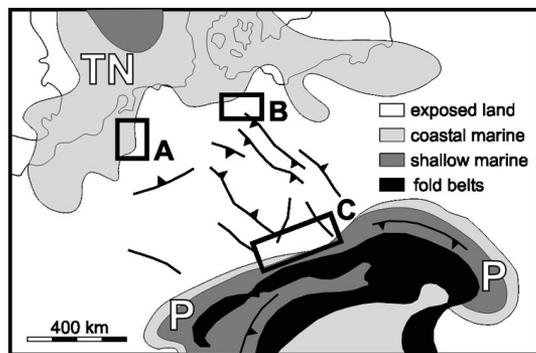


Fig. 1. Paleogeographic setting of Central Europe in the Paleogene. TN, Cenozoic North Sea; P, Paratethys. The frames indicate the positions of the Cenozoic basins for which climate records are presented. A, Lower Rhine Basin; B, Weisselster Basin; C, Molasse Basin.

The present analysis refers to the global chronostratigraphic concept of Gradstein *et al.* (12). For the correlation of regional stages, data are used from Hager (13), Schäfer *et al.* (11), Steininger *et al.* (14), Rögl (15), and the *Stratigraphic Table of Germany 2002* (16). With respect to the different methods of dating, the error obtained for the absolute age of a flora varies, ranging from <500 thousand years up to a few million years. In the latter case, however, the relative age-relation between floras succeeding in a geological record is known (see Table 1).

The time span represented by a flora depends not only on how the material was collected, but also on taphonomic conditions. For the present analysis, floral lists compiled for single horizons are preferred and considered to represent a time span below 100 thousand years, a value far below the error bars of the stratigraphic dating. In rarer cases, only floral lists combined from different locations are available (localities 1, 2, 3, 5, 7, and 8 from

the Molasse Basin; cf. Fig. 2) that may represent longer time periods.

In the present analysis, three quantitative climate records for three Cenozoic basin complexes (i.e., Lower Rhine Basin, Weisselster/Lausitz Basin, and Molasse Basin) were calculated to produce climate curves for well defined adjacent geographic regions of Central Europe. Thus, aberrations caused by spatial paleoclimatic differences are largely excluded. The temporal resolution obtained for the climate curves in each case depends on the presence of suitable floras that are not evenly spaced over the stratigraphic column, being separated by some 100 thousand years to several million years. The climate record of the Lower Rhine Basin is combined from the curves published by Utescher *et al.* (9) and new results calculated for the Tiglian. It covers a time span of ≈ 26 My extending from the late Oligocene to the late Pliocene, and is based on an analysis of 17 floras. The record of the Weisselster Basin covers a time span from the middle Eocene to the Oligocene. Together with floras from the neighboring Lausitz Basin, it can be extended to the middle/late Miocene transition, with a total time span of ≈ 32 My. The record is based on data from 22 floras. In addition, Seifhennersdorf and Kleinsaubernitz volcanic floras, both from the Oberlausitz district, are included (Fig. 2). The geologic record of the South German Molasse Basin extends from the Oligocene to the middle Miocene (time span of ≈ 22 My). Because only scant paleobotanical information is available for the Oligocene portion of the paleofloristic data, analysis from the Western Swiss Molasse is also included. Three localities were included to complete the reconstruction: Oberdorf Mine (Styrian Basin) and two well dated floras from the Vienna Basin (Türkenschanze and Lerch) (Fig. 2).

With an average temporal resolution of ≈ 1.0 My in the Neogene portions of the records, and ≈ 2.1 My in the Eocene to Oligocene parts, the data set allows only for an analysis of long-term climate trends. Short-term climate oscillations with

