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Cenozoic paleotemperatures and leaf physiognomy — A European perspective

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Abstract

For 21 European leaf-floras (with a focus on Central Europe), which span a stratigraphic range from the Late Eocene to the Pliocene, paleoclimate estimates have been calculated using five different quantitative techniques: (a) leaf margin analysis (LMA_1), using a regression model based on data from East Asia, (b) the multivariate Climate Leaf Analysis Multivariate Programm (CLAMP) technique, based on data from East Asia and N.-America, (c) a recently developed multivariate technique based on modern European vegetation (ELPA), (d) a provisional LMA regression model based on the vegetation of several wet localities from N.-America (LMA_2), and e) the Coexistence Approach (CA), a technique based on comparisons with the nearest living relatives (NLRs) of fossil taxa. According to our results there seems to be certain discrepancies where the different techniques are compared for paleotemperatures estimates, depending mainly on the stratigraphic age of the floras. For Paleogene floras, both multivariate leaf physiognomic techniques are in rather good agreement with CA, although both techniques may differ considerably from each other. In contrast, for the Neogene, CLAMP shows a tendency to produce estimates that are considerably colder than CA, whereas ELPA, provides generally warmer estimates, and is in better agreement with CA and other independent evidence. Our results and interpretations add some *caveats* to temperature reconstructions based on leaf physiognomy, especially when applied to European floras from older periods (i.e. Paleogene, Cretaceous). Possible changes of the relationship between climate and leaf physiognomy over time should be taken into account as a possible source of error whenever such techniques are used. There is the possibility that the actual correlation between climate and leaf form may be modified by long-time evolutionary responses or floral changes, leading to erroneous paleoclimate estimates, if a calibration data-set is used, which is not suited for the region and time-interval in question. However, further research will be needed to test whether such changes in the relationship between climate and leaf physiognomy over time can also be detected on other continents, or whether this is a problem restricted to Europe.

Keywords: Paleotemperatures; Cenozoic; Nearest living relatives; Leaf physiognomy; Europe

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1. Introduction

Understanding paleoclimate may be essential for our understanding of future climatic situations evolving during contemporary and future global climate change. For the terrestrial realm, fossil plants are generally considered to represent excellent paleoclimatic proxies. Consequently, in recent decades a number of different techniques have been developed for the estimation of paleoclimate parameters relying on fossil plant remains. Unlike taxonomically based techniques established by comparisons with the nearest living relatives (NLRs) of fossil plants (e.g., Kershaw and Nix, 1988; Mosbrugger and Utescher, 1997; Mosbrugger, 1999), non-taxonomically based techniques depending on correlations between certain climatic parameters and leaf physiognomy are considered by many authors to represent powerful and reliable tools for the estimation of paleoclimatic parameters. This is because such methods are considered to be independent of the correct identification of fossil leaves (e.g., Wolfe, 1979, 1993; Wing and Greenwood, 1993; Wolfe, 1995; Wilf, 1997; Wolfe and Spicer, 1999; Roth-Nebelsick et al., 2004). Despite the general acceptance of leaf physiognomic methods by many authors, there is still intense debate on the applicability of certain leaf physiognomic techniques for the reconstruction of Cenozoic paleotemperatures (e.g. Boyd, 1994; Mosbrugger and Utescher, 1997; McIver and Basinger, 1999). For example, several applications of leaf physiognomic techniques to paleofloras of the European and Asian Neogene yielded mean annual temperatures (MAT) which were considerably lower than those derived by other paleobotanical techniques (e.g. NLR techniques), and also than those indicated by independent geological and paleontological evidence (e.g. Mosbrugger and Utescher, 1997; Utescher et al., 2000; Kvaček et al., 2002; Liang et al., 2003; Kowalski and Dilcher, 2003; Uhl et al., 2006).

Kowalski and Dilcher (2003) suggested that leaf physiognomic reconstruction techniques may tend to underestimate paleotemperatures since paleofloras are dominated by leaves from wet environments, which show a greater proportion of toothed leaves in modern vegetation than has been documented from “standard” correlations between climate and leaves from less mesic habitats, a fact first recognized by Burnham et al. (2001). To overcome such a bias, Kowalski and Dilcher (2003) proposed an alternative, though provisional, regression model for these floras, based on a modern calibration data-set derived from wet environments. Although this approach yielded temperature estimates for both fossil and modern assemblages that were closer to other (independent) evidence, persistent lower paleotemperature estimates for a number of European Neogene paleofloras left the discussion still open (e.g. Mosbrugger and Utescher, 1997; Utescher et al., 2000; Kvaček et al., 2002; Liang et al., 2003; Kowalski and Dilcher, 2003; Uhl et al., in press). Further, considering paleotemperature reconstructions not only from the Neogene, but also from the Paleogene of Europe, it is evident that in many cases the estimates derived from leaf physiognomic techniques are actually in good agreement with other paleoclimatic evidence, despite the fact that at least some of these Paleogene floras certainly also originated from wet environments (e.g. Uhl et al., 2003; Roth-Nebelsick et al., 2004; Kvaček and Walther, 2004). To elucidate whether these observations can be generalized or not, we compared the paleotemperature estimates derived from several quantitative techniques for thirteen Neogene and eight Paleogene floras from Europe. For this purpose, we used methods based on different modern calibration data sets originating from different continents, to see whether there are any systematic patterns.

