Reconstructing palaeotemperatures using leaf floras – case studies for a comparison of leaf margin analysis and the coexistence approach

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Abstract

In the past the problems and advantages of the nearest-living-relative (NLR) and leaf physiognomy approaches have been repeatedly discussed and it has been demonstrated that both approaches frequently show broad agreement with each other. However, detailed comparisons of the various methods for accuracy in estimation of palaeoclimate at individual localities are still lacking. Such studies are needed before data obtained from different approaches can be integrated in palaeoclimate maps and models. Moreover, there are some indications that leaf physiognomy and NLR approaches may lead to different results. In this study we applied a physiognomic method based on leaf margin analysis and the coexistence approach, a recent variation of the NLR approach, to two Tertiary palaeofloras (Schrotzburg, Middle Miocene, south Germany; Kleinsaubernitz, Upper Oligocene, east Germany). We demonstrated that both approaches can produce reasonable and consistent results if the standard error of the leaf physiognomy palaeoclimate data is taken into account. However, our results and interpretations indicate that reconstructions based on leaf physiognomy are influenced by factors not related to climate, such as sample size and differential preservation or transport. In contrast, reconstructions for the same fossil assemblages based on the coexistence approach seem to be less affected by taphonomic variables, but may be less sensitive to minor climate changes.
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1. Introduction

Fossil land plants represent excellent palaeoclimate proxies and various methods have been developed to extract climate information from them. Only a few of these methods, however, provide quantitative palaeoclimate data. A frequently used quantitative technique of palaeoclimate reconstruction is based on fossil leaf assemblages and makes use of the correlation between leaf physiognomy and climate parameters. Bailey and Sinnott (1915, 1916) were the first to observe that the percentage of woody species with entire-margined leaves is higher in tropical floras than in cooler climatic zones. Wolfe (1971, 1979) further analysed this correlation between leaf margin

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types of floras and climate and used it to reconstruct Tertiary climates of North America. Later, Wolfe (1993) proposed the Climate Leaf Analysis Multivariate Program (CLAMP) approach which represents a multivariate analysis of leaf physiognomy considering 29 (or even more) leaf characters simultaneously in relation to several climate variables. More recently, Wilf (1997) demonstrated that the CLAMP approach does not significantly improve the mean annual temperature reconstructions as compared to the classic leaf margin analysis, which relates one variable, the proportion of species having entire-margined leaves, to mean annual temperature (e.g. Wolfe, 1971, 1979). However, Wiemann et al. (2001) showed that in a test on Recent floras from Connecticut canonical correspondence analysis (the mathematical basis of CLAMP) gave better results than leaf margin analysis, whereas in a test on Recent floras from Florida leaf margin analysis gave better results.

The leaf physiognomy approach to terrestrial palaeoclimate reconstruction has several advantages. Its application is relatively simple, it can provide quantitative estimates for several climate parameters and does not require a detailed taxonomic study of fossil floras thus being largely independent of taxonomic revisions. On the other hand, the leaf physiognomy approach is not completely independent of taxonomy because it requires that the number of species in a leaf flora is identified and hence depends on the (morpho-) species concept (cf. the discussion in Wolfe, 1999; Davies-Vollum, 1999). Moreover, the quality of palaeoclimate reconstructions based on the leaf physiognomy approach depends on various factors other than taxonomy (Wolfe, 1993; Wiemann et al., 1998; Jacobs, 1999). In particular, the type of calibration data set (based on modern floras) plays a significant role (cf. Wilf, 1997; Gregory-Wodzicki, 2000) and there is still a debate about the best strategy to obtain a calibrating data set (e.g. Stranks and England, 1997). The species richness also influences palaeoclimate reconstructions based on leaf physiognomy. Wolfe (1985) suggested that leaf margin analysis requires a species richness of at least 30 species; according to Povey et al. (1994) leaf physiognomy analysis

needs more than 15 taxa to produce reliable results. Local variations within the standing vegetation may represent another source of errors. Burnham et al. (2001) observed that the vegetation along an Amazonian river consisted of more species with toothed margins than the adjacent vegetation. Correspondingly, they found that in modern lakeside and riparian floras, resembling the environments where most of the fossil plant remains may come from, the standard correlation underestimates the real temperatures. Additionally, taphonomy and sampling techniques for fossil plants also have an impact on leaf physiognomy approaches (e.g. Boyd, 1994; Jordan, 1997; Wolfe, 1993, 1995), although little is known about the impact of these factors and there is conflicting evidence. For instance, Burnham (1989) performed a leaf margin analysis for the litter and the standing vegetation of a paratropical forest and found no serious taphonomic effect: 91% of the species in the standing vegetation had entire-margined leaves whereas in the litter the entire-margined species varied between 77 and 100%. However, in a similar actualistic study Greenwood (1992) observed overrepresentation as well as underrepresentation of entire-margined species in the litter as compared to the standing vegetation.

Another widely used technique for reconstructing palaeoclimate with the help of fossil plants is based on comparisons of fossil with Recent species and is known as the 'nearest-living-relative' (NLR) method (e.g. Chaloner and Creber, 1990). Here it is assumed that the climatic requirements of fossil species are more or less similar to those of their NLRs. This approach, which has its roots in the early days of palaeobotany and palaeoclimatology (e.g. Heer, 1855, 1856, 1859), can be used not only with leaves, but also with other plant remains (e.g. fruits, seeds, pollen, spores) for which nearest living relatives can reliably be identified. A recent variation of the NLR approach, the so-called coexistence approach (CA), has been described by Mosbrugger and Utescher (1997) and was applied repeatedly for Tertiary palaeoclimate reconstructions in Europe (e.g. Pross et al., 1998; Utescher et al., 2000). The CA determines for all taxa of a given fossil flora the nearest living

relatives and their climatic tolerances (i.e. minimum and maximum values) with respect to various climate parameters such as mean annual temperature or mean annual precipitation; for these climate parameters the coexistence intervals are determined within which all nearest living relatives of the fossil flora can coexist. It is assumed that the coexistence intervals best describe the palaeoclimate of the fossil flora.

