ORIGINAL ARTICLE

Vegetation, climate and palaeoaltitude reconstructions of the Eastern Alps during the Miocene based on pollen records from Austria, Central Europe

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ABSTRACT

Aim To reconstruct the flora, vegetation, climate and palaeoaltitude during the Miocene (23.03–5.33 Ma) in Central Europe.

Location Six outcrop sections located in different basins of the Central Paratethys in Austria.

Methods Pollen analysis was used for the reconstruction of the vegetation and climate. The altitude of the Eastern Alps that are adjacent to the Alpine Foreland and Vienna basins has been estimated using a new quantification method based on pollen data. This method uses biogeographical and climatological criteria such as the composition of the modern vegetation belts in the European mountains and Miocene annual temperature estimates obtained from fossil pollen data.

Results Pollen changes from Early to Late Miocene have been observed. The vegetation during the Burdigalian and Langhian (20.43–13.65 Ma) was dominated by thermophilous elements such as evergreen trees, typical of a present-day evergreen rain forest at low altitudes (i.e. south-eastern China). During the Serravallian and Tortonian (13.65–7.25 Ma) several thermophilous elements strongly decreased, and some disappeared from the Central European region. This kind of vegetation was progressively substituted by one enriched in deciduous and mesothermic plants. Middle-altitude (*Cathaya*, *Cedrus* and *Tsuga*) and high-altitude (*Abies* and *Picea*) conifers increased considerably during the Langhian and later on during the Serravallian and Tortonian.

Main conclusions Pollen changes are related to climatic changes and to the uplift of the Alpine massifs. The vegetation during the Burdigalian and Langhian reflects the Miocene climatic optimum. The decrease in thermophilous plants during the Serravallian and Tortonian can be interpreted as a climatic cooling and can be correlated with global and regional climatic changes. This study shows that the palaeoaltitude of the eastern part of the Eastern Alps during the Burdigalian was not high enough for *Abies* and *Picea* to form a forest. Therefore, we inferred that the summits of most of the mountains would have been less than 1800 m. The substantial increase of middle- and high-altitude conifers in the pollen spectra suggests that the uplift rate increased during the Langhian in this region. Based on higher palaeoaltitude estimations for the pollen floras from the studied sections of Austria, we infer that the uplift of the easternmost part of the Alpine chain continued during the Serravallian and Tortonian.

Keywords

Altitude, Austria, climate, Eastern Alps, Miocene, palynology, tectonic uplift, vegetation reconstruction.

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INTRODUCTION

Pollen analysis has been proven to be a very efficient tool for reconstructing vegetation and climate for the Miocene in the Central Paratethys (Ivanov *et al.*, 2002; Jiménez-Moreno, 2005, 2006; Jiménez-Moreno *et al.*, 2005).

Reconstruction of palaeoaltitudes is fundamental to improving our knowledge of European palaeogeography during the Miocene. However, palaeogeographical reconstructions of palaeoaltitudes of Alpine massifs during the Neogene are scarce. They are based primarily on the sedimentary record, the flux of terrigenous sediments accumulated in sedimentary basins and facies distribution (Schmid *et al.*, 1996; Frisch *et al.*, 1998; Kuhlemann & Kempf, 2002; Braga *et al.*, 2003; Martín *et al.*, 2003; Kuhlemann, 2007) and thermochronology (i.e. fission track measurements: Hejl, 1997; Dunkl *et al.*, 1998; Bigot-Cormier *et al.*, 2000; Bistacchi & Massironi, 2000; Spiegel *et al.*, 2001; Herwegh & Pfiffner, 2005; Kuhlemann *et al.*, 2006; Zattin *et al.*, 2006).

A new method of quantification of palaeoaltitudes has been developed (Fauquette *et al.*, 1999) and is applied here to estimate palaeoaltitudes of the eastern part of the Eastern Alps during the Miocene. This method takes into account pollen floras accumulated near the coastline, providing both a regional view of the vegetation from the littoral to the uppermost altitudinal belts and climatic reconstructions. This new method improves upon previous work using macrofloras to estimate past altitudes (Axelrod, 1965, 1968; Axelrod & Bailey, 1976; Meyer, 1992). These previous studies were based on macroremains that provided a fragmentary and very circumscribed idea of the vegetation. They were located at mid to high altitudes in north-western America and have no direct link to the altitudinal climatic gradient from sea level. This method has been successfully applied to Early Pliocene pollen spectra from the Mercantour Massif in the Southern Alps (Fauquette *et al.*, 1999) and the Canigou Mountain in the eastern Pyrenees (Pérez Villa *et al.*, 2001). In both studies the results were validated by geomorphology (Fauquette *et al.*, 1999; Clauzon *et al.*, 2002).

The aims of this study are to reconstruct the vegetation developed around the Alpine Foreland and Vienna basins (Austria) during the Miocene and give an interpretation in terms of climate and palaeoaltitudes. Our analyses are based on pollen analysis of several sections distributed throughout the Miocene using botanical taxonomy and a quantitative analysis of the pollen data.

PALAEOGEOGRAPHICAL FRAMEWORK

Palaeogeographical changes influence climate and floral and faunal exchanges. Tectonic processes were very active during the studied time period and played a major role by causing important palaeogeographical changes, which produced modifications in oceanic/atmospheric circulation (such as the marine gateway openings of the Denmark Strait and Drake Passage and the closure of the seaway between the Mediterranean Sea and the Indian Ocean) that generated the Miocene climatic cooling (Pagani *et al.*, 2000; Billups *et al.*, 2002; Ogasawara, 2002; Diekmann *et al.*, 2003; Hall *et al.*, 2003; Meulenkamp & Sissingh, 2003).