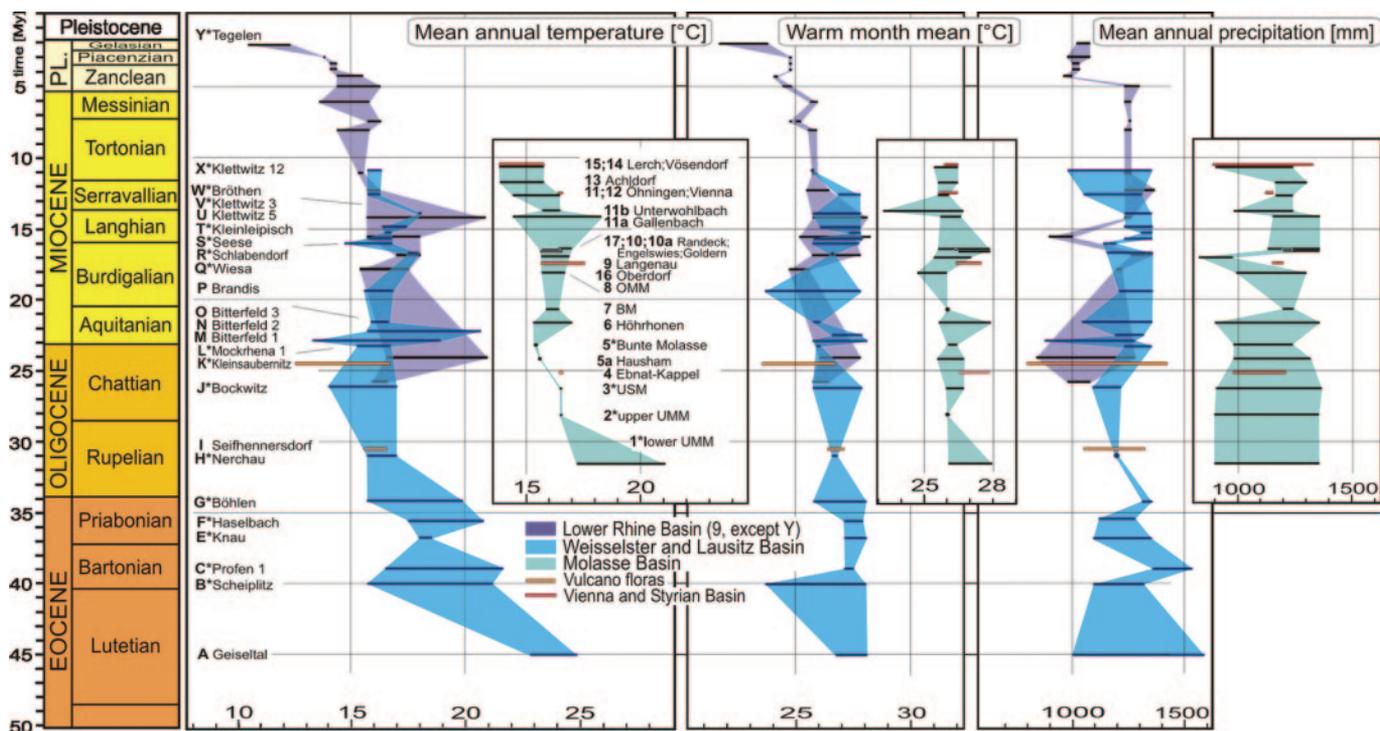


Fig. 2. Records for MAT, MAP, and WMM as calculated by the CA. The bars represent coexistence intervals. The records of the Lower Rhine Basin are from Utescher *et al.* (9), with the results for a Tiglian flora (code Y) added. Additional information about stratigraphical dating, and references, as well as a complete set of climate data are provided in Tables 1 and 2. Code numbers marked with an asterisk indicate floras with no mammal or nannoplankton dating available.