2. Material and methods

2.1. Material

For this meta-analysis we have chosen 21 European leaf-floras (with a focus on Central Europe) which span a stratigraphic range from the Late Eocene to the Pliocene (cf. Table 1). The floras have been selected based on the following criteria:

1) diversity of the flora, with well known taxonomic composition
2) extremely good preservation and documentation of leaf physiognomy
3) coverage of a wide area of depositional environments by individual floras.

Stratigraphic and taxonomic details for the individual floras, as well as their depositional settings can be found in the citations given in Table 1 and will not be repeated here.

2.2. Methods

We applied several frequently used leaf physiognomic techniques including (a): leaf margin analysis (LMA_1) (using a regression model established by Wing and Greenwood (1993); based on data from East Asia from Wolfe (1979)) and (b) the multivariate Climate Leaf Analysis Multivariate Program (CLAMP) technique (based on data from East Asia and N.-America;

Table 1
Palaeofloras considered in the present study

Locality	Age	Depositional literature	environment
1. Berga/Thuringia	Pliocene	fluviatile–lacustrine (?)	Mai and Walther (1988)
2. Willershausen	Pliocene	lacustrine	Knobloch, 1998; Knobloch and Gregor, 2000; Gregor and Storch, 2000
3. Frankfurt	Pliocene	lacustrine (?)	Mädler (1939)
4. Hambach 9A	Late Miocene	fluviatile	Utescher et al. (2000)[a]
5. Garzweiler 8o	Late Miocene	fluviatile	Utescher et al. (2000)[a]
6. Hambach 8u	Late Miocene	fluviatile	Utescher et al. (2000)[a]
7. Hambach 7f	Late Miocene	fluviatile	Utescher et al. (2000)[a]
8. Bergheim 7o	Late Miocene	fluviatile	Utescher et al. (2000)[a]
9. Frechen 7o	Late Miocene	fluviatile	Utescher et al. (2000)[a]
10. Sprendlingen	Late Miocene	fluviatile	Meller (1989)
11. Schrotzburg	Middle Miocene	fluviatile	Hantke, 1954; Uhl et al., 2003, 2006[a, b, c, d]
12. Kövágó-oldal	Middle Miocene	lacustrine	Erdei and Hir, 2003; Traiser, 2004[a, b, c, d]
13. Wackersdorf	Early Miocene	fluviatile–lacustrine	Knobloch and Kvaček (1976)
14. Enspel	Late Oligocene	lacustrine (maar lake)	Köhler, 1998; Utescher et al., 2000[a]
15. Kleinsaubernitz	Late Oligocene	lacustrine (maar lake)	Walther, 1999; Uhl et al., 2003[a, c]
16. Monod-Rivaz	Late Oligocene	lacustrine	Berger, 1994; Traiser, 2004[a, b, d]
17. Hammerunterwiesenthal	Early Oligocene	lacustrine (maar lake)	Walther (1998)
18. Kundratice	Early Oligocene	lacustrine (maar lake)	Kvaček and Walther (1998)
19. Haselbach	Early Oligocene	fluviatile–lacustrine	Mai and Walther, 1978; Roth-Nebelsick et al., 2004[a]
20. Weiβelster Basin	Late Eocene	fluviatile–lacustrine	Mai and Walther (1985)
21. Stare Sedlo	Late Eocene	fluviatile–lacustrine	Knobloch et al. (1996)

[a] CA values taken from this publication.
[b] CLAMP value taken from this publication.
[c] LMA_1 value taken from this publication.
[d] ELPA value taken from this publication.

e.g. Wolfe, 1993, 1995; Wolfe and Spicer, 1999), (c) a recently developed multivariate ordination technique based on modern European vegetation (European Leaf Physiognomic Approach, ELPA) (Traiser, 2004; Traiser et al., 2005; Uhl et al., in press), and (d) the provisional LMA regression model (LMA_2) developed by Kowalski and Dilcher (2003) (for a detailed discussion of techniques a, b, and c see Uhl et al. (2006) and citations therein).

In most cases the leaf physiognomic composition of the floras was scored based on descriptions and illustrations from the literature (cf. Table 1). In the case of the localities Monod-Rivaz and Kövago-Oldal leaf physiognomy was scored directly from voucher specimens (Traiser, 2004). In a few cases existing values derived from leaf physiognomic techniques have been taken from the literature (cf. Table 1).