In contrast to leaf margin analysis, the NLR method and thus the CA depend largely on the quality of the determination of the fossil flora, of its NLRs and of the climatic requirements of these NLRs. Hence, errors in the palaeoclimate reconstruction may occur if some fossil taxa or their NLRs are misidentified, if the determination of the climatic requirements of the NLRs is partly incorrect and if the fossil taxa and their NLRs have different climatic requirements. However, these errors are assumed to become apparent when no coexistence interval can be found in which all NLRs of a given fossil flora can coexist (for details see Mosbrugger and Utescher, 1997). On the other hand, the CA does not take into account the relative abundance of taxa and thus is largely independent of taphonomic filters and collecting bias. For instance, if some taxa are missing in a fossil flora because of taphonomic or sampling effects this may influence the width of the calculated coexistence interval, but the coexistence interval would still represent a valid palaeoclimate estimate. Theoretically, this method will function with a flora that contains at least one taxon for which a nearest living relative can be reliably determined (Mosbrugger and Utescher, 1997, p. 63). The width of the coexistence interval generally increases with decreasing species richness of the fossil flora. Additionally, the accuracy of this method probably decreases with increasing age of the floras investigated, due to the increasing taxonomic differences between the fossil taxa and their assumed NLRs.

In the past the problems and advantages of the different approaches have been repeatedly discussed (e.g. Wing and Greenwood, 1993; Herman and Spicer, 1997; Mosbrugger and Utescher, 1997) and it has been demonstrated by several authors that the NLR and leaf physiognomic approaches frequently show broad agreement with each other (e.g. Wing and Greenwood, 1993; Wilf, 2000). However, detailed comparisons of the various methods for individual localities are still lacking. Such studies demonstrating the consistency of the results of the different methods are needed before palaeoclimate data obtained from different approaches can be integrated in palaeoclimate maps and models. Moreover, there are some indications that leaf physiognomy and NLR approaches may lead to different results. Mosbrugger and Utescher (1997) compared temperature data from the Neogene Lower Rhine Embayment (west Germany) obtained with CLAMP and the CA. Surprisingly, the temperatures from CLAMP are consistently below the temperature ranges obtained with the CA. However, up to now it is unclear whether this observation can be generalised or not.

In this paper we compare results of palaeotemperature estimates based on leaf margin analyses and the CA. For this purpose we apply the regression equation of Wing and Greenwood (1993; based on the data set of Wolfe, 1979), as well as the CA (Mosbrugger and Utescher, 1997) to a Middle Miocene leaf flora in south Germany which was collected from 26 distinct layers over a 4 m thick profile and to an Upper Oligocene leaf flora from east Germany which was collected from a 300 m thick core. From our study it turns out that the different approaches can both produce reasonable and consistent results if the standard error of the leaf physiognomy palaeoclimate data is taken into account. However, it appears that the CA is more robust against taphonomic disturbances, but is probably less sensitive to small climatic changes.

2. Study sites, material, and methods

2.1. Study sites and material

As our study sites we chose the localities Schrotzburg near Lake Constance in south Germany (Middle Miocene) and Kleinsaubernitz near Bautzen in east Germany (Upper Oligocene) (Fig. 1). The two floras were chosen because of the fact
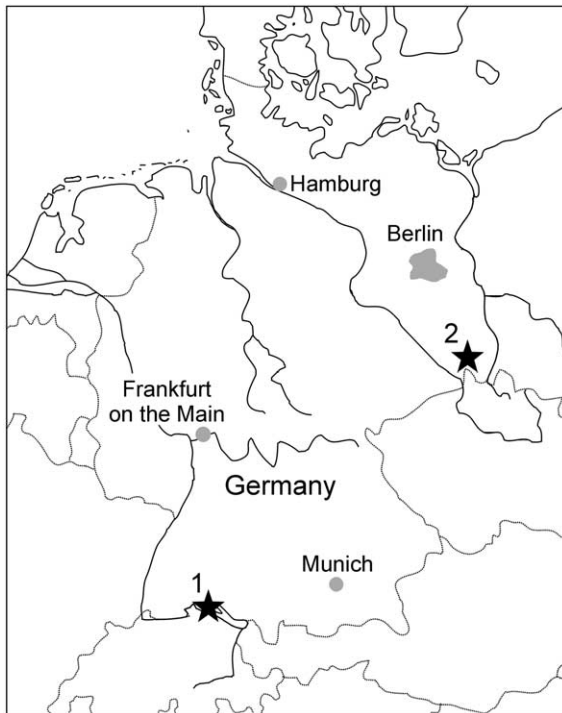
Fig. 1. Schematic map of the investigated localities, marked by ★. 1: Schrotzburg; 2: Kleinsaubernitz.

that in both floras all plant remains were collected (no bias towards known taxa or specific leaf size classes), the very good documentation of the distribution of the plant remains in the sedimentary sequences, which allowed the reconstruction of the sampling procedures, and because of their differences in stratigraphic age, source vegetation, environmental conditions and depositional setting.

The Schrotzburg locality is Middle Miocene (Sarmatian) in age and contemporary with the Upper Oehningen beds (Stauber, 1937) from which the flora was first described by Heer (1855, 1856, 1859). Hantke (1954) studied the Schrotzburg leaf flora in detail and – based on the climatic requirements of NLRs of a few taxa of the fossil flora – estimated mean annual temperature (MAT) to be about 16°C. In the following years more taxonomic publications on the Schrotzburg flora appeared (e.g. Nötzold, 1956, 1957; Hantke, 1965, 1966, 1980; Gregor and Hantke, 1980; Gregor, 1982) which considered

only one or a few taxa. Although there is no recent revision, the Schrotzburg flora, most likely representing a riparian forest vegetation, is still one of the best known Miocene leaf floras in Europe (cf. Mai, 1995) and has yielded about 40 species (represented by angiosperm leaves, fruits, seeds and conifers) and several thousand specimens. Identification of most of the taxa is based on the morphology of a large number of complete specimens. Our study is based on the more than 15 000 specimens investigated by Hantke (1954) stored in the collection of the Eidgenössische Technische Hochschule Zürich, Switzerland.

The Schrotzburg plant-bearing sediments are very uniform and consist of marls attaining a thickness of about 4 m (Rutte, 1956). Initially, the flora was collected from 28 distinct layers which possibly represent single flooding events (Hantke, 1954). Based on mammalian remains, the marls and underlying sandstones have been dated as being of lower Sarmatian age (Schreiner, 1974).