Alpine uplift started 35 million years ago (Ma), during the Eocene–Oligocene transition (Meulenkamp & Sissingh, 2003; Jolivet *et al.*, 2006; Popov *et al.*, 2006), principally due to two contemporary processes: (1) migration of the African plate northward, then collision with the European plate producing subduction of the European plate below Apulia; and (2) slab retreat and coeval back-arc basin opening (Jolivet *et al.*, 2006; and references therein). The subduction and ensuing collision processes led to the formation of mountain belts from the Betic Cordillera and the Rif in the west, to the Hellenides and Taurides in the east. The formation of the Alps and Carpathians was due to the subduction of the European plate below Apulia, part of the African plate. The retreat of the European slab allowed the formation of the Pannonian Basin to the east, although its dynamics cannot be compared simply to the true back-arc basins of the Mediterranean region (Linzer, 1996; Horvath & Tari, 1999; Wortel & Spakman, 2000; Cloething *et al.*, 2004). The convergence between the African and Eurasian plates led to the Tethys becoming a geo- and biogeographical palaeoentity and the development of two distinct physiographical realms during the Miocene and Pliocene (23.03–1.81 Ma): the Mediterranean and Paratethys seas (Rögl, 1998; Meulenkamp & Sissingh, 2003). Because of this convergence, numerous marine and continental basins were generated on the northern Mediterranean margin and on the Paratethys. During the Miocene and Pliocene, these basins experienced a long-term trend of decreasing marine influence and concomitant reduction in the size of their marine depositional domains (Rögl, 1998; Meulenkamp & Sissingh, 2003; Popov *et al.*, 2006). Furthermore, also due to this convergence, the Eurasian plate drifted northward (Meulenkamp & Sissingh, 2003). Several palaeomagnetic studies estimate a drifting value of *c.* 10° since the Early Miocene until the Present. Average values for the studied span [Early Burdigalian (20 Ma)–Late Tortonian (8–7 Ma)] are *c.* 3°–4° (Rögl, 1998; Meulenkamp & Sissingh, 2003). This would have contributed to the general climate cooling on these moving continental masses during the Miocene and thus has to be taken into account.

MATERIALS AND METHODS

Studied sections

In this study, 48 samples from six outcrop sections, previously well dated by different methods, were analysed for pollen grains. Samples came from different basins of the Central Paratethys in Austria (Fig. 1). The sections studied from Burdigalian to Tortonian are (from west to east): Strass-Eberschwang [Alpine Foreland Basin, Ottnangian (Burdigalian) *c.* 18 Ma; Faupl & Roetzel, 1987]; Göllersdorf [Alpine

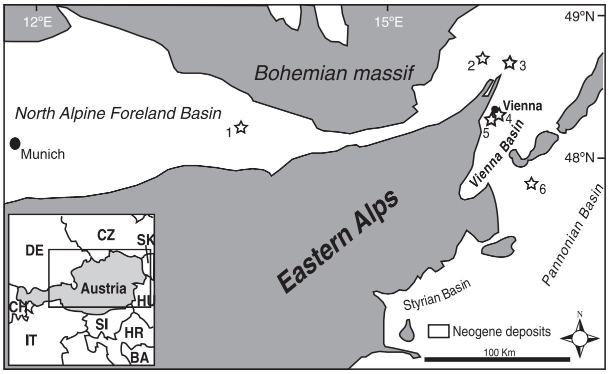

Figure 1 Geographical map with the location of the studied sections (white stars): (1) Strass-Eberschwang; (2) Göllersdorf; (3) Siebenhirten; (4) Hennersdorf; (5) Baden-Sooss 1 and 2; and (6) St Margarethen. Modified from Jiménez-Moreno (2005).

Foreland Basin, Karpatian (Upper Burdigalian), *c.* 16.5 Ma; Roetzel *et al.*, 1999]; Baden-Sooss-1 [Vienna Basin, Lower Badenian (Langhian), *c.* 14.5 Ma; Fuchs & Stradner, 1977]; Siebenhirten [Vienna Basin, Lower Sarmatian (Upper Serravallian), *c.* 12.4 Ma; Harzhauser & Piller, 2004a]; Baden-Sooss-2 [Vienna Basin, Upper Sarmatian (uppermost Serravallian), *c.* 12 Ma; Brix, 1988]; St Margarethen [Eisenstadt-Sopron Basin, Upper Sarmatian (uppermost Serravallian), *c.* 11.8 Ma; Harzhauser & Kowalke, 2001; Harzhauser & Piller, 2004b]; and Hennersdorf [Vienna Basin, Pannonian (Tortonian), *c.* 10.3 Ma; Magyar *et al.*, 1999; Harzhauser & Mandic, 2004].

Pollen analysis

Sampling was done by taking *c.* 150 g of sediment per sample. In the chemical treatment, only 15–20 g of sediment were used. The samples were processed with cold HCl (35%) and HF (70%), removing carbonates and silica. Separation of the palynomorphs from the remaining residue was carried out using $ZnCl_2$ (density = 2). Sieving was done using a 10-μm nylon sieve. The pollen residue, together with glycerin, was prepared on slides. A transmitted light microscope, using ×250 and ×1000 (oil immersion) magnifications, was used for botanical identification and counting of palynomorphs, palynomorphs being very abundant in these sediments. Spores were not considered due to their low abundance.

Identification of the pollen grains was done by comparing the Miocene grains with their present-day relatives using the pollen and photograph collections stored in the laboratory in Lyon, several pollen atlases (China, Taiwan, Africa, North America, Mediterranean region, etc.) and the Photopal website (http://medias.obs-mip.fr/photopal). A minimum of 150 terrestrial pollen grains, *Pinus* and indeterminable Pinaceae excluded, were counted in each sample.

Detailed pollen diagrams and standard synthetic diagrams (Suc, 1984), without *Pinus* and indeterminable Pinaceae, have been plotted (Figs 2–4). In Fig. 4, taxa have been grouped into 10 different groups based on ecological criteria (Nix, 1982) in order to clearly visualize the composition of the past vegetation (see Jiménez-Moreno, 2005, 2006; Jiménez-Moreno *et al.*, 2005, for an explanation of the grouping). Complete pollen data will be made available on the web in the 'Cenozoic Pollen and Climatic values' database (CPC) (http://cpc.mediasfrance.org).