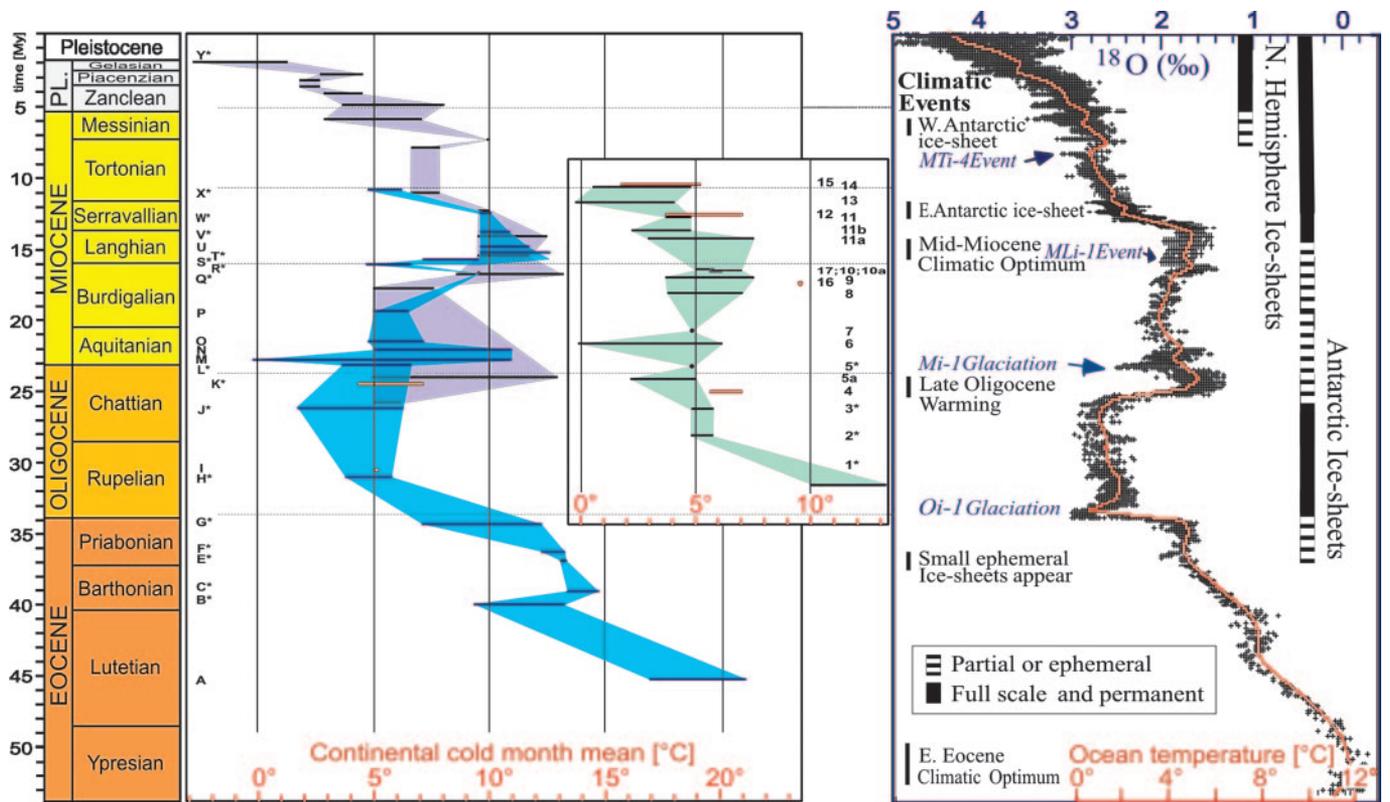


Fig. 3. Continental temperature curves (CMM) for Central Europe during the last 45 My in comparison with the global marine oxygen isotope record of Zachos *et al.* (1) adapted to the International Commission on Stratigraphy 2004 time scale (12). For code numbers and bar colors, see Fig. 2.

periods below 1 My, such as orbital scale climate variability, as observed in marine isotope records (e.g., ref. 1), cannot be resolved. However, for some intervals of the early and middle Miocene, a higher resolution between 0.5 and 1 My is obtained in our data set, thus providing the possibility to detect short-term variations.

Method of Paleoclimate Reconstruction

We apply the coexistence approach (CA) (6, 9) as a tool for calculating quantitative climate data from these fossil floras. This method uses the climate tolerances of all nearest living relatives (NLR) known for a given fossil flora. The climatic requirements of these extant taxa are obtained by listing the climate conditions of the plant distribution area. By using this database of extant taxa and climatic requirements with respect to a variety of different variables, a “coexistence interval” can be calculated for each climate variable considered that allows the majority of NLR of a fossil flora to coexist. The resulting coexistence intervals are then interpreted as the most probable ranges of different paleoclimate variables for a fossil flora.