For our investigation we directly use the species lists for the Schrotzburg flora and the individual plant-bearing layers as published in Hantke, 1954; however, we combine Hantke's layers 12, 12a and 12b to a single layer because they are particularly close to each other (less than 1 cm) and relatively poor in specimens. Hence, in our study we consider a total of 26 plant-bearing layers (instead of the 28 layers distinguished in Hantke, 1954), which we analyse both as individual floras and as a combined flora. Table 1 provides some statistical information about the number of taxa and specimens recorded from these 26 layers. Because these layers differ considerably in their number of leaf taxa and specimens, the Schrotzburg flora is ideal for testing the influence of these parameters on palaeoclimate reconstructions. Possibly, these differences in the number of taxa and specimens do not reflect true changes in the source vegetation but may be explained by taphonomic processes and differences in sampling efforts (i.e. sampling area).

The Kleinsaubernitz flora near Bautzen was collected from a core (cf. Walther, 1999) and is of Upper Oligocene age on the basis of the plant macro remains (Walther, 1999) and the palyno-

flora (Suhr and Goth, 1999). Walther (1999) studied the Kleinsaubernitz leaf flora and estimated MAT to be about 13–15°C, again using the climatic requirements of selected NLRs. In comparison to the Schrotzburg locality the Kleinsaubernitz flora is more diverse (63 species; represented by angiosperm leaves, fruits, seeds and conifers) but because it was collected from a core, it yielded only a few hundred specimens including more than 300, often incomplete, angiosperm leaf remains. Identification of most of the taxa is based not only on morphological characters, like at the Schrotzburg locality, but also on cuticular anatomy. More than 50% of the taxa are evergreen thermophilous elements (Walther, 1999).

The plant-bearing sediments mainly consist of diatomite and oil shale deposited in a Maar lake (Suhr and Goth, 1999; Walther, 1999). Within the core the plant remains are more or less equally distributed in the uppermost 200 m of the plant-bearing part and less frequent in the lower 100 m (Walther, 1999).

Our investigation is based on the published species list for the Kleinsaubernitz flora as well as on the stratigraphic column of the core indicating the occurrences of the individual taxa (Walther, 1999). Moreover, we divided the 300 m of the core, which contained plant remains, into three parts of 100 m each; these three parts of the core with their (more or less arbitrarily separated) florules were treated as individual subsamples. Table 1 provides some statistical information about the number of taxa and specimens recorded from the entire core and from the three subsamples.

2.2. Methods

2.2.1. Palaeoclimate

For comparison of the leaf physiognomy and the NLR approaches as tools for terrestrial palaeoclimate reconstructions we use the leaf margin analysis (LMA) and the CA as two typical representatives.

2.2.1.1. Leaf margin analysis. LMA is based on the fact that today the proportion of dicot woody species with entire-margined leaves within a given

flora is correlated with MAT (e.g. Bailey and Sinnott, 1915, 1916; Wolfe, 1979; Wilf, 1997). We used the following regression equation which describes the correlation between MAT and the proportion (P) of woody species with entire-margined leaves in a flora:

$$MAT = 30.6P + 1.14$$

(Wing and Greenwood, 1993; calibrating data set of Wolfe, 1979, based on mesic forests of East Asia). The standard deviation or 'sampling error' of MAT was calculated after Wilf (1997; his equation 4) as:

$$\sigma[MAT] = c[P(1-P)/r]^{0.5}$$

with P ($0 < P < 1$) representing the proportion of leaf species with entire margins of the r species in the flora and c being the constant in the regression equation (here 30.6).

2.2.1.2. Coexistence approach. This technique (described in detail in Mosbrugger and Utescher, 1997) is based on the NLR philosophy and determines for a given fossil flora and climate parameter (e.g. MAT) the climatic interval of coexistence within which all (more realistic: most) NLRs of the fossil taxa can coexist. For a given climate parameter these coexistence intervals represent minimum and maximum values which are assumed to encompass the 'real' palaeoclimate value. Sometimes it may occur that not all NLRs of the fossil flora can coexist within a single climatic interval and that some taxa form 'climatic outliers'. The climatic outliers are neglected in the palaeoclimate reconstructions; they are caused by misidentifications of a fossil taxon or its NLR, by incorrect determinations of the climatic requirements of a NLR or by a discrepancy between the climatic requirement of the fossil taxon and its NLR (see the discussion in Section 1 and in Mosbrugger and Utescher, 1997).

The CA is largely computer-assisted. There is a data base which for several hundred Palaeogene and Neogene taxa provides information about the NLRs and their climatic tolerances with respect to 10 different climate parameters (parts of the most recent version of the data base are available on the internet at http://www.palaeoflora.de). More-

over, the computer program CLIMSTAT is available (from V. Mosbrugger or T. Utescher), which for a given fossil flora extracts the relevant information from the data base and calculates the co-existence intervals for the palaeoclimate parameters of interest.

Since LMA can only estimate MAT, we restrict our palaeoclimate reconstructions to this parameter.

2.2.2. Taphonomy

For the reconstruction of sampling curves the relevant subsamples are first sorted according to increasing specimen numbers; in a second step the number of specimens and taxa of the layers are summed up stepwise, beginning with the layer containing the fewest specimens. Rarefaction curves (sensu Raup, 1975) were calculated using the software package Biodiversity Professional, version 2 (©1997, The Natural History Museum/Scottish Association for Marine Science).

3. Results

3.1. Temperature reconstruction

3.1.1. Schrotzburg

In the following climate analysis of the Schrotzburg leaf flora and its subsamples (individual layers) using the LMA and the CA, we first analysed the entire flora by combining the leaf taxa of all individual layers; the corresponding MAT estimates are termed LMAT(s) (s = Schrotzburg) and CAT(s), respectively; then the 26 plant-bearing layers were treated as separate floras and analysed individually resulting in estimates termed LMAT(sl) (sl = Schrotzburg, individual layers) and CAT(sl).

3.1.1.1. Leaf margin analysis. Table 2 shows the result of the application of the regression equation (see above) to the entire flora (i.e. combining all layers). Obviously LMAT(s) (17.8°C) is higher than the upper boundary of the CAT(s) interval (16.5°C). However, the standard deviation of the LMAT(s) estimate is about ± 2.6°C when calculated according to Wilf (1997; see above). Thus,

when including the standard deviation the equations provide a LMAT(s) result consistent with the CAT(s) interval. This also implies, however, that in this case the climatic resolution of the LMA has only half the precision (about 5°C) as compared to that of the CA (2°C).