Climate reconstruction

Climate reconstructions, based on pollen data, were estimated using the climatic amplitude method (Fauquette *et al.*, 1998a,b). This method has been applied to many pollen sequences of the western Mediterranean area (Fauquette *et al.*, 1998a, 1999; Fauquette & Bertini, 2003; Jiménez-Moreno *et al.*, 2005, 2007; Fauquette *et al.*, 2006) and has also been applied to the pollen sequences presented herein. This will allow us to estimate the climate in Austria throughout the Miocene period. The climatic amplitude method is a method in which the past climate is estimated by transposing the climatic requirements of the maximum possible number of modern taxa to the fossil data. The most probable climate for a set of taxa is estimated as the climatic interval suitable for the highest number of taxa. High-latitude/high-altitude taxa were excluded from the reconstruction process. The identification and exclusion of high-latitude/high-altitude plants is based on numerous palynological studies (Suc *et al.*, 1995a,b, 1999; Jiménez-Moreno, 2005) that show that the Neogene vegetation zonation followed a similar latitudinal and altitudinal zonation to the one observed in present-day south-eastern China (Wang, 1961), where most of the taxa that disappeared from Europe by the Late Neogene can be found. Therefore, the estimates obtained correspond to the climate at low to middle–low altitude (Fauquette *et al.*, 1998a). The pollen grains of *Pinus* and indeterminable Pinaceae have been excluded from the pollen sum as they are, in some cases, over-represented.

The results are presented, as potential climate ranges and a 'most likely value' corresponding to a weighted mean, for two climatic parameters: (1) mean annual temperature (Ta); and (2) mean annual precipitation (Pa).

Palaeoaltitude reconstruction

Altitudinal zonation of plants reflects their latitudinal distribution. For example, today, the *Abies–Picea* vegetation belt ranges between 0 and 500 m a.s.l. in altitude in southern Sweden and southern Norway (Noirfalise *et al.*, 1987), but it is situated between 1400 and 2000 m in the southern French Alps (Ozenda, 1961) (Fig. 5). The vertical shift of the vegetation belts in relation to latitude is obvious but difficult to quantify, as the elevational range of plant species is controlled not only by climatic parameters (decreasing temperature and increasing precipitation with increasing altitude), but also by local conditions (nature of soils, slope orientation, etc.). Ozenda (1975) attempted to quantify the vertical shift in relation to latitude in Europe based on three

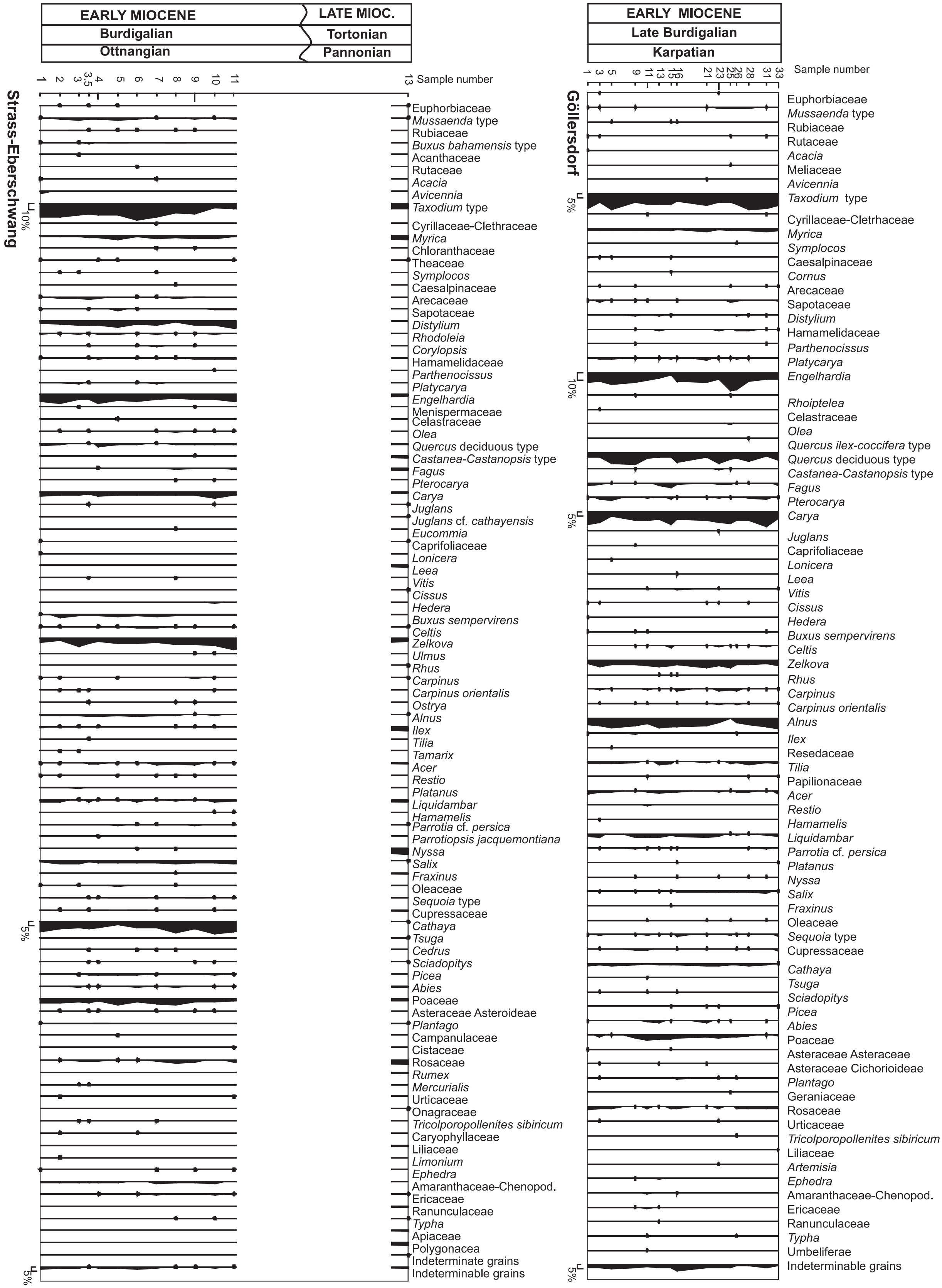

Figure 2 Detailed pollen diagrams showing percentages of taxa of the Strass-Eberschwang and Göllersdorf sections without *Pinus* and indeterminable Pinaceae. A solid dot indicates taxa recorded in the counts but at percentages below 1%.