The results obtained from the leaf physiognomic methods are compared to estimates derived from the Coexistence Approach (CA), a quantitative technique based on the NLR Approach (Mosbrugger and Utescher, 1997) representing a source of information independent from leaf physiognomy. In some cases existing CA values were taken from the literature (cf. Table 1).

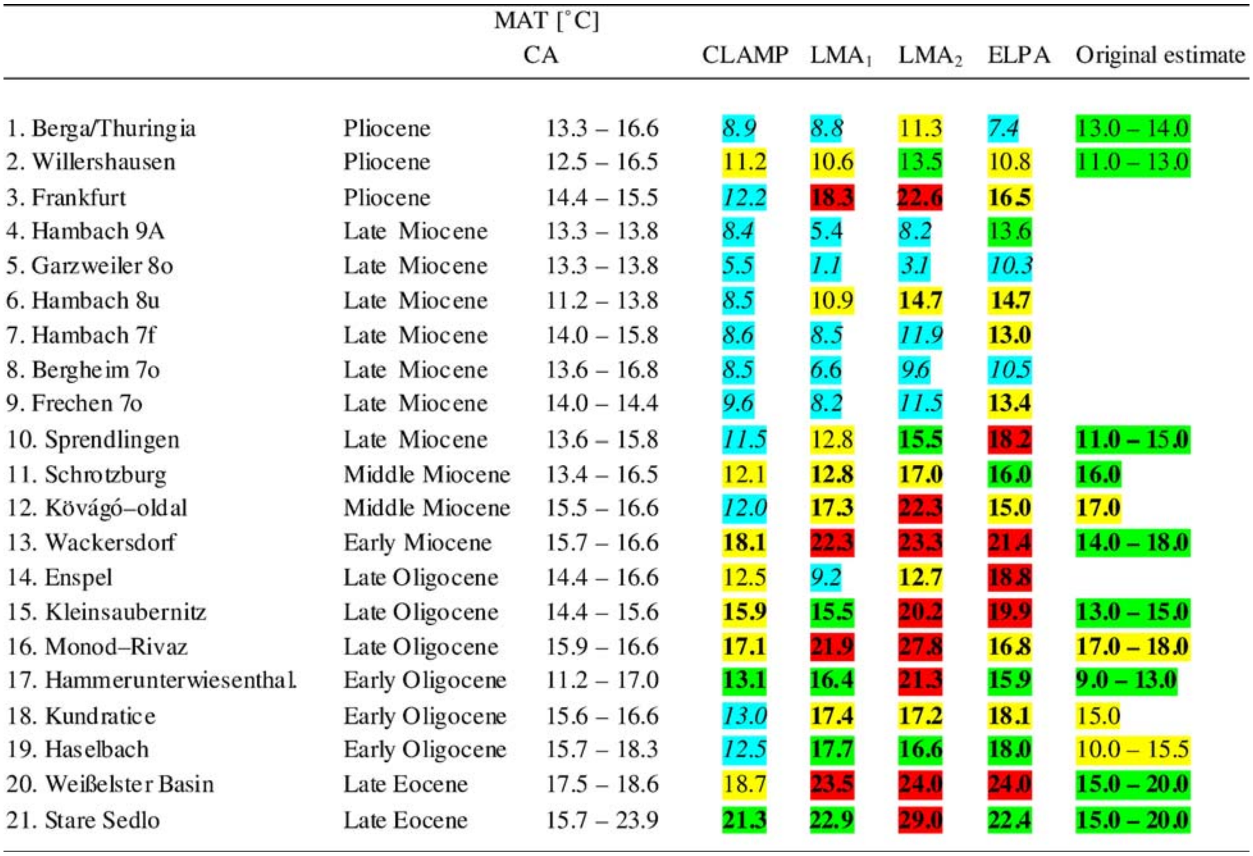
To provide an assessment of the deviations from the CA results, we divided the estimates derived from the leaf physiognomic methods into five different classes relying on standardized errors: 1) absolute agreement with CA, 2) up to 2 °C warmer, 3) up to 2 °C colder, 4) more than 2 °C warmer, and 5) more than 2 °C colder than CA. When available, information on MAT estimates provided by previous studies, based mostly on general comparisons with selected NLRs, is added.

However, it should be emphasized here, that such a procedure does not imply *a priori* that the CA estimates are implicitly "true", although the reliability of this method has been shown repeatedly not only for the European Neogene (e.g. Mosbrugger and Utescher, 1997; Utescher et al., 2000; Uhl et al., 2003, Mosbrugger et al., 2005; Uhl et al., 2006), as well as the Paleogene (e.g. Pross et al., 1998; Utescher et al., 2000; Uhl et al., 2003; Roth-Nebelsick et al., 2004; Kvaček and Walther, 2004; Mosbrugger et al., 2005). Here we use it *a priori* only as a widely supported and reliable source of information about paleotemperatures, which can be considered to be independent from leaf physiognomy.