The MAT of the entire flora can also be calculated by applying the regression equation to all layers separately and calculating the mean LMAT(sl) of the layers. The result of this procedure is also shown in Table 2 (mean all layers). Here the mean LMAT(sl) estimate is in good agreement with the CA (cf. Table 2). Because the entire flora contains more taxa than each of the 26 layers (cf. Table 1) and because the quality of the LMA largely depends on the number of taxa (cf. Povey et al., 1994; Wilf, 1997) it is indeed surprising that the mean LMAT(sl) estimates are in better agreement with the CAT(s) than the LMAT(s) estimate. An explanation for this phenomenon is provided when looking at the LMAT(sl) estimates of the individual layers.

Fig. 2A illustrates the LMAT(sl) estimates for the individual layers; for comparison, the CAT(sl) intervals are also included. The LMAT(sl) estimates show significant oscillations near the base and minor oscillations in the middle and upper parts of the sequence. Moreover, and in contrast to the results of the CA, an overall warming trend towards the top of the sequence is observable. Fig. 2B considers only those layers which provided at least 15 taxa because this has been proposed to be the minimum species richness required for LMA (e.g. Povey et al., 1994). But even then major climatic oscillations and a warming trend towards the top are recognisable. The warming trend revealed from the LMAT(sl) estimates crosses the – more or less constant – CAT(sl) intervals (see trend line in Fig. 2A). This may explain the previously described phenomenon that the mean LMAT(sl) is well within the CAT(s) interval whereas the LMAT(s) estimate is not (Table 2).

In absolute terms the LMAT(sl) varies between 8.8 and 20.3°C when all layers are considered and between 13.0 and 19.8°C when layers with fewer than 15 taxa are excluded (Tables 1 and 2, Fig. 2A,B). Only for six of the 26 layers the LMAT(sl)

Table 1
Some relevant data for the investigated floras

	Number of specimens	Number of entire-margined specimens	Proportion of entire-margined specimens	Number of taxa	Number of entire-margined taxa	Proportion of entire-margined taxa
Schrotzburg (layer)						
1 (top)	2411	661	0.27	30	18	0.60
2	1098	390	0.36	17	10	0.59
3	3678	583	0.16	23	13	0.57
4	77	31	0.40	17	9	0.53
5	1057	192	0.18	21	11	0.52
6	1054	278	0.26	24	12	0.50
7	456	204	0.45	24	13	0.54
8	1626	371	0.23	26	14	0.54
9	42	8	0.19	9	3	0.33
10	73	38	0.52	11	5	0.45
11	143	74	0.52	15	8	0.53
12	410	56	0.14	11	6	0.55
13	553	147	0.27	18	7	0.39
14	103	25	0.24	12	7	0.58
15	30	8	0.27	9	3	0.33
16	11	2	0.18	6	2	0.33
17	92	9	0.10	12	5	0.42
18	159	35	0.22	12	6	0.50
19	332	38	0.11	11	5	0.45
20	33	5	0.15	8	3	0.38
21	21	5	0.24	9	4	0.44
22	17	6	0.35	8	5	0.63
23	7	2	0.29	5	2	0.40
24	8	3	0.38	4	1	0.25
25	26	4	0.15	8	3	0.38
26 (base)	1023	259	0.25	23	14	0.61
All layers	14540	3434	0.24	35	18	0.54
Kleinsaubernitz						
Complete flora	309	141	0.46	51	24	0.47
Upper part	167	67	0.40	34	13	0.38
Middle part	125	66	0.53	32	20	0.63
Lower part	17	8	0.47	9	4	0.44

For every single layer and subsample number of specimens, the number of entire-margined specimens, the proportion of entire-margined specimens, the number of taxa, the number of entire-margined taxa and the proportion of entire-margined taxa (data only for the angiosperm leaves) are given (data compiled from Hantke, 1954 [Schrotzburg] and Walther, 1999 [Kleinsaubernitz]).

values lie within the corresponding coexistence intervals; when layers with fewer than 15 taxa are included, only one of the remaining 11 layers falls into this category (Fig. 2B). Thus, when the layers are analysed individually, there is a particular difference between the MAT estimates of the LMA and CA. This difference vanishes, however, when the standard deviation of the LMA data is considered: it overlaps with (or in two layers is extremely close to) the corresponding coexistence

intervals. The width of the standard deviation varies between ±2.7°C and ±6.7°C; accordingly in all layers, the climatic resolution of the CA at least doubles that for the LMA (cf. Table 2, Fig. 2A).

3.1.1.2. Coexistence approach. When applied to the entire flora (i.e. combining all 26 plant-bearing layers) the CA yields a CAT(s) interval between 14.4 and 16.5°C (Table 2). Considering the plant-

Table 2
Application of LMA and CA to the investigated floras

	LMAT [°C]	CAT [°C]
Schrotzburg		
All layers combined	17.8 ± 2.6	14.4–16.5
1 (top)	19.5 ± 2.7	14.4–16.5
2	19.1 ± 3.7	14.4–16.5
3	18.4 ± 3.2	14.4–16.5
4	17.3 ± 3.7	14.4–16.5
5	17.2 ± 3.3	14.4–16.5
6	16.4 ± 3.1	14.4–16.5
7	17.7 ± 3.1	14.4–16.5
8	17.6 ± 3.0	14.4–16.5
9	11.3 ± 4.8	14.4–16.5
10	15.0 ± 4.6	13.5–16.5
11	17.5 ± 3.9	14.4–16.5
12	17.8 ± 4.6	14.4–16.5
13	13.0 ± 3.5	14.4–16.5
14	19.0 ± 4.4	14.4–16.5
15	11.3 ± 4.8	13.5–16.5
16	11.3 ± 5.9	13.5–16.5
17	13.9 ± 4.4	13.5–16.5
18	16.4 ± 4.4	13.5–16.5
19	15.0 ± 4.6	13.5–16.5
20	12.6 ± 5.2	13.5–16.5
21	14.7 ± 5.1	13.5–16.5
22	20.3 ± 5.2	14.4–16.5
23	13.4 ± 6.7	14.4–16.5
24	8.8 ± 6.6	13.5–20.5
25	12.6 ± 5.2	14.4–16.5
26 (base)	19.8 ± 3.1	14.4–16.5
Mean all layers	15.7	
Kleinsaubernitz		
Complete flora	15.5 ± 2.1	14.4–15.6
Upper part	12.3 ± 2.6	14.0–15.6
Middle part	20.3 ± 2.6	14.4–15.6
Lower part	14.7 ± 5.1	14.4–15.8
Mean subsamples	15.8	