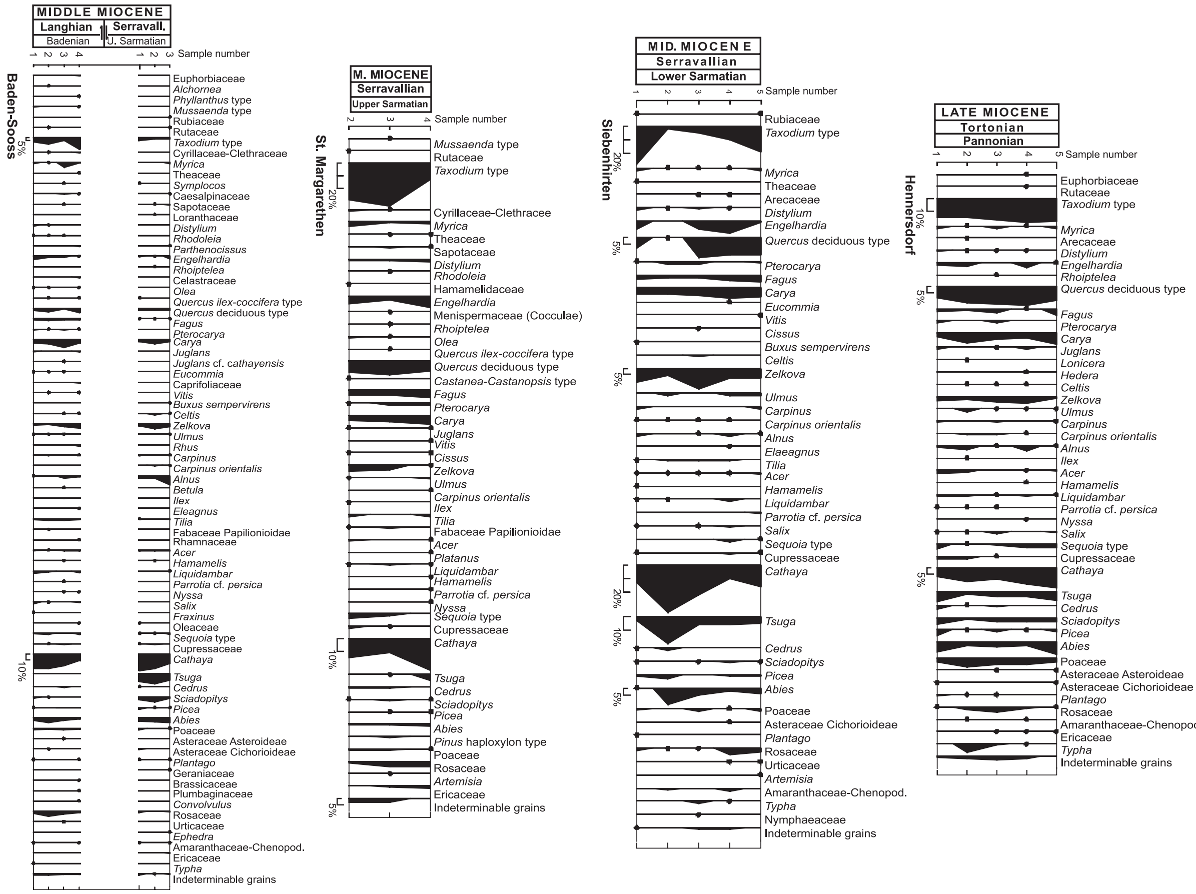

Figure 3 Detailed pollen diagrams showing percentages of taxa of the Baden-Sooss 1 (lower portion) and 2 (upper portion), St Margarethen, Siebenhirten and Hennersdorf sections without *Pinus* and indeterminable Pinaceae. A solid dot indicates taxa recorded in the counts but at percentages below 1%.

observations: (1) vegetation belts occur at different altitudes at different latitudes; (2) in temperate regions, mean annual temperatures vary *c.* 0.6°C per degree in latitude (1° in latitude = *c.* 110 km); and (3) temperature decreases in relation to altitude at *c.* 0.55°C per 100 m of elevation. Ozenda (1989) established the following relationship: a shift of 1 km to the north is equivalent, from a bioclimatic point of view, to a shift of 1 m in altitude. As a result, today, in general, vegetation belts shift 110 m in altitude per degree in latitude. Using this relationship, the vegetation distribution during the Miocene and the pollen-based climate estimates, it is possible to estimate the altitude of the Eastern Alps throughout the Miocene. In this study, conifers from high-elevation vegetation belts (mainly *Abies* and *Picea*) are used as the best indicators of palaeoaltitude in the pollen spectra. Based on modern pollen spectra from marine sediments close to the Alps (Suc *et al.*, 1999), a threshold value of 3% for *Abies* and *Picea* has been used to infer the presence of *Abies* and *Picea* forests in the past. In order to estimate palaeoaltitudes, the following assumptions have been made: (1) the present climatic limits of the closest living taxa are the same as those of the Miocene plants; (2) the pole-to-equator climatic gradient was similar to that of today, and hence the poleward lowering of the elevational limits of plant species or zones would be similar to that of today; and (3) the elevational zonation of plants during the Miocene in Central Europe was similar to the present-day zonation in south-eastern China.

RESULTS

Vegetation belts

A very rich and diverse flora has been recorded in this study (Figs 2 & 3). The vegetation has been compared with the one growing today in subtropical to temperate south-eastern China (Wang, 1961), the most reliable present-day model (Suc, 1984; Axelrod *et al.*, 1996; Jiménez-Moreno, 2005, 2006; Jiménez-Moreno *et al.*, 2005). The following plant ecosystems can be distinguished in the pollen data:

(1) A coastal marine environment characterized by the presence of an impoverished mangrove composed of *Avicennia*, which is mainly accompanied by halophytes (such as Amaranthaceae–Chenopodiaceae and *Armeria*).

