ELSEVIER

Review of Palaeobotany and Palynology 91 (1996) 1–21

REVIEW
OF
PALAEOBOTANY
AND
PALYNOLOGY

# Criteria to distinguish parautochthonous leaves in Tertiary alluvial channel-fills

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Received 15 November 1994; revised and accepted 19 May 1995

**Abstract**

The plant taphonomic character of fluvial channels in the Upper Oligocene strata of the Weißelster basin, near Borna, Germany, has been studied to determine if concentrated macrofloral-bearing intervals represent allochthonous or parautochthonous accumulations. Single bedding planes or leaf accumulations that represent a single cluster of leaves, the taphonomic signature of leaf fall, were examined representing 1.6 m$^2$ of surface area. Unequivocal autochthonous elements, such as the floating water fern, *Salvinia*, were excluded from the data set. Each assemblage was evaluated separately. Criteria useful in identifying parautochthonous leaf assemblages include: (1) a heterogenous mixture of plant parts with phytoclast concentration increasing upsection in the fill; (2) a log-normal distribution of leaf sizes in the assemblage; (3) a gaussian or log-normal distribution of leaf size in all dominant taxa; (4) a random directional orientation of leaves or, in the case of taxodiaceous conifers, short shoots on any particular bedding surface; and (5) a biased leaf-surface orientation (one leaf surface predominantly facing upwards). Actualistic data are provided as justification for establishing these criteria.

## 1. Introduction

The preservation of local elements near their growth site affords an opportunity to assess plant community structure and potentially resolve spatial distribution. Autochthonous assemblages provide the best means of fixing plant communities in space and time (e.g. Basinger, 1991; Wing et al., 1993). Parautochtonous assemblages (those having been transported from the death or discard site but remaining within the original habitat; Behrensmeyer and Hook, 1992), on the other hand, provide a more representative sample of riparian vegetation. The identification of parautochthonous plant parts generally has been a subjective exercise. This is particularly true of well-preserved Tertiary fossil plants recovered from fluvial channel fills in alluvial plain settings. The life habits of taxa found in these assemblages include those that are fully aquatic (the water-fern *Salvinia*), semi-aquatic (*Sparganium*), flood-tolerant (the bald cypress *Taxodium*), or fully terrestrial (*Fagus*; Kvaček and Walther, 1991; Mai and Walther, 1991). Most phytoclasts, those with affinities to taxa living in par-

*SSDI* 0034-6667(95)00071-2

tially flooded or fully terrestrial environs, preserved within the fine-grained clastic portion of a channel-fill sequence (commonly referred to as clay lenses), have been considered, a priori, to have originated from vegetation growing in close proximity to the depositional site (e.g. Potter and Dilcher, 1980; Wing, 1984; Christophel and Greenwood, 1987, 1989). As a result, such assemblages have been regarded as reflecting the contribution from local vegetation (Greenwood, 1991) and utilized accordingly in paleoecological and paleoclimatological reconstructions.

The sedimentary sequence characterizing the abandonment phase of a river channel reflects the hydrodynamic conditions under which sediment and phytoclasts accumulated (for example, see differentiation by Burnham, 1990). In most instances, plant part accumulation in this setting conforms to our preconceived ideas, but anomalies do occur. For example, accumulations of logs within a channel-fill usually are considered as one good criterion to assist in distinguishing the base of channels. Such accumulations are believed to represent emplacement via bedload transport, subsequently overridden by the migration of down-river bedforms. When masses of logs are preserved near the top of a channel-form structure, though, one of several different mechanisms may have been responsible for their emplacement and preservation (Liu and Gastaldo, 1992). Not all within-channel log accumulations have the same origin. This is also true for other phytoclast assemblages within the same depositional regime (see Gastaldo and Huc, 1992). The stratigraphic position of the plant assemblage in association with the sedimentological features of the channel-fill must be evaluated together in order to provide the most accurate assessment of phytoclast origin.

We have examined plant fossil assemblages within the Upper Oligocene Thierbach Schichten, a fluvial complex located in the Weißelster basin, Germany (Eißmann, 1968; Bellman et al., 1982). Well-preserved adpressions (Shute and Cleal, 1987) occur within the sedimentary fills of abandoned channel-forms. The purpose of this paper is to present our results from one locality in the Weißelster basin, along with data from actualistic studies, in an effort to define objective criteria useful in identifying these assemblages as being parautochthonous in origin. These criteria can be applied directly to Cretaceous–Tertiary–Quaternary plant fossil assemblages in similar depositional settings.