The results are given for both floras and the corresponding subsamples. For further explanations see text.

bearing layers individually, the CAT(sl) intervals are also between 14.4 and 16.5°C for layers 1–9, 11–14, 22–23 and 25–26; layers 10 and 15–21 show slightly cooler lower boundaries (13.5°C) whereas layer 24 yields a wider interval then all the other layers (13.5–20.5°C; Table 2, Fig. 2). Obviously in the lower part of the profile there are more layers with a cooler lower boundary (and hence with a wider coexistence interval) than in the upper parts of the profile. This may

or may not indicate slightly lower temperatures during the sedimentation of these lower layers. Another, probably more plausible interpretation is indicated from Fig. 2A in combination with Fig. 3, which shows the variation of number of taxa, number of specimens and width of the coexistence interval over the 26 layers investigated. From these figures it appears that the wider coexistence intervals are related to floras (layers) which are less diverse and contain fewer specimens. This is particularly evident for layer 24, which shows the widest interval of coexistence and the lowest number of taxa and the second lowest number of specimens. In contrast, all layers with at least 15 species have the same interval of coexistence (14.4–16.5°C; cf. Fig. 2).

As a whole, the CA gives more or less the same results for MAT over the whole profile and there is only a minor variation (0.9°C) of the lower boundary of the coexistence interval in the lower part of the section. These results, both for the entire flora and for the individual layers, are consistent and in perfect agreement with the MAT estimated by Hantke (1954) for the Schrotzburg flora (16°C), which was based on the climatic demands of the nearest living relatives of few selected taxa of the fossil flora.

3.1.2. Kleinsaubernitz

In the following climate analysis of the Kleinsaubernitz leaf flora using the LMA and the CA, we first analysed the entire flora by combining all leaf taxa; the corresponding MAT estimates are termed LMAT(k) (k = Kleinsaubernitz) and CAT(k), respectively; then the whole plant-bearing part of the core (300 m) was divided in three 100-m parts and the florules of the three parts were treated as individual subsamples termed LMAT(kss) (kss = Kleinsaubernitz, subsamples) and CAT(kss).

3.1.2.1. Leaf margin analysis. Table 2 also shows the results of LMA for the different samples of the Kleinsaubernitz flora. When applied to the whole flora LMAT(k) is in good agreement with the MAT given by Walther (1999) (13–15°C) as well as the CAT(k). However, as seen above for the Schrotzburg flora, the resolution
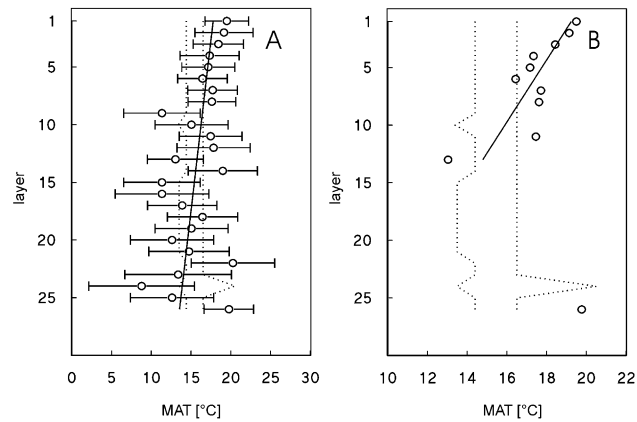
Fig. 2. Comparison between LMAT and CAT for the individual layers of the Schrotzburg locality. (A) All layers. (B) Only layers with 15 or more taxa. ○ = LMAT, solid line = trend line for LMAT, dotted line = CAT, error bars = standard deviations.

of LMA is only half as good as the resolution of the CA, when the standard deviation, according to Wilf (1997), is considered.

The mean LMAT, calculated from the individual LMAT(kss), is in very good agreement with the LMAT(k). Comparison with CAT(k) shows that the mean LMAT is only slightly higher than the upper boundary of CAT(k).

When looking at the (arbitrary) subsamples the results are more complicated. LMAT(kss) and CAT(kss) of the upper part of the fossiliferous region marginally overlap with a slightly higher upper boundary for CAT(kss). In the middle part CAT(kss) is significantly cooler than LMAT(kss) and in the lower part the results from both methods are again in good agreement. Here no correlation can be seen between the number of species per subsample and the temperature values and ranges. In the upper part with 34 species we have the lowest and in the middle part with virtually the same number of species (32) we have the highest temperatures. In the lower part, which gives MAT estimates which are in very good agreement with the whole flora and the results obtained by CA, we only have nine species.

3.1.2.2. Coexistence approach. CAT(k) and CAT(kss) show no great differences. Only CAT(kss) from the upper part shows a slightly cooler lower boundary than all the other samples

and only CAT(kss) from the lower part shows a slightly warmer upper boundary than all the other samples. All results are in perfect agreement with the temperature estimates (13–15°C) of Walther (1999).

3.2. Taphonomic and sampling effects

3.2.1. Schrotzburg

In LMAs MAT directly depends on the percentage of entire-margined leaves. From Fig. 4A,B it can be seen that at the Schrotzburg locality in all layers the number of entire-margined specimens is lower than the number of toothed specimens (Fig. 4B), whereas the number of entire-margined taxa is only lower in those samples with fewer than about 100–200 specimens (Fig. 4A). In fact, Fig. 4A clearly indicates that with increasing specimen number the species richness of entire-margined taxa increases more rapidly than the species richness of toothed taxa thus leading to an increase in the proportion of entire-margined leaf taxa (Fig. 3A) and of MAT (Fig. 2A). Correspondingly, entire-margined leaf taxa are underrepresented in specimen-poor floras, as is evident from Fig. 4A.