3. Results

The results of the applications are shown in Table 2 and Fig. 1. CLAMP estimates derived for most of the Paleogene floras, as well as for one Early Miocene and

Table 2
Quantitative comparison of MAT estimates for the different floras and methods



		MAT [°C] CA	CLAMP	LMA$_1$	LMA$_2$	ELPA	Original estimate
1. Berga/Thuringia	Pliocene	13.3 – 16.6	*8.9*	*8.8*	11.3	*7.4*	13.0 – 14.0
2. Willershausen	Pliocene	12.5 – 16.5	11.2	10.6	13.5	10.8	11.0 – 13.0
3. Frankfurt	Pliocene	14.4 – 15.5	*12.2*	**18.3**	**22.6**	**16.5**	
4. Hambach 9A	Late Miocene	13.3 – 13.8	*8.4*	5.4	*8.2*	13.6	
5. Garzweiler 8o	Late Miocene	13.3 – 13.8	*5.5*	*1.1*	*3.1*	*10.3*	
6. Hambach 8u	Late Miocene	11.2 – 13.8	*8.5*	10.9	**14.7**	**14.7**	
7. Hambach 7f	Late Miocene	14.0 – 15.8	*8.6*	*8.5*	*11.9*	**13.0**	
8. Bergheim 7o	Late Miocene	13.6 – 16.8	*8.5*	*6.6*	*9.6*	*10.5*	
9. Frechen 7o	Late Miocene	14.0 – 14.4	*9.6*	*8.2*	*11.5*	**13.4**	
10. Sprendlingen	Late Miocene	13.6 – 15.8	*11.5*	12.8	**15.5**	**18.2**	**11.0 – 15.0**
11. Schrotzburg	Middle Miocene	13.4 – 16.5	12.1	**12.8**	**17.0**	**16.0**	**16.0**
12. Kövágó–oldal	Middle Miocene	15.5 – 16.6	*12.0*	**17.3**	**22.3**	**15.0**	**17.0**
13. Wackersdorf	Early Miocene	15.7 – 16.6	**18.1**	**22.3**	**23.3**	**21.4**	**14.0 – 18.0**
14. Enspel	Late Oligocene	14.4 – 16.6	12.5	*9.2*	**12.7**	**18.8**	
15. Kleinsaubernitz	Late Oligocene	14.4 – 15.6	**15.9**	**15.5**	**20.2**	**19.9**	**13.0 – 15.0**
16. Monod–Rivaz	Late Oligocene	15.9 – 16.6	**17.1**	**21.9**	**27.8**	**16.8**	**17.0 – 18.0**
17. Hammerunterwiesenthal	Early Oligocene	11.2 – 17.0	**13.1**	**16.4**	**21.3**	**15.9**	**9.0 – 13.0**
18. Kundratice	Early Oligocene	15.6 – 16.6	*13.0*	**17.4**	**17.2**	**18.1**	15.0
19. Haselbach	Early Oligocene	15.7 – 18.3	*12.5*	**17.7**	**16.6**	**18.0**	10.0 – 15.5
20. Weißelster Basin	Late Eocene	17.5 – 18.6	18.7	**23.5**	**24.0**	**24.0**	**15.0 – 20.0**
21. Stare Sedlo	Late Eocene	15.7 – 23.9	**21.3**	**22.9**	**29.0**	**22.4**	**15.0 – 20.0**

XXX=overlap with CA; XXX=up to 2 °C colder than CA; XXX=up to 2 °C warmer than CA; XXX=more than 2 °C colder than CA; XXX=more than 2 °C warmer than CA. CA = Coexistence Approach; LMA$_1$ = Leaf Margin Analysis (regression model from Wing and Greenwood, 1993); LMA$_2$ = Leaf Margin Analysis (provisional regression model for riparian elements from Kowalski and Dilcher, 2003); ELPA = European Leaf Physiognomic Approach; Orig. estimate=previous estimates from the literature (cf. Table 1).

Pliocene flora, are in good agreement (overlap, or ±2 °C) with estimates derived by CA. Only two Paleogene, but eleven Neogene CLAMP estimates are colder than CA estimates (Table 2). Five out of eight LMA$_1$ estimates for Paleogene floras are in good agreement with CA estimates, and two are significantly warmer and one colder. For the Neogene, five LMA$_1$ estimates agree with CA, two are warmer and six colder (Table 2). Using the provisional LMA$_2$ regression model for wet environments we find that for the Paleogene five estimates are significantly warmer and only two are in agreement with CA. For the Neogene, three floras are warmer, five colder than CA and five agree with estimates derived from this technique (Table 2). Concerning ELPA, we see that for the Paleogene three estimates are significantly warmer than CA estimates and five agree. For the Neogene, one estimate is warmer and three colder than CA, whereas eight ELPA estimates agree with CA estimates (Table 2).