In this study, intervals for MAT, WMM, CMM, and MAP are calculated. The widths of the climate intervals calculated, i.e., the climatic resolution of the method, strongly depends on the parameter analyzed in each case. Coexistence intervals calculated for MAT range from 0.2°C to 5°C. The precision of the paleoclimate reconstruction increases with the diversity of the fossil flora analyzed (6). Therefore, diverse floras were selected for this study when available. For the localities considered, diversity ranges from 9 to 89 taxa (mean = 26.5). A quality indicator of climate reconstruction based on the CA is the percentage of taxa coexisting in the resulting climate intervals. Theoretically, for all climate parameters there exists an interval within which all NLR (i.e., 100%) of a fossil flora can coexist.

There are, however, several factors biasing the results, such as taphonomic conditions, misidentifications of NLR, or imprecise information of their climatic requirements. Therefore, not all NLR of a fossil flora may coexist or fit into a single interval as defined by world climates today (6). The percentage of NLR of a given fossil flora that coexist in a single climate interval is commonly used to estimate the accuracy and significance of the reconstruction obtained from the CA (6), but this could also be regarded as a measure of how unusual or nonanalogue a paleoclimate might have been by modern standards. There may also be unique combinations of different climate variables causing a non coexistence of taxa in today’s climates that would suggest the presence of a “fossil” or “extinct” climate that exists nowhere in the world today (17, 18).

The CA, when applied to Neogene floras (e.g., refs. 6, 9, and 19), has been shown to be reliable and robust. In addition, it has been demonstrated that the climate amplitude method of Faquette *et al.* (7) and the CA produce entirely consistent results when applied to a set of Messinian microfloras (20). The question arises about how reliable the CA is for Paleogene floras because this method is based on the assumption that the climatic tolerances of the fossil taxa do not differ significantly from the climatic tolerances of their NLR. This assumption may not be valid for all Paleogene plant taxa, thus making the climate reconstructions in the Paleogene, based on the CA, less reliable. In this study, our Paleogene floras show coexistence percentages of 89–100% that are almost identical to those obtained for Neogene floras. Such results are highly significant (significance level $\ll 0.01\%$), as shown by Monte Carlo simulations in which climate data are calculated for random floras of 25 taxa extracted from a data pool of 100 taxa (6). A complete list of climate data and coexistence percentages of the floras analyzed in this study is provided in Table 2, which is published as supporting information on the PNAS web site.

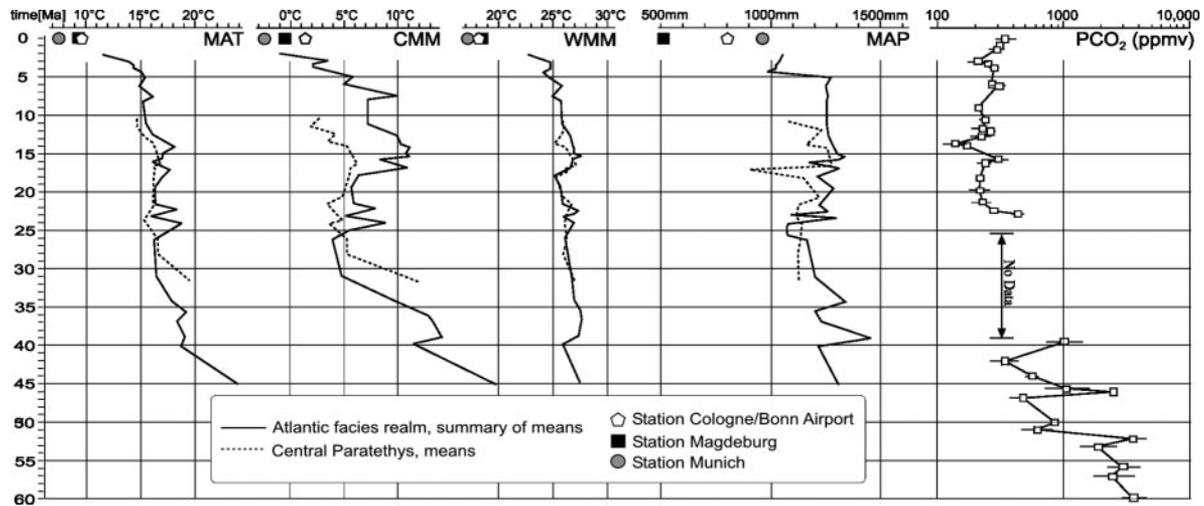


Fig. 4. Climate records for the Atlantic realm (summary of the Lower Rhine Basin and Weissenlöhle Basin records) and the Paratethys compared to the Cenozoic atmospheric pCO_2 variations as derived from boron isotopes ratios of planktonic foraminifers (21). The isotope record is adapted to the ICS 2004 time scale (12). All of the continental curves are tentatively interpolated, using the means of coexistence intervals. Present climate data for the different regions are indicated.