This phenomenon is even more evident when the various layers are not treated as individual floras but are assumed to be independent samples of the same flora. Then a sampling curve can be reconstructed from the available data reflecting
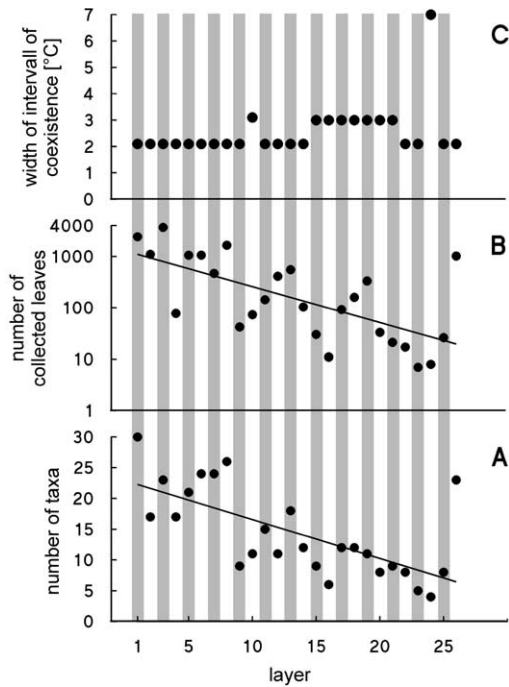
Fig. 3. Variation of various parameters over the 26 layers at Schrotzburg. (A) Number of taxa. (B) Number of collected leaves. (C) Width of coexistence intervals. Solid lines = trend lines.

how the number of taxa increases during sampling. For this purpose the layers are first sorted according to increasing specimen numbers; in a second step the number of specimens and taxa of the layers are summed up stepwise, beginning with the layer containing the fewest specimens. The resulting cumulative sampling curve is shown in Fig. 5A. Fig. 5B,C illustrates how for this sampling curve the number of entire and toothed taxa and the LMAT vary with increasing number of specimens. Similar to Fig. 4A, Fig. 5B shows the fact that with an increasing number of specimens the ratio of taxa with entire margins to toothed margins changes, with a greater increase of entire-margined taxa. The LMAT exhibits some oscillations with an increasing number of specimens, with a more or less stable result after more than 1000 collected specimens.

Hence, in our Schrotzburg example not only the species richness, but also the proportion of entire-margined leaf taxa depends on the sample size pointing to a taphonomic filter favouring

toothed leaf taxa in specimen-poor samples at this locality. In addition, all these correlations clearly suggest that the oscillations and the overall warming trend in the LMAT(sl), as revealed in Fig. 2A,B, are most likely due to sampling and taphonomic effects and may not reflect climatic changes.

3.2.2. Kleinsaubernitz

Here the cumulative number of collected leaves (from top to bottom) is significantly correlated with LMAT ($r^2 > 0.99$; Fig. 6). This indicates that even after the total flora from this core was collected, no stable relation between entire and toothed taxa was reached, such as was found for the Schrotzburg locality after more than 1000 collected specimens (Fig. 5C). This indicates that the resulting LMAT for the Kleinsaubernitz flora has to be seen with great care and that the good agreement between LMAT and CAT is probably highly coincidental.
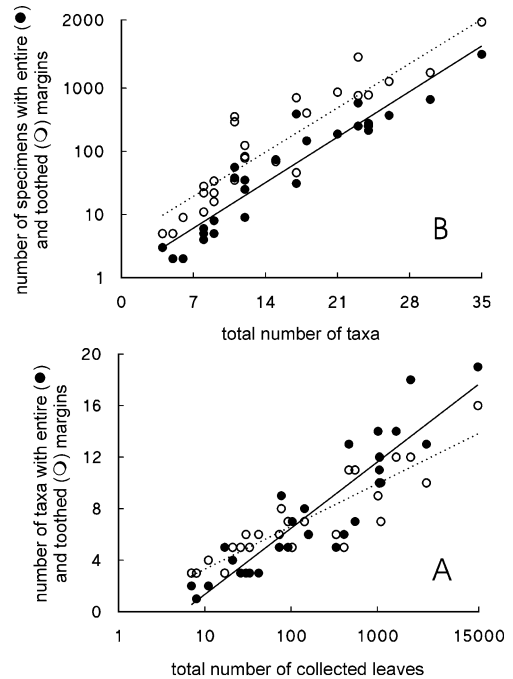

Fig. 4. (A) Correlation between total number of taxa and number of collected leaves at the locality Schrotzburg (note log scale for the *y*-axis). (B) Correlation between total number of collected leaves (note log scale for the *x*-axis) and number of taxa at the locality Schrotzburg.
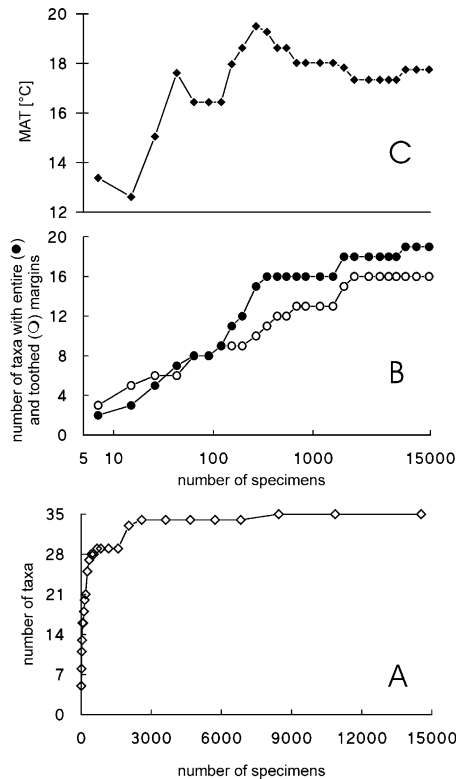
Fig. 5. (A) Sampling curve for the Schrotzburg flora. (B) Correlation between number of specimens (note log scale for *x*-axis) and number of taxa with entire and toothed margins from the sampling curve. (C) Development of LMAT with increasing specimen number (note log scale for *x*-axis). For further information see text.
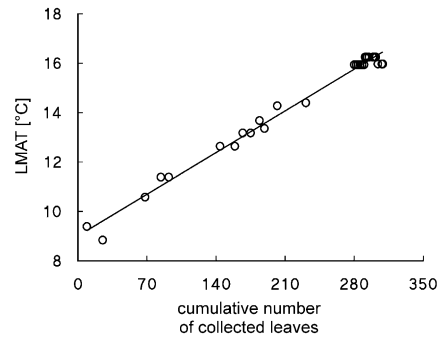

Fig. 6. Correlation between the cumulative number of collected leaves and the resulting LMAT at the locality Kleinsaubernitz.

may have influenced the species composition of the samples.