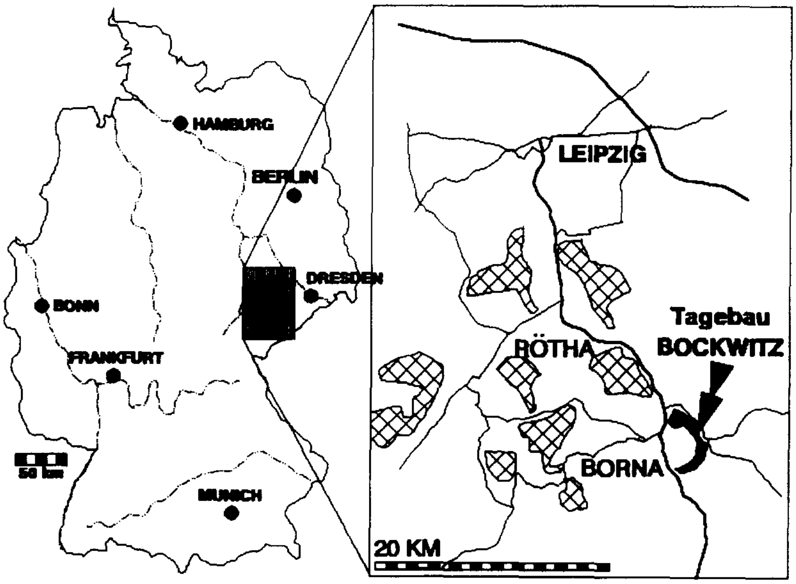

Fig. 1. Map indicating the geographic position of Tagebau Bockwitz, near Borna, Germany. Cross-hatched areas represent active mines in 1991.

## 2. Materials and methods

### 2.1. Fossil data collection

One continuous section of the channel-fill sequence, approximately 1 m in thickness and 0.25 $m^3$ in volume, was excavated from within an erosional ditch in Tagebau Bockwitz, Saxony, Germany (Figs. 1 and 2). Blocks were subdivided vertically for various subsampling regimes (systematic paleobotany, palynology, organic geochemistry; Walther et al., 1992), with one complete section subsequently slabbed and smoothed. Tracings were made directly onto transparent acetate in order to evaluate the sedimentological sequence of, and disposition of phytoclasts within, the channel-fill. Larger prepared bedding surfaces, collected in the mid- to late-1980s and curated at the Staatliches Museum für Mineralogie und Geologie, Dresden, were also studied. These slabs are labelled BOB (Borna — Ost Bockwitz). All large prepared surfaces were examined, totalling a surface area of 1.6 $m^2$, because of the limited area of any particular bedding surface within collected blocks of the channel-fill sequence. Unfortunately, orientations of the curated slabs relative to magnetic north were not recorded when these specimens were collected.

A variety of phytotaphonomic data were recorded for the channel-fill sequence, excluding known autochthonous (fully aquatic and semi-aquatic) elements such as *Salvinia*. These data included the spatial arrangement of individual leaves and leaf clusters (leaf mats sensu Burnham, 1990) relative to the distribution of lithologies. Individual bedding surfaces or leaf clusters (defined as a group of stratigraphically successive leaves spaced not more than 3 mm apart) were examined, photographed, and traced. Entire leaves were systematically identified (Mai and Walther, 1991), and their length (from the point of petiolar attachment to leaf apex) and width (widest part of the leaf) measurements recorded. Because *L*:*W* relationships are an accurate reflection of leaf area (Burnham, 1986), leaf outlines were not digitized to calculate leaf area. Length and width leaf measurements of several taxa (*Fagus saxonica*, *Carpinus grandis*, *Alnus rostaniana*, *Ulmus carpinoides*,