Results

Continental climate change of Central Europe during the last 45 My is primarily characterized by decrease of CMM, of nearly 20°C between the Eocene and Pliocene (Figs. 2 and 3). In contrast, MAT and WMM did not undergo as significant a change from the Eocene to the Pliocene. Only near the end of the Pliocene do these variables show a notable decrease (Fig. 2). Change in precipitation is also small, with over 1,000 mm during most of this interval. CMM and WMM trends clearly diverged during the Cenozoic, implying an increase of seasonality in Central Europe during this time. In the following, the climate curves will be discussed in detail.

Temperature Evolution. The middle Eocene to early Oligocene portion of the continental temperature changes are documented by the record of the Weissenlöhle Basin. It starts in the Lutetian (Geiseltal flora, code A in Fig. 3) with the warmest climate conditions observed in this reconstruction. With MAT ranges from 23°C to 25°C, MAP from 1,000 mm to 1,600 mm (Fig. 2), and CMM from 17°C to 21°C (Fig. 3), almost tropical climate conditions are indicated. However, a mean annual range of temperature between 9°C and 12°C is more characteristic for warm temperate climates. During the middle and late Eocene, a pronounced decrease of MAT and CMM by at least 5°C is observed (codes A, E, and G in Fig. 3), whereas WMM remains at a uniformly high level. During most of the Oligocene, lower temperatures are recorded with CMM around 5°C (codes H, I, J, and K of the Weissenlöhle Basin record; codes 2 and 3 of the Molasse Basin record). The latest Chattian is marked by a temperature peak (record of the Lower Rhine Basin) corresponding to the Late Oligocene Warming known from isotope records (Fig. 3) (1). During the early Miocene, an overall trend of increasing temperature is observed persisting to the middle Miocene. However, this warming seems to be more stepwise, and the curves show several short-term variations. In the Weissenlöhle Basin record, there is evidence for a short-term cooling at the base of the Aquitanian (code M in Fig. 3). There, the absence of floral elements with high temperature requirements results in a pointed shift of the lower boundary of the MAT range to cooler conditions. In the later Burdigalian, temperature increased again. The succeeding warm time span persisted through the earlier part of the Serravallian, and corresponds to the Mid-Miocene Climatic Optimum that is also globally observed. At the

base of the middle Miocene, there is a second short-term temperature depression observed in the MAT and CMM records of the Lausitz Basin (codes R and S).

The Mid-Miocene Climatic Optimum is reflected by increases of all of the temperature records of the three Cenozoic basins. For MAT and WMM, similar values are obtained from the floras of different Cenozoic basins during that time. However, CMM records indicate regional differences for the first time. Very high CMMs of 9–13°C are calculated for the floras from the Lausitz and Lower Rhine Basins (e.g., codes T, U, V, and W), even reaching the late Eocene level. High values are also reported for the late Burdigalian of the Styrian Basin (Oberdorf Mine flora, code 16). However, considerably lower CMMs of only 4–7.5°C are indicated for contemporaneous floras from the South German Molasse Basin. These regional differences are probably caused by paleogeographic settings. The Lower Rhine and the Weissenlöhle/Lausitz Basins are close to the Cenozoic North Sea, moderating the climate during the cold season. In the case of the Molasse Basin, orographic movements in the nearby area might be reflected by paleoclimate. The onset of the Miocene cooling seems to be between 13.0 and 14.0 My when considering all of the different records and climate variables analyzed. In the Molasse Basin, CMM decreased more rapidly than in both other regions, and, at the end of the middle Miocene, CMM dropped below 4°C (code 13).