These results show a tendency for most leaf physiognomic methods to produce estimates which agree with those of the CA for Paleogene floras, but which are colder than CA estimates for Neogene floras. LMA$_2$ and to a lesser degree ELPA also show a tendency towards warmer estimates for Paleogene floras. In contrast to the other physiognomic methods, ELPA also produces estimates which are mostly in agreement with those of CA (Table 2) for the Neogene floras. Nevertheless, as mentioned above, the CA estimates are not considered *a priori* to be implicitly true. But the reliability of this method for the European Neogene and Paleogene has been accepted repeatedly by various authors, and estimates derived from this technique are usually in good agreement with qualitative and quantitative temperature-data derived form other geological and paleontological evidence.

Nevertheless, when we compare our CLAMP estimates with MAT estimates given in previous works on the

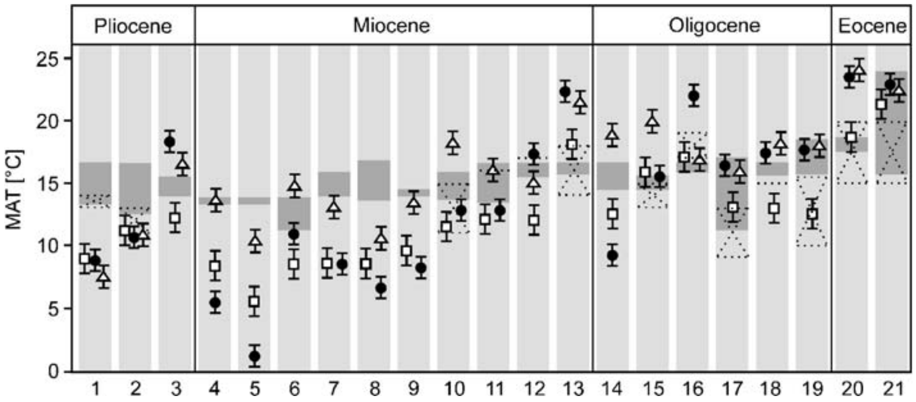


Fig. 1. Graphical comparison of MAT estimates derived from LMA (●), CLAMP(□), ELPA (Δ), CA (dark grey boxes) and "original estimates" based on comparison with NLRs, taken from preceding publications on individual floras (cf. Table 1) (dotted boxes).

corresponding floras, which were based mostly on the climatic requirements of selected NLRs, we see that CLAMP estimates are mostly in agreement with these estimates for Paleogene floras, or come very close to these estimates (i.e. Stare Sedlo, Kundratice) (Table 2, Fig. 1). Interestingly, CLAMP is also in good agreement with some of the Neogene estimates from previous works (Table 2, Fig. 1). LMA estimates are only occasionally in agreement with estimates given in previous published works and generally show a greater variability than estimates derived from all other techniques (Table 2, Fig. 1). For most of the floras analyzed, ELPA provides estimates that are warmer than the "original" estimates given in previous published reports. Only for two floras (i.e. Monod-Rivaz, Willershausen) do the ELPA estimates agree with these old estimates and only in one case (Berga) does ELPA provide a colder estimate. CA estimates are similar to the old estimates, although in some cases there are slight differences. In some cases, however, CA estimates are somewhat warmer, or have warmer upper limits than the old estimates, although no stratigraphic tendency can be seen at this time.

Results from both LMA regression models show a great variability, a fact that is probably related to the high susceptibility of this technique to taphonomic disturbances (e.g. Uhl et al., 2003, 2006). In contrast, both multivariate techniques show smaller variability, with ELPA almost constantly providing warmer estimates than CLAMP (mean difference 3.6 °C), although for some floras CLAMP estimates are in fact warmer than ELPA estimates (cf. Table 2, Fig. 1).

4. Discussion

According to our results there seems to be a certain discrepancy in the comparability of the different techniques for the estimation of paleotemperatures, depending largely upon the stratigraphic age of the flora. For Paleogene floras, both multivariate leaf physiognomic techniques are in rather good agreement with CA, although both techniques may differ considerably from each other. In contrast, for the Neogene, CLAMP shows a tendency to produce estimates that are considerably colder than CA, whereas ELPA, generally provides warmer estimates, and is better in agreement with CA. A possible explanation for the tendency of CLAMP to produce colder temperature estimates in the Neogene may be due to an intrinsic shortcoming of the underlying dataset. Within this dataset, MAT and CMMT of the individual calibration floras show a linear correlation ($r^2=0.898$) and as demonstrated in previous studies, the Neogene cooling in Europe, as represented by CA estimates, is most pronounced for CMMT rather than MAT (e.g. Utescher et al., 2000; Mosbrugger et al., 2005). Considering the close correlation of both parameters in the CLAMP calibration dataset (in contrast to the climate dataset provided by New et al. (1999) used for ELPA; cf. Traiser, 2004; Traiser et al., 2005) it may be possible that CLAMP estimates for MAT are biased, at least to some part, by a decrease of CMMT, leading to a possible underestimation of MAT values.