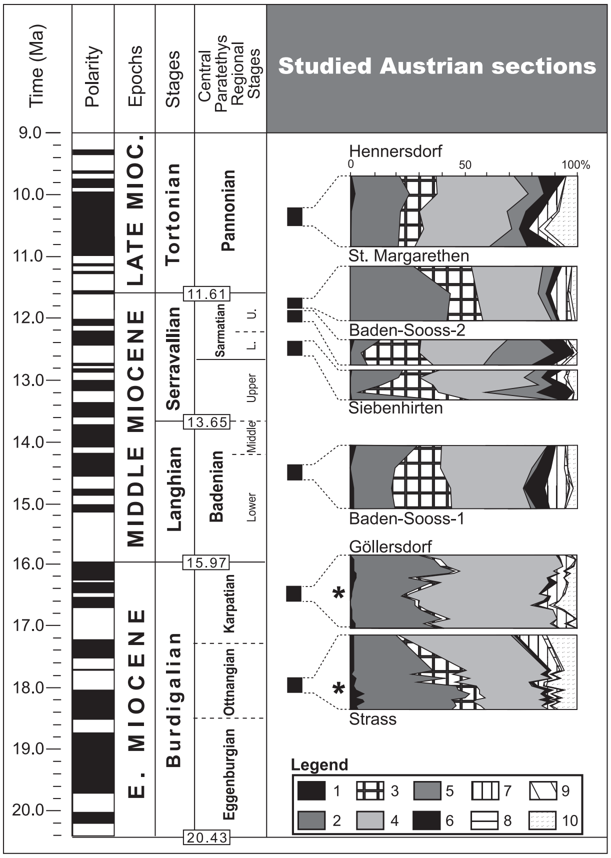

Figure 4 Chronostratigraphical situation (according to the time-scale of Harzhauser & Piller, 2007) and pollen synthetic diagrams without *Pinus* and indeterminable Pinaceae of the studied sections from Austria. The stratigraphical lengths of the sections are approximate (see references in the text for more details). Grouping was done regarding the ecology of the plants (see text for explanation). Legend numbers are: (1) megathermic elements (i.e. tropical); (2) mega-mesothermic elements (i.e. subtropical); (3) *Cathaya*; (4) mesothermic elements (i.e. warm-temperate); (5) meso-microthermic elements (mid-altitude conifers); (6) microthermic elements (high-altitude conifers, mainly *Abies* and *Picea*); (7) non-significant elements; (8) Cupressaceae; (9) Mediterranean xerophytes; (10) herbs and shrubs. The asterisk indicates the presence of pollen of *Avicennia* (mangrove plant).

(2) A broad-leaved evergreen forest, from sea level to around 700 m in altitude, featuring *Taxodium* or *Glyptostrobus*, *Myrica*, *Rhus*, Cyrillaceae–Clethraceae, Euphorbiaceae, *Distylium*, *Castanopsis*, Sapotaceae, Rutaceae, *Mussaenda*, *Ilex*, *Hedera*, Hamamelidaceae, *Engelhardia* and *Rhoiptelea*.

(3) An evergreen and deciduous mixed forest above 700 m in altitude, characterized by deciduous *Quercus*, *Engelhardia*, *Platycarya*, *Carya*, *Pterocarya*, *Fagus*, *Liquidambar*, *Parrotia*, *Carpinus*, *Celtis* and *Acer*. Within this vegetation belt, a riparian vegetation has been identified, composed of *Salix*, *Alnus*, *Carya*, *Carpinus*, *Zelkova*, *Ulmus* and *Liquidambar*. The shrub layer was dominated by Ericaceae, *Ilex* and Caprifoliaceae.

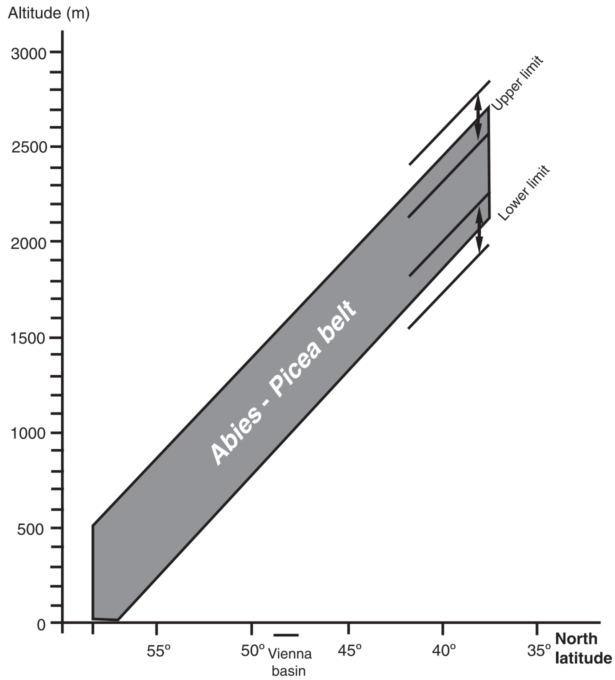

Figure 5 Altitudinal variation of the *Abies–Picea* belt in relation to latitude, from north to south, and the present latitudinal position of the Vienna Basin.

(4) From 1000 m up, a mid-altitude deciduous and coniferous mixed forest with *Betula*, *Fagus*, *Cathaya*, *Cedrus* and *Tsuga*.

(5) Lastly, above 1800 m in altitude, a coniferous forest with *Abies* and *Picea*.

Vegetation dynamics

Burdigalian–Langhian (Ottnangian to Middle Badenian)

Pollen spectra from Strass-Eberschwang, Göllersdorf and Baden-Sooss-1 demonstrate the regular occurrence and abundance of thermophilous species typical of the lowest altitudinal belts described above and the relative scarcity of altitudinal elements (Figs 2 & 3).