The late Miocene to Pliocene continental paleoclimate record is only available for the northwest German Cenozoic (Lower Rhine Basin) and has been described in detail by Utescher *et al.* (9). In all of the other basins, the later part of the late Miocene and the Pliocene are missing. The temperature curves show a further, stepwise cooling mainly affecting CMM, with short-term warming in the late Tortonian and early Zanclean. The Pliocene climate can still be characterized as warm temperate, but MAT fell below 15°C and CMM below 3°C for the first time in this region. Near the top of the Pliocene (Tiglian), a significant decline in temperature occurred, and, for the first time, CMM has fallen below the freezing point.

Changes in Seasonality. When comparing the tentative CMM and WMM curves in Fig. 4, which are interpolated by using means of coexistence intervals, it is obvious that the continental climate variations during the Cenozoic of Central Europe primarily are changes in seasonality of temperature. From the middle Eocene to the present, an overall increase of seasonality can be observed.

Periods of low seasonality existed during the middle Eocene ($\approx 13^{\circ}\text{C}$) and the middle Miocene ($\approx 17^{\circ}\text{C}$), whereas the later part of the Oligocene, as well as the later Pliocene, are characterized by high seasonal temperature variations ($\approx 20^{\circ}\text{C}$ and 23°C , respectively). Today, seasonal temperature variations of $\approx 17\text{--}18^{\circ}\text{C}$ in north Germany are on an intermediate level, with respect to the Cenozoic climate history. In south Germany, the diminished oceanic influx and the nearby alpine orogen have a significant impact on the degree of seasonal temperature variation. Considering interval means, a seasonality of 23.5°C is calculated for the early late Miocene of the South German Molasse Basin, whereas for contemporaneous floras from the Lower Rhine Basin only 19°C are obtained. Also today, the seasonality recorded in south Germany (e.g., at the meteorological station Munich; mean annual range of temperature = 24.7°C) is considerably higher ($7\text{--}8^{\circ}\text{C}$) than is observed in the area of the north German Cenozoic Basins.

Precipitation. As shown in Fig. 2, MAP rates show some minor variations and weak trends, but commonly were on a high level of more than 1,000 mm throughout the Central European Cenozoic. MAP rates are not affected by the Late Miocene Cooling, and stayed stable until the early Pliocene. Very high rates of ca. 1,500 mm are calculated for the Eocene. At the base of the Oligocene, MAP decreased slightly. From the upper part of the late Oligocene on, MAP increased again. In the time span between the later Burdigalian and the Langhian, dryer conditions with MAP below 1,000 mm result for only two of the floras (Fig. 2). During the late Miocene and earliest Pliocene, MAP remained at a constant level of ca. 1250 mm, and then significantly dropped by ca. 250 mm within the Zanclean (Lower Rhine Basin record; ref. 9).

Comparison with the Global Marine Isotope and pCO_2 Records

The availability of consistent quantitative terrestrial temperature records for Central Europe covering the major part of the Cenozoic allows for a correlation with ocean data. For the comparison of continental and marine temperature variations, the global deep-sea oxygen isotope record of Zachos *et al.* (1) is selected. The authors provide the most recent synthesis of global climate change during the Cenozoic. The isotope record and ocean water temperatures derived from the analysis of benthic deep-sea foraminifera are based on >40 Deep Sea Drilling Project and Ocean Drilling Project sites. Deep ocean water is commonly derived from the sinking of cool water masses in the polar regions, and thus its temperature can be regarded as a proxy for sea-surface temperatures in higher latitudes (1). To compare the continental and marine temperature variations, the CMM curves are selected because they provide the highest variability among all temperature parameters analyzed. Fig. 3 shows that the major trends observed in the marine record are clearly reflected by the continental curves. First of all, the marine and continental records show a long-term cooling trend beginning at the Early Eocene Climatic Optimum and ending with the Pleistocene glaciation. The degree of cooling in the continental data set ($\approx 14^{\circ}\text{C}$) is $\approx 4^{\circ}\text{C}$ higher than is known for the marine bottom water ($\approx 10^{\circ}\text{C}$). However, a certain percentage of cooling observed in the continental record can be referred to plate tectonics. During the time span of the last 45 My, a movement of the European tectonic plate relative to the magnetic reference frame of $\approx 3.8^{\circ}$ to the north occurred (Ocean Drilling Stratigraphic Network plate reconstruction service). Assuming a zonal gradient of 0.4°C per degree of latitude for MAT, the latitudinal shift of the European plate would account for $\approx 11\%$ of the overall observed temperature decrease.