Similarly as was demonstrated for the Schrotzburg flora above (Fig. 4), it can also be seen that in Kleinsaubernitz the cumulative number of entire-margined specimens is lower than the cumulative number of toothed specimens (Fig. 8B), independent of the number of taxa. In contrast to the Schrotzburg flora here also the number of entire-margined taxa is always lower (Fig. 8A). However, it can be seen from Fig. 8A that the cumulative number of taxa with toothed margins increases not in a linear way. Therefore the increase in toothed taxa is at first more rapid than

To get an idea about the reason for the different temperature values for the subsamples of the Kleinsaubernitz flora, rarefaction plots have been calculated, according to Raup (1975), for the entire flora and the individual subsamples. As expected all three subsamples show a slightly lower species richness than the complete flora (Fig. 7). Interestingly there are no obvious differences in the curves for the individual subsamples, pointing to a different species richness for the middle subsample which could have been a possible explanation for the higher LMAT(kss). It seems that in this case [two floras with almost the same number of taxa (32 and 34) and specimen counts in the same order of magnitude (167 and 125)] other (taphonomic?) factors, which greatly influence the temperature reconstructions based on LMA,
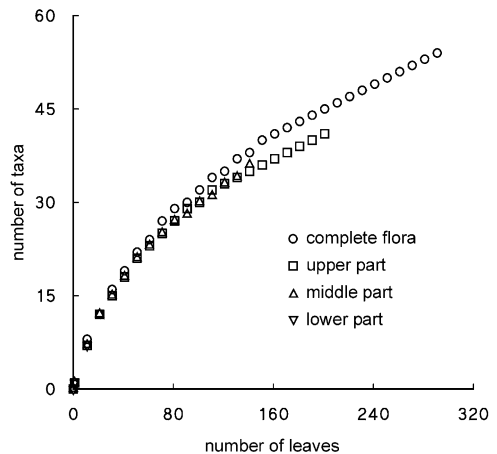

Fig. 7. Rarefaction curves for the Kleinsaubernitz flora and its (artificial) subsamples.

the increase in taxa with entire margins, leading to almost similar taxon numbers after about 300 collected specimens. This pattern explains why here LMAT is significantly correlated with the number of collected leaves. In comparison with Fig. 4 it can be speculated that, if we could collect more specimens we would probably get more entire-margined taxa than toothed taxa, leading to even higher values for LMAT.

These results also point to taphonomic filters favouring toothed leaf taxa in specimen-poor samples, which have great effects on temperature reconstructions based on LMA. However, there are also perturbations of LMAT by other taphonomic effects which are not correlated with species richness, as is indicated by the totally different LMAT values of subsamples with almost similar diversities (Table 2, Fig. 7).

Interestingly for both floras no great taphonomic or sampling effects can be seen with regard to CAT. Only at the locality Schrotzburg can a slight correlation between the width of the inter-

val of coexistence and the number of taxa in some layers be observed (cf. Fig. 7). At the locality Kleinsaubernitz no such correlation can be seen.

4. Discussion

Our study provides interesting information regarding the robustness of the different approaches used and their sensitivity to taphonomic and sampling effects. First of all it turns out that in our case studies the MAT estimates produced by LMA and CA are more or less consistent, but only when the standard deviation of the LMAT and the CA interval are considered. This emphasises that both approaches can produce reasonable results. It also corroborates statements by other authors (e.g. Wilf, 1997; Jordan, 1997) that the standard deviation has to be taken into account in all climate interpretations derived from LMA or other leaf physiognomic approaches. Furthermore, our analysis suggests that the climatic resolution of the LMA, characterised by a standard deviation of at least ±2°C, is only about half that of the CA which yielded coexistence intervals of mostly about 2°C in width (cf. Table 2, Fig. 2).

Another noteworthy result is the possible dependence of MAT on the mode of application of the LMA. Results for the whole Schrotzburg flora [LMAT(s)] are consistently 2°C higher than the means of the single layers [mean LMAT(sl)], and even about 2°C warmer than the CAT. However, at the locality Kleinsaubernitz no such differences can be seen between LMAT(k), the mean LMAT(kss) and CAT(k) (cf. Table 2). Though this difference between LMAT(s) and the mean LMAT(sl) at the locality Schrotzburg can be explained by a combination of taphonomic and sampling effects, as shown in Section 3, one should be aware of the underlying problem when analysing fossil floras which are more or less contemporary but come from different localities and facies. Presumably, there may be a difference in the LMAT (and probably CA) reconstructions if such floras are pooled and analysed as a single data set or if they are treated as individual floras. This problem also exists in calibration
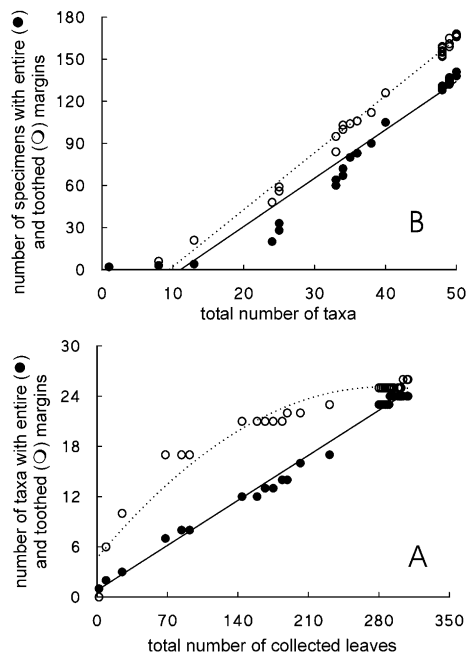

Fig. 8. (A) Correlation between total number of taxa and number of collected leaves at the locality Kleinsaubernitz. (B) Correlation between total number of collected leaves and number of taxa at the locality Kleinsaubernitz.

studies investigating the relationships between MAT and leaf margins in modern floras. As Wilf (1997) stated, LMA can be confused by small calibration data sets which are influenced by uneven species abundance patterns. Again the question is: is it justified to pool such small data sets, each coming from a specific microclimate and maybe differing MAT, and use all the taxa together for correlations with MAT? Or should these data sets be handled as individual samples? As our example from the Schrotzburg locality shows, these different approaches may give results which differ markedly from each other. It should be tested in modern floras which of these two approaches gives better results.