The coastal marine environment was generally composed of the *Avicennia* mangrove (its presence during the Burdigalian in Strass-Eberschwang and Göllersdorf and during the Langhian in other sections from Central Europe was recorded in Nagy, 1990; Nagy & Kókay, 1991; and Plaziat *et al.*, 2001) and several halophytes.

In the hinterland, the lowlands were populated by a broad-leaved evergreen forest, depicted by *Alchornea*, *Rhus*, Theaceae, Rubiaceae, Chloranthaceae, Euphorbiaceae, *Distylium*, *Castanopsis*, Sapotaceae, Rutaceae, *Mussaenda*, *Ilex*, *Hedera*, Hamamelidaceae, *Engelhardia*, *Rhoiptelea*, etc. Within this vegetation belt, the swamp forests were also well developed during this time period. Its components, such as *Taxodium* or *Glyptostrobus*, *Nyssa*, *Myrica* and Cyrillaceae–Clethraceae, show comparatively high abundances in the pollen spectra. Very humid conditions at that time most likely favoured the wide distribution of swamp forests and of ecologically related riparian forests with *Platanus*, *Liquidambar*, *Zelkova*, *Carya*, *Pterocarya* and *Salix*.

An evergreen and deciduous mixed forest composed mainly of elements such as *Quercus*, *Carya*, *Pterocarya*, *Fagus*, Ericaceae, *Ilex*, Caprifoliaceae, *Liquidambar*, *Parrotia*, *Carpinus*, *Celtis* and *Acer*, but also *Engelhardia* and *Platycarya*, characterized areas of higher altitude. Within this vegetation belt, a riparian vegetation has been identified, mainly composed of *Salix*, *Alnus*, *Carya*, *Carpinus*, *Zelkova* and *Ulmus*.

Mid- and high-altitude elements (*Tsuga*, *Cedrus*, *Abies* and *Picea*) and *Cathaya* increased significantly during the Langhian (Baden-Sooss-1 section; Figs 3 & 4).

Serravallian–Tortonian (c. Late Badenian to Pannonian)

Important changes in the vegetation are observed in Siebenhirten, Baden-Sooss-2, St Margarethen and Hennersdorf sections: *Avicennia*, which previously populated the coastal areas, vanished and several megathermic elements (*Buxus bahamensis* group, *Alchornea* and Melastomataceae), typical of the broad-leaved evergreen forest, became rare and most of them disappeared from the region (Figs 3 & 4). This is in accordance with previous studies that also show the disappearance of *Avicennia* and several megathermic plants from Central Europe during the same time-span (Plaziat *et al.*, 2001; Jiménez-Moreno, 2005).

The evergreen–deciduous mixed forest suffered a great transformation due to the loss and decrease in the abundance of several mega-mesothermic evergreen plants. Deciduous mesothermic plants, such as deciduous *Quercus*, and *Fagus*, *Alnus*, *Acer*, *Eucommia*, *Betula*, *Alnus*, *Carpinus*, *Ulmus*, *Zelkova* and *Tilia*, progressively substituted this kind of vegetation. Thus, the vegetation shows a tendency towards increasing proportions of mesothermic deciduous elements, which most likely came from higher altitudes. However, the swamp forest continued to be very well developed.

At the same time, the vegetation from mid-altitude (*Cathaya*, *Tsuga* and *Cedrus*) and high-altitude (*Picea* and *Abies*) belts clearly increased (Fig. 4). A similar vegetation change is observed during the same time interval in other areas of Europe (e.g. Spain, southern France, Switzerland and Hungary: (Bessedik, 1985; Jiménez-Moreno, 2005, 2006; Jiménez-Moreno *et al.*, 2005).

Palaeoaltitude estimation

Burdigalian–Langhian

During the middle Burdigalian (*c.* 18 Ma), the estimated mean annual temperature on the coastline at Strass-Eberschwang was *c.* 20°C (Fig. 6). Therefore, the *Abies* and *Picea* belt would have developed at a high altitude in order to compensate for the high temperatures. Today, such a temperature occurs in south-eastern China where *Abies* is present above an altitude of 1800 m (Wang, 1961). Pollen percentages in samples from the Strass-Eberschwang locality show a maximum value of 1.3% of the high-altitude elements *Abies* and *Picea* (Fig. 4). These elements are not abundant in the pollen spectra, indicating altitudes < 1800 m. On the contrary, *Cathaya*, growing today between 900 and 1900 m in south-eastern China (Liu *et al.*, 1997), is quite abundant in the samples. Therefore, we can infer a maximum elevation between 900 and 1800 m for the eastern part of the Eastern Alps at *c.* 18 Ma.

Later, during the late Burdigalian (*c.* 16.5 Ma) at Göllersdorf, the maximum values of *Abies* and *Picea* were 2.15%