Although such an explanation may be possible, there is an additional explanation, which may also influence the reliability of leaf physiognomic techniques: recently it has been repeatedly demonstrated that in the modern vegetation the relationship between leaf physiognomy (i.e. leaf margin type) and climate is substantially the same for N.-America, S.-America, East-Asia and Europe (e.g. Wilf, 1997; Wiemann et al., 1998; Gregory-Wodzicki, 2000; Burnham et al., 2001; Kowalski, 2002; Traiser et al., 2005). Nevertheless, some minor differences between these different regions have been observed (e.g. Kowalski, 2002; Traiser et al., 2005), and in the case of Africa (e.g. Jacobs, 1999, 2002) and Australia (Greenwood et al., 2004) even larger differences of this relationship became obvious. Although Greenwood et al. (2004) observed almost the same slope in the linear regression between leaf margin type and MAT as seen on other continents, the proportion of non-entire (toothed) taxa was always lower as seen on the other continents. Despite the discrepancies, this result indicates that the evolutionary response of leaf form to climate (i.e. temperature) may be globally convergent. In the case of Australia the discrepancies may be explained by the different evolutionary and climatic history of this continent during the Cenozoic. This may indicate that the relationship between climate and leaf physiognomy changed during the Cenozoic within Australia, a possibility that should also be considered for Europe and the rest of the world. During the Paleogene–Neogene transition a significant floral change took place in Europe (e.g. Mai, 1995), gradually replacing many "paleotropical" elements typical for European Paleogene floras with modern "arctotertiary" elements (e.g. Mai, 1995; Kvacek and Walther, 2001). This change may have had a drastic influence on the relationship between climate and leaf physiognomy within European vegetation. Following such a possible explanation we can conclude that the relationship represented by the LMA and CLAMP calibration datasets may be well suited for European Paleogene floras, whereas the ELPA calibration dataset may probably be better suited for European Neogene floras (although the latter dataset still has to be seen as provisional; Traiser et al., 2005).

Our results and interpretations add some *caveats* to temperature reconstructions based on leaf physiognomy, especially when applied to European floras from older periods (i.e. Paleogene, Cretaceous). Possible changes of the relationship between climate and leaf physiognomy over time should be taken into account as a possible source of error whenever such techniques are used. Such an interpretation contradicts at first sight (at least partly) the assumption, underlying all attempts to reconstruct quantitative paleoclimate parameter from angiosperm leaf physiognomy, that convergent evolution of leaf form in response to climate is more influential than evolutionary constraints based upon phylogeny. Although there is evidence that the evolutionary response of leaf form to climate (i.e. temperature) may be globally convergent (e.g. Greenwood et al., 2004), there is also the possibility that the actual correlation between climate and leaf form may be modified by long-term evolutionary responses or floral changes. This would lead to erroneous paleoclimate estimates if a calibration dataset is used which is not suited for the region and time-interval in question, as already proposed by Wolfe and Upchurch (1987) for the Late Cretaceous of North America. These authors used a southern hemispheric calibration data-set for leaf physiognomic analysis of Late Cretaceous floras from North America, because these fossil assemblages, as well as modern southern hemispheric vegetation, are dominated by evergreen taxa, whereas Northern hemisperic calibration data-sets have high percentages of deciduous taxa. However, further research will be needed to test whether the proposed changes in the relationship between climate and leaf physiognomy over time can also be detected on other continents, or whether this is a problem restricted to the European Tertiary and the Cretaceous of North America.

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References

Berger, J.P., 1994. Paleontologie de la Molasse de Suisse Occidentale. Manuscrit d'habilitation, Université de Fribourg. 403 pp.

Boyd, A., 1994. Some limitations in using leaf physiognomic data as a precise method for determining paleoclimates with an example from the Late Cretaceous Pautût Flora of West Greenland. Palaeogeogr. Palaeoclimatol. Palaeoecol. 112, 261–278.

Burnham, R.J., Pitman, N.C.A., Johnson, K.R., Wilf, P., 2001. Habitat-related error in estimating temperatures from leaf margins in a humid tropical forest. Am. J. Bot. 88, 1096–1102.

Erdei, B., Hir, J., 2003. Vegetation and climate reconstruction of Sarmatian (Middle Miocene) sites from NE and W Hungary. Acta Univ. Carol., Geol. 46, 75–84.

Greenwood, D.R., Wilf, P., Wing, S.L., Christophel, D.C., 2004. Paleotemperature estimation using leaf-margin analysis: is Australia different? Palaios 19, 129–142.