The contrasting pattern of the LMAT estimates as compared to the CAT reconstructions, especially at the locality Schrotzburg, is also of particular interest: when ignoring the standard deviation, the LMAT(sl) data seem to indicate an overall warming trend with highly variable MAT estimates ranging from 9 to 19°C when all layers are considered and from 13 to 19°C when layers with fewer than 15 taxa are excluded (cf. Fig. 2). In contrast, the CA reconstructs stable climatic conditions over the whole sequence, although the width of the coexistence intervals may vary; moreover, the larger coexistence intervals are correlated with a smaller number of taxa as was observed before for other floras (e.g. Pross et al., 1998). The data and correlation analyses presented in Section 3 provide good evidence that the LMA-derived temperatures are influenced by sampling and taphonomic artefacts: specimen-poor floras are characterised not only by a low species richness but also by an underrepresentation of entire-margined leaf types and hence yield mostly relatively low LMAT(sl) estimates (cf. Figs. 5 and 6). This result is not in conflict with the observation of Greenwood (1992) in his study of Recent leaf litter that not only the proportion of entire-margined leaf taxa but also the proportion of entire-margined leaf specimens is correlated with MAT.

The finding of a statistical bias towards fewer entire-margined species in specimen-poor samples is surprising to some extent but can possibly be explained by taphonomic effects. For example en-

tire-margined angiosperm leaves very often belong to evergreen species (e.g. Spicer, 1989). Hence, on average they have a longer life-span than the – mostly toothed – leaves of deciduous trees and are therefore numerically underrepresented in leaf litter and in taphofloras. This pattern is clearly evident in Figs. 4 and 7: in all layers the proportion of entire-margined leaf specimens is well below the proportion of toothed leaf specimens, in the Schrotzburg flora even in those layers in which entire-margined leaf taxa predominate (Fig. 4). However, this scenario is not necessarily true for all taphofloras. In some taphofloras leaves of evergreen species may represent the majority of collected leaves (e.g. Kvacek and Walther, 1995; Walther, 1998). Such overrepresentations can possibly be caused by the fact that evergreen trees also periodically shed their leaves, but not always in a strict annual rhythm (Ebel et al., 1980), like most deciduous trees. In extreme cases such shedding events may lead to taphofloras which consist of virtually a single taxon, which, however, must not be exclusively taxa with entire-margined leaves (e.g. Uhl and Walther, 2000). In some cases the slower biodegradation of tough, coriaceous evergreen leaves may also lead to an overrepresentation of such leaves.

In order to compensate for the observed taphonomic effect, LMA requires a specimen-rich sample. The curves in Fig. 5 seem to indicate that at least at the Schrotzburg locality more than 1000 specimens are required before a more or less stable number of taxa and proportion of entire-margined leaf taxa is attained. This interpretation, however, is not fully justified because the best-fit regressions between the number of specimens and the number of taxa as well as between the number of specimens and the proportion of entire-margined taxa are logarithmic and not asymptotic. Hence, the pattern of the regression curve cannot be used to infer the minimum sample size required because the form of the logarithmic regression curve shows a self-similarity which is independent of the sample size. Correspondingly, plotting the number of entire-margined and toothed taxa versus the logarithm of the total number of specimens results in a linear regression curve shown

in Fig. 4A. The fact that this regression line shows no asymptotic behaviour at all indicates that even with 15 000 specimens we are far not only from the real species richness (which is not surprising considering that the maximum species richness recorded for the Schrotzburg flora is only 35 taxa) but also from a stable proportion of entire-margined taxa.

This result is indeed frustrating. It implies that a lot of effort has to be put into sampling before a sound LMA becomes possible. Obviously, sampling a taphoflora for LMA should always be accompanied by the construction of sampling curves similar to Figs. 5A and 6. Correspondingly, our study adds another uncertainty to all those published LMAs which are based on small sample size or which provide no information about sample size at all. In fact, many published applications of LMA do not include information on sample size (e.g. Povey et al., 1994; Davies-Vollum, 1997) or sample size is well below 1000 specimens [e.g. Wiemann et al., 1998 (>500); Gregory, 1994 (177); Gregory-Wodzicki, 1997 (537)]. Presumably, previous LMAs without sampling control may underestimate or overestimate the proportion of entire-margined leaves and hence MAT, depending on taphonomic effects. Therefore, future applications of the LMA should be restricted to those leaf floras for which sample size, which depends on the original species richness of the source flora, is known to be sufficient, as has already been stated by previous authors (e.g. Burnham, 1989, 1994a,b; Burnham et al., 1992).

Finally, the taphonomic and sampling effects observed in our study raise questions regarding the validity of the two standard techniques used to compile calibrating data sets for LMA. One technique consists of collecting leaves from forest vegetation in order to obtain a 'representative', species-rich sample with at least 20 species (cf. Wolfe, 1993). According to another strategy published floral lists of Recent vegetation stands are evaluated with respect to the leaf margin types (e.g. Wilf, 1997; Jacobs, 1999; Wiemann et al., 1998). Theoretically, both strategies should yield calibration data sets suitable for LMA of fossil floras as long as the Recent leaf floras used for calibration show the same sensitivity to taphonomic and sampling effects as the taphofloras. However, according to our results, this latter assumption is questionable in many cases.

Obviously, further studies regarding the influence of taphonomy and sampling on LMA and other leaf physiognomic approaches are required. It may be expected that the observed taphonomic and sampling effects are less serious problems to multivariate leaf physiognomic approaches using many uncorrelated leaf parameters (e.g. CLAMP); this hypothesis, however, needs to be tested. Moreover, the common strategies to compile calibrating data sets for leaf physiognomic approaches have to be scrutinised if they yield calibrations which can reasonably be applied to taphofloras.

Interestingly, it turned out that the CA was only marginally influenced by the observed taphonomic and sampling effects. Here only the width of the intervals of coexistence was wider in some samples (but not in all) with a low number of taxa, an effect which has been reported before (e.g. Pross et al., 1998). From a certain point of view it would be easy to argue, based on this observation, that this method is much more robust than LMA or other leaf physiognomic methods and therefore more reliable. However, this can still be called into question: a sceptic could argue that this method is not robust, but insensitive to small climatic changes, at least in some cases. However, our analysis cannot solve this particular problem and more investigations on this subject are needed to test (verify or falsify) the proposed reliability of the CA.

Acknowledgements

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