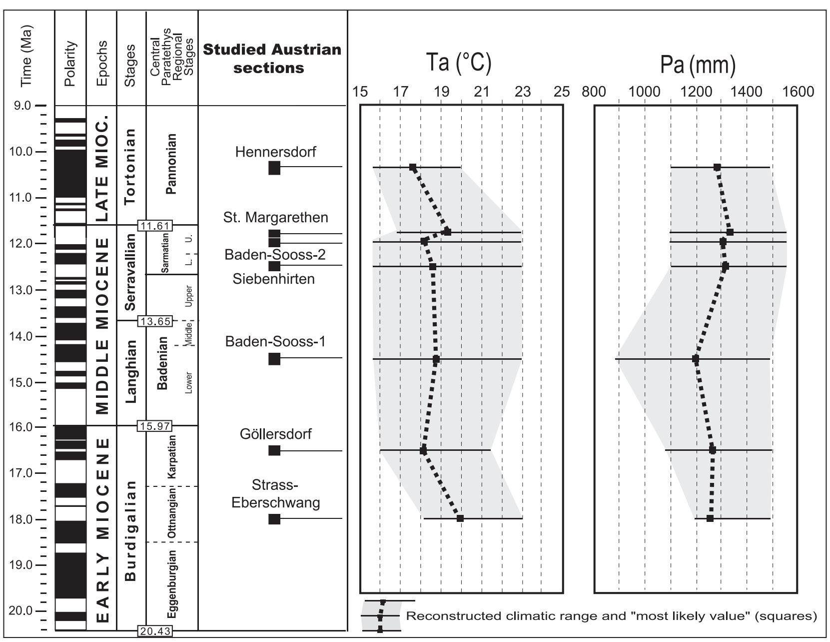

Figure 6 Chronostratigraphical situation (according to the time-scale of Harzhauser & Piller, 2007) and climatic reconstruction based on the pollen data (mean annual temperature and mean annual precipitation) from the studied sections. The stratigraphical lengths of the sections are approximate (see references in the text for more details). Only the average temperature (Ta, °C) and precipitation (Pa, mm) for all the pollen samples in each section has been plotted.

(Fig. 4). Therefore, as in Strass-Eberschwang, palaeoaltitudes would be < 1800 m.

In the samples from Baden-Sooss-1 of Langhian age (*c.* 14.5 Ma), the maximum value of *Abies* and *Picea* of 3.98% (Fig. 4) indicates that this vegetation belt was well developed in the mountains close to Baden-Sooss. The estimated mean annual temperature was around 18.8°C (range between 15.6°C and 22.9°C). Today, such a temperature occurs at *c.* 36° latitude (e.g. in Malta), *c.* 12° lower in latitude than Baden-Sooss. However, we have to take into account that during the Langhian, Europe was located around 3° lower in latitude than today (Meulenkamp & Sissingh, 2003). Therefore, after this subtraction (12°–3°), we can estimate a latitude of *c.* 9° lower for the above estimated temperature. Using the ratio established by Ozenda (1989), a shift of 9° in latitude would correspond to a shift of *c.* 990 m in altitude. Today, the lower altitudinal limit of *Abies* in the closest mountains is situated around 600 m (Ozenda *et al.*, 1979). Taking into account the shift of 990 m in vegetation belts between the Langhian and present day, *Abies* would be present above 1590 m. This indicates that, during the Langhian, the eastern part of the Eastern Alps was at least 1600 m above sea-level.

Serravallian–Tortonian

Pollen spectra younger than the Langhian (Siebenhirten, Baden-Sooss-2, St Margarethen and Hennersdorf; *c.* 12.4, 12, 11.8 and 10.3 Ma, respectively) show high percentages of *Abies* and *Picea* (Fig. 4). This implies that since the Langhian, this vegetation belt would have been fully developed and we are no longer able to estimate palaeoaltitudes. Therefore, the Eastern Alps were at least 1600 m high.

DISCUSSION

Climatic evolution

The large number of thermophilous elements during the Early and early Middle Miocene suggests a warm, subtropical climate. The climate was also quite humid, which was necessary to support the development of such a large association of thermic elements, which require very humid conditions all year (Wang, 1961). The estimated climatic parameters indicate mean annual temperatures of around 18–20°C and mean annual precipitations between 1200 and 1300 mm (Fig. 6). The floral assemblages and climatic parameters during the Early and early Middle Miocene clearly reflect the Miocene Climatic Optimum (MCO: Zachos *et al.*, 2001; Shevenell *et al.*, 2004). These results are in accordance with other palaeobotanical data from Central Europe that also indicate very warm floras and high temperature estimations for the Early and early Middle Miocene. For example, Jiménez-Moreno *et al.* (2005) show, from estimates based on Karpatian and Early Badenian (Langhian) pollen floras from Hungary, a good correspondence not only in temperature [mean annual temperature (MAT) = 18–20°C], but also in precipitation [mean annual precipitation (MAP) = 1200–1400 mm]. Mosbrugger *et al.* (2005), using abundant palaeobotanical data from Germany, noticed increases in all of the temperature records in three Cenozoic basins during the mid-MCO. Böhme *et al.* (2007), studying xylofloras from the North Alpine Foreland Basin (in southern Germany), also showed very high temperature estimations of *c.* 22.2–24.2°C (MAT) during the Late Ottnangian (Early Miocene) and 17.4–20.5°C (MAT) for the early Middle Miocene. A mean annual temperature of around 18°C was estimated using macrofloras for the mid-Miocene climate optimum in Serbia (Utescher *et al.*, 2007). Erdei *et al.* (2007) also calculated high temperatures of *c.* 18.8–16.5°C (MAT) for the Early Miocene using macrofloras from the Pannonian Basin.

The major change in the pollen spectra is the observed impoverishment in plant diversity produced by the disappearance of some of the most thermophilous plants and the consequent enrichment in mesothermic and altitudinal plants, from the Serravallian up to the Tortonian. Palaeoclimatic parameter estimates show the lowest MAT values in Hennersdorf (Tortonian) of *c.* 17–18°C (Fig. 6). Despite a general decreasing trend in our temperature estimates during the Middle and Late Miocene (Fig. 6), there is also a positive excursion during the Late Sarmatian (St Margarethen section; Fig. 6). This warm peak during the Late Sarmatian has also been observed by Piller & Harzhauser (2005) and Harzhauser *et al.* (2007) (who report positive δ^{18}O and δ^{13}C values and a low sea level) and could be related to orbital climate forcing (see Jiménez-Moreno *et al.*, 2005, for explanation). This is related to a gradual decrease in temperatures immediately following the MCO, which has also been observed in several palaeobotanical studies in Central Europe, with decreases in temperature of *c.* 1.5°C in the Forecarpathian Basin (Ivanov *et al.*, 2002), 2–3°C in Hungary (Jiménez-Moreno *et al.*, 2005), *c.* 2°C in the Pannonian Basin (Erdei *et al.*, 2007) and 2–3°C in Serbia (Utescher *et al.*, 2007) and Germany (Mosbrugger *et al.*, 2005). This gradual temperature decrease is well documented on a world-wide scale and has been correlated with the general decrease in temperature observed by several studies: a gradual increase in the isotopic δ^{18}O values took place [DSDP Sites 608 (Miller *et al.*, 1991) and 588 (Zachos *et al.*, 2001)] during this time-span called the 'Monterey cooling event' and is related to the increase in the development of the East Antarctic Ice Sheet (Zachos *et al.*, 2001). The isotopic values also indicate that this cooling dynamic continued during the Late Miocene and Pliocene (Zachos *et al.*, 2001).