Looking more closely, the long-term oxygen isotope record shows characteristic steps and peaks that are related to global temperature change and degree of glaciation. Most of these

episodes documented in the marine record are also mirrored in the continental record, but there are also some differences between the marine and the terrestrial data set. The prominent decrease in the European continental temperature during the Eocene is correlated to the 17-My-long cooling after the Early Eocene Climatic Optimum (EECO) (50–51 My) reflecting a prominent decline in deep-sea temperature and build-up of the Antarctic ice-sheet at the end of the Eocene. The lower temperatures in the Oligocene continental record correspond to the overall heavy isotope values observed in the marine record related to a persistent Antarctic ice-sheet during that time. The positive temperature increase observed at ≈ 25 My in the record of the Lower Rhine and Molasse Basins (Ebnat-Kappel flora; code 4) probably can be attributed to the so-called Late Oligocene Warming and the corresponding reduction of Antarctic ice volume. During the early and middle Miocene, the oxygen isotope record forms a saddle-like plateau caused by reduced ice volume and a warming trend of deep ocean water culminating in the Mid-Miocene Climatic Optimum (17–15 My). The continental record (e.g., CMM record of the Lower Rhine Basin) shows a similar pattern with temperature rapidly increasing at ≈ 17 My. After the Mid-Miocene Climatic Optimum, the isotope curve shows a gradual trend to heavier values attributed to the cooling of deep ocean water, the growing ice shield on Antarctica, and the beginning of Arctic glaciation, later on. This change starts with deep ocean water temperatures rapidly dropping by $\approx 3^{\circ}\text{C}$ between 15 My and 13 My. However, in the continental records of north Germany, the most prominent temperature decrease is observed between 12 My and 10 My, and is possibly correlated with the prominent drop of global sea level at the Ser4/Tor1 sequence boundary (3). During the late Miocene and the Pliocene, mean $\delta^{18}\text{O}$ values rose continuously. This is also reflected in the continental record (Lower Rhine Basin) where CMM decreased by $\approx 2.5^{\circ}\text{C}$ during this time span. Similar to the marine records, Pliocene temperatures before 3 My were still comparatively high.

Currently, the mean temporal resolution of our terrestrial data sets (1.2 My and 1.6 My, respectively), and in many cases the climatic resolution, are still insufficient to allow an identification of short-term climate oscillations on an orbital scale (10^4 to 10^5 years). In principle, this is also true for short-term aberrations or increases described as stable isotope events (e.g., ref. 3). These aberrations in many cases are characterized by a high magnitude of change that stands out above the normal climate variability (1), and are often connected to sequence boundaries. In the continental records, there are some distinct temperature peaks that are possibly related to stable isotope events. The cool aspect of the Bitterfeld flora dating from the basal part of NN1 (code M) corresponds quite well to the prominent Mi-1 heavy isotope event at the Oligocene/Miocene transition (cf. ref. 3), also identifiable in the Zachos curve (Fig. 3). The rapid drop in temperature at the early/middle Miocene transition shown by the Weissenlöhle Basin record (Schlabendorf Well flora, code R) is about time-equivalent to the MLI-1 isotope event (cf. ref. 3). In the Neogene climate record of the Lower Rhine Basin, the temperature increase in the later Tortonian probably is correlated to warming succeeding the MTi-4 isotope event (cf. ref. 3). The following temperature depression within the Messinian is supposed to be correlated with one of the two MMi isotope events (cf. refs. 3 and 9).

The CMM record for Central Europe correlates surprisingly well with the global marine oxygen isotope record. In contrast, the pCO_2 curves, as derived from boron and carbon isotopes (1, 21), are not closely linked with the marine oxygen isotope record (1) or with temperature and precipitation records of Central Europe (Fig. 4). High CO_2 concentrations of $>2,000$ ppm are reported for the late Paleocene and early Eocene abruptly dropping below 1,000 ppm at ≈ 52 My while deep ocean water