Gregor, H.-J., Storch, D., 2000. Die Flora von Willershausen-kritische Bemerkungen zu den bisherigen Florenlisten und Elementen sowie zur Paläoökologie, Soziologie und zum Paläoklima der Fundstelle. Doc. Nat. 132, 37–63.

Gregory-Wodzicki, K.M., 2000. Relationships between leaf morphology and climate, Bolivia: implications for estimating paleoclimate from fossil floras. Paleobiology 26, 668–688.

Hantke, R., 1954. Die fossile Flora der obermiozänen Oehninger-Fundstelle Schrotzburg. Denkschr. Schweiz. Nat.forsch. Ges. 80, 27–118.

Jacobs, B.F., 1999. Estimation of rainfall variables from leaf characters in tropical Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 145, 231–250.

Jacobs, B.F., 2002. Estimation of low-latitude paleoclimates using fossil angiosperm leaves: examples from the Miocene Tugen Hills, Kenya. Paleobiology 28, 399–421.

Kershaw, A.P., Nix, H.A., 1988. Quantitative palaeoclimatic estimates from pollen data using bioclimatic profiles of extant taxa. J. Biogeogr. 15, 589–602.

Knobloch, E., 1998. Der pliozäne Laubwald von Willershausen am Harz (Mitteleuropa). Doc. Nat. 120 302 pp..

Knobloch, E., Gregor, H.-J., 2000. Ergänzung zur Flora von Willershausen am Harz-Material im Naturmuseum Augsburg. Doc. Nat. 132, 27–35.

Knobloch, E., Kvaček, Z., 1976. Miozäne Blätterfloren vom Westrand der Böhmischen Masse. Rozpr. Úst. Geol. 42, 1–129.

Knobloch, E., Konzalova, M., Kvaček, Z., 1996. Die obereozäne Flora der Stare Sedlo-Schichtenfolge in Böhmen (Mitteleuropa). Rozpr. Ces. Geol. Ust. 49 (260 pp.).

Köhler, J., 1998. Die Fossillagerstätte Enspel– Vegetation, Vegetationsdynamik und Klima im Oberoligozän. Unpublished Dissertation, Tübingen University, 211 pp.

Kowalski, E.A., 2002. Mean annual temperature estimation based on leaf morphology: a test from tropical South America. Palaeogeogr. Palaeoclimatol. Palaeoecol. 188, 141–165.

Kowalski, E.A., Dilcher, D.L., 2003. Warmer paleotemeratures for terrestrial ecosystems. Proc. Natl. Acad. Sci. 100, 167–170.

Kvaček, Z., Walther, H., 1998. The Oligocene volcanic flora of Kundratice near Litomerice, Ceske Stredohorí volcanic complex (Czech republic) — a review. Acta Mus. Natl. Pragae, Ser. B, Hist. Nat. 54, 1–42.

Kvaček, Z., Walther, H., 2001. The Oligocene of Central Europe and the development of forest vegetation in space and time based on megafossils. Palaeontogr. B 259, 125–148.

Kvaček, Z., Walther, H., 2004. Oligocene Flora of Bechlejovice ar Decin from the neovolcanic area of the Ceske Stredohori mountains, Czech Republic. Acta Mus. Natl. Pragae, Ser. B, Nat. Hist. 60, 9–60.

Kvaček, Z., Velitzelos, D., Velitzelos, E., 2002. Late Miocene Flora of Vegora, Macedonia, N. Greece. University of Athens, Athens Greece. 175 pp.

Liang, M.-M., Bruch, A., Collinson, M., Mosbrugger, V., Li, Ch.-S., Sun, Q.-G., Hilton, J., 2003. Testing the climatic estimates from different palaeobotanical methods: an example from the Middle Miocene Shangwang flora of China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 198, 279–301.

Mädler, K., 1939. Die pliozäne Flora von Frankfurt am Main. Abh. Senckenb. Naturforsch. Ges. 446 (202 pp.).

Mai, D.H., 1995. Tertiäre Vegetationsgeschichte Europas. Gustav Fischer, Jena. 691 pp.

Mai, D.H., Walther, H., 1978. Die Floren der Haselbacher Serie im Weiβelster-Becken (Bezirk Leipzig) DDR. Abh. Staatl. Mus. Mineral. Geol. Dresd. 28, 1–200.

Mai, D.H., Walther, H., 1985. Die obereozänen Floren des Weiβelster-Beckens und seiner Randgebiete. Abh. Staatl. Mus. Mineral. Geol. Dresd. 33, 1–260.

Mai, D.H., Walther, H., 1988. Die pliozänen Floren von Thüringen, Deutsche Demokratische Republik. Quartärpaläontology 7, 55–297.

McIver, E.E., Basinger, J.F., 1999. Early tertiary floral evolution in the Canadian High Arctic. Ann. Mo. Bot. Gard. 86, 523–545.