Regional vs. global climatic change

The decrease in thermophilous plants and, on the contrary, the noticeable increase in mesothermic plants and altitudinal trees, can be interpreted as a result of the abovementioned climatic cooling, or from the uplift of the surrounding mountains in this area, which was very intense during the studied time period (Kuhlemann, 2007). In both cases, altitudinal elements would increase. However, the estimated climate, using only taxa growing at low to middle–low altitude, seems to confirm a decrease in mean annual temperatures, which was most likely not sufficient on its own to explain the development of an *Abies–Picea* forest. The two phenomena coexisted, and it is quite difficult to separate one process from the other (global climatic forcing vs. regional relief uplift) due to the tectonic situation of the studied area and the fact that the two may have interacted with one another. What is clear is that even if the uplift of the surrounding mountains may have influenced the regional climate and the increase in conifers observed in the pollen spectra, the evolution of the vegetation during the Miocene was very dependent on the global climatic signal, as shown in previous studies (Ivanov *et al.*, 2002; Jiménez-Moreno, 2005, 2006; Jiménez-Moreno *et al.*, 2005; Mosbrugger *et al.*, 2005; Böhme *et al.*, 2007; Erdei *et al.*, 2007; Utescher *et al.*, 2007).

Palaeoaltitude of the Eastern Alps during the Miocene

Pollen data do not allow us to estimate the altitudinal range of the *Abies* belt, or know whether the alpine herbaceous and perpetual-snow belts above it existed. This is because herbaceous elements from the alpine belt cannot be differentiated from herbaceous taxa growing at lower elevations. Taking this into account, this study shows the following:

(1) During the Burdigalian, the Eastern Alps were lower than 1800 m. This is in accordance with the structural and sedimentological data from previous studies (Schmid *et al.*, 1996; Frisch *et al.*, 1998; Kuhlemann & Kempf, 2002) that interpret a moderate elevation for the eastern part of the Eastern Alps for the same time period. Kuhlemann (2007) also shows that the proto-Carpathians were most probably elevated below 500 m.

(2) Palaeoaltitudes of the Eastern Alps increased during the Langhian with estimations higher than 1600 m. This coincides with the palaeogeographical and palaeotopographical reconstructions from Kuhlemann (2007), who demonstrates a rapid uplift of the eastern part of the Eastern Alps and the Carpathians at this time.

(3) Pollen records from the Serravallian and Tortonian sections indicate an active uplift since the middle Miocene. This increase in high-altitude conifers is also evident in other sections from the Western Alps and Jura (Jiménez-Moreno, 2005).

These estimations coincide with the sedimentological and tectonic interpretations from previous studies in the Eastern Alps that stated that the main uplift took place during the Late Miocene (Frisch *et al.*, 1998) and that an important exhumation rate occurred between 22 and 13 Ma (Hejl, 1997; Dunkl *et al.*, 1998; Kuhlemann *et al.*, 2006). Similar to the Eastern Alps, moderate to rapid uplift created the moderately elevated Carpathian chain in the Late Miocene, partly starting from lowland levels (Kuhlemann, 2007).

CONCLUSIONS

The pollen analysis of sediments from several sections taken from the Central Paratethys in Austria allowed us to characterize the vegetation and climate during the Miocene in this part of Central Europe. It also permitted the reconstruction of palaeoaltitudes of the eastern part of the Eastern Alps during the Early to Middle Miocene.

The abundance of thermophilous elements in the pollen spectra and the high temperature estimations during the Early and early Middle Miocene indicate that the climate was subtropical. This has been correlated with the warmest period during the Miocene: the MCO. During the Serravallian and Tortonian, important changes in the vegetation occurred as several thermophilous elements strongly decreased, many of them disappearing from the Central European region. They were substituted by deciduous and mesothermic plants. This is interpreted as a progressive climatic cooling that is universally known in the literature as the 'Monterey cooling event' and was mainly related to an increase in the volume of the Eastern Antarctic ice sheet.

This study also shows an increase in conifers typical of high elevations (*Cathaya*, *Cedrus*, *Tsuga*, *Picea* and *Abies*) during the Miocene in Austria. This was mainly related to the effects of the intense regional tectonics, generating the uplift of the Alps, as the climatic cooling was certainly not sufficient to develop an *Abies–Picea* forest. Therefore, using a new method based on pollen and climatic data, palaeoaltitudes of the Eastern Alps have been reconstructed. This shows that during the Burdigalian, the Eastern Alps had an altitude of less than 1800 m. Palaeoaltitudes increased during the Langhian with estimations higher than 1600 m. Pollen records from the Serravallian and Tortonian sections indicate an intense uplift during the Middle Miocene. These palaeoaltitude results correspond to minimum values, but show an important increase in elevation during the Early Miocene. They also demonstrate increasing values of palaeoaltitudes in the Eastern Alps due to an increase in the rate of uplift during the Middle and Late Miocene.

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BIOSKETCHES

Gonzalo Jiménez-Moreno works on European Miocene palaeoecological and palaeoclimatic records using pollen and other proxies. He has also conducted several high-resolution pollen studies on Late Pleistocene and Holocene sediments from the USA.

Séverine Fauquette works on climate reconstructions based on pollen data using the 'climatic amplitude method', which she developed. This method has been applied to many pollen sequences from the western Mediterranean area. She has also established a new method for palaeoaltitude estimation using the pollen data.

Jean-Pierre Suc has worked extensively on pollen analysis of the Neogene and Quaternary marine and continental sediments from Europe. He has published more than 100 papers and has supervised more than 20 doctoral students.

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