Meller, B., 1989. Eine Blatt-Flora aus den obermiozänen Dinotherien-Sanden (Vallesium) von Sprendlingen (Rheinhessen). Doc. Nat. 54, 1–10.

Mosbrugger, V., 1999. The nearest living relative method. In: Jones, T.P., Rowe, N.P. (Eds.), Fossil Plants and Spores: Modern Techniques. Geological Society, London, pp. 261–265.

Mosbrugger, V., Utescher, T., 1997. The coexistence approach—a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. Palaeogeogr. Palaeoclimatol. Palaeoecol. 134, 61–86.

Mosbrugger, V., Utescher, T., Dilcher, D.L., 2005. Cenozoic continental climatic evolution of Central Europe. Proc. Natl. Acad. Sci. 102, 14964–14969.

New, M., Hulme, M., Jones, P., 1999. Representing 20th century space-time climate variability. Part I: Development of a 1961–1990 mean monthly terrestrial climatology. J. Climate 12, 829–856.

Pross, J., Bruch, A., Kvaček, Z., 1998. Paläoklima-Rekonstruktionen für den Mittleren Rupelton (Unter-Oligozän) des Mainzer Beckens auf der Basis mikro-und makrobotanischer Befunde. Mainzer Geowiss. Mitt. 27, 79–92.

Roth-Nebelsick, A., Utescher, T., Mosbrugger, V., Diester-Haass, L., Walther, H., 2004. Changes in atmospheric CO_2 concentrations and climate from the Late Eocene to Early Miocene: palaeobotanical reconstruction based on fossil floras from Saxony, Germany. Palaeogeogr. Palaeoclimatol. Palaeoecol. 205, 43–67.

Traiser, C., 2004. Blattphysiognomie als Indikator für Umweltparameter: Eine Analyse rezenter und fossiler Floren. Dissertation, Tübingen University, 113 pp., URN:urn:nbn:de:bsz:21-opus-14947.

Traiser, C., Klotz, S., Uhl, D., Mosbrugger, V., 2005. Environmental signals from leaves — A physiognomic analysis of European vegetation. New Phytol. 166, 465–484.

Uhl, D., Mosbrugger, V., Bruch, A., Utescher, T., 2003. Reconstructing palaeotemperatures using leaf floras- case studies for a comparison of leaf margin analysis and the coexistence approach. Rev. Palaeobot. Palynol. 126, 49–64.

Uhl, D., Bruch, A.A., Traiser, C., Klotz, S., 2006. Palaeoclimate estimates for the Middle Miocene Schrotzburg flora (S-Germany) – A multi-method approach. Internat. J. Earth Sci. 95, 1071–1085.

Utescher, T., Mosbrugger, V., Ashraf, A.R., 2000. Terrestrial climate evolution in Northwest Germany over the last 25 million years. Palaios 15, 430–449.

Walther, H., 1998. Die Tertiärflora von Hammerunterwiesenthal (Freistaat Sachsen). Abh. Staatl. Mus. Mineral. Geol. Dresd. 43/44, 239–264.

Walther, H., 1999. Die Tertiärflora von Kleinsaubernitz bei Bautzen. Palaeontogr. B 249, 63–174.

Wiemann, M.C., Manchester, S.R., Dilcher, D.L., Hinojosa, L.F., Wheeler, E.A., 1998. Estimation of temperature and precipitation from morphological characters of dicotyledonous leaves. Am. J. Bot. 85, 1796–1802.

Wilf, P., 1997. When are leaves good thermometers? A new case for Leaf Margin Analysis. Paleobiology 23, 373–390.

Wing, S.L., Greenwood, D.R., 1993. Fossils and fossil climate: the case for equable continental interiors in the Eocene. Philos. Trans. R. Soc. Lond., B 341, 243–252.

Wolfe, J.A., 1979. Temperature parameters of humid zo mesic forests of eastern Asia and relation to forests of other regions of the northern hemisphere and Australia. U. S. Geol. Surv. Prof. Pap. 1106, 1–37.

Wolfe, J.A., 1993. A method of obtaining climatic parameters from leaf assemblages. U.S. Geol. Surv. Bull. 2040, 1–71.

Wolfe, J.A., 1995. Paleoclimatic estimates from Tertiary leaf assemblages. Annu. Rev. Earth Planet. Sci. 23, 119–142.

Wolfe, J.A., Spicer, R.A., 1999. Fossil leaf character states: multivariate analysis. In: Jones, T.P., Rowe, N.P. (Eds.), Fossil Plants and Spores: Modern Techniques. Geological Society, London, pp. 233–239.

Wolfe, J.A., Upchurch Jr., G.R., 1987. North American nonmarine climates and vegetation during the Late Cretaceous. Palaeogeogr. Palaeoclimatol. Palaeoecol. 1, 33–77.