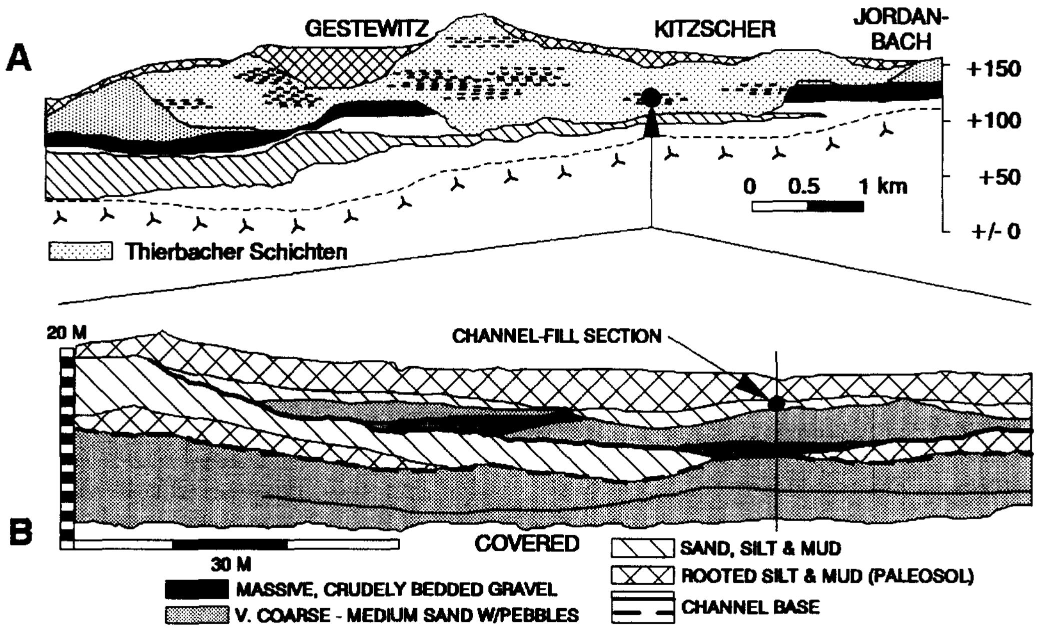

Fig. 2. (A) Generalized stratigraphic section of Paleogene strata in the Weißelster Basin showing the distribution of the Thierbacher Schichten. (B) Partial section of Tagebau Bockwitz mine highwall indicating lithological relationships. Samples described in this report were recovered from indicated channel-fill section.

*Ulmus drepanodonta*, and *Liquidambar europaea*) were made from specimens in the curated collection to supplement the limited leaf size distribution data set obtained from bedding surfaces. To test whether or not the distribution of $L:W$ data was gaussian, the Kolmogorov-Smirnov analysis was used. The planar orientation of individual leaves was determined for each bedding surface examined. Orientation measurements were made in the direction of the leaf apex, in the case of individual laminae, in the direction of the terminal leaflet, in the case of compound leaves (e.g. *Cyclocarya cyclocarpa*), or towards the apex of short shoots (i.e. *Taxodium dubium*). Data were organized into 15° intervals and plotted as rose diagrams. The disposition of individual leaves relative to adaxial or abaxial side up also was recorded. The exposed leaf surface was determined to be abaxial if venation was in surficial relief.

### *2.2. Modern analog data collection*

Observations were made in an oxbow lake of the Macareo River in the middle delta plain of the Orinoco delta, Venezuela, during the 1987 field season (Pfefferkorn et al., 1988; Rabold, 1990). The oxbow is an open system, with the downstream end connected with the active river. The upstream end is closed, separated from the active river by accumulated sediments that are now vegetated by grasses, shrubs and small trees. Data collection consisted of grab samples from the sediment–water interface throughout the channel length, and cores of 3 m length (3 cm and 5 cm diameter corers) in shallow water near the closed end of the oxbow.

A large diameter coring device (15 cm diameter; Burnham, 1988) was used to recover leaves at the sediment–water interface in an inactive channel of the Tensaw River, AL, USA, in March 1993. Logisitics within the Wash Branch of Dennis Lake, Basin Quadrangle, AL, resulted in the recovery of a single core. The orientation of angiosperm leaf apices and taxodiaceous short shoots relative to North were measured with a Brunton compass. Orientation data were compiled into rose diagrams. Data on adaxial/abaxial distribution were not taken due to severe degradation of the leaves. In order to obtain adaxial/abaxial data, recently fallen leaves were investigated in an alluvial swamp adjacent to Maple Bayou, the Basin Quadrangle, AL. All leaves were collected from shallow water depressions in the swamp floor and originated from either the air–water or the sediment–water interface. A select group of *Quercus laurifolia* leaves, all of which were found with their adaxial surface facing upwards, were returned to Auburn University where they were used in experiments to determine if these leaves had a predisposed preferential orientation (see below). An additional adaxial/abaxial data set was noted from abandoned and infilled channels of the Danube River alluvial plain (Lobau) to the east of Vienna, Austria.

To confirm the validity of preferential leaf adaxial/abaxial orientation, a number of different genera were dropped from various heights under natural conditions. *Ligustrum vulgare* and *Ilex opaca* (evergreen) were dropped from a height of 9.2 m at Auburn University. *Ulmus campestris* (s.l.) and *Populus alba* were dropped from approximately 5 m from a hunting blind in the Lobau.

Additional adaxial–abaxial orientation data sets were collected from 0.5 m$^2$ quadrats of forest floor litters in the Göttinger Wald, a temperate forest in central Germany, and a temperate forested area in Auburn, AL. The Göttinger Wald data were collected in July 1992 and represented the previous autumnal loss. Leaves were adhering to one another in the litter. The data set from Auburn was collected during November 1992 during Fall. A sample of 501 *Juglans regia* leaflets were examined in November 1993 from beneath a single tree in Neckargemünd, near Heidelberg, Germany. A data set of 165 *Acer platanoides* leaves was collected from a mixed hardwood forest near Dresden, Germany, during September 1993. A data set for macrophylls was collected in a tropical peat swamp forest in Sarawak, East Malaysia, in October–November 1992. Due to the size of the macrophylls, there was no limit set on the quadrat size and this data set reflects all fallen leaves accessible around a single parent tree.

## 3. Thierbach Schichten

The Upper Oligocene Thierbach Schichten is an unconformable unit overlying Upper Eocene

(Oberflöz II) and Lower Oligocene (Oberflöz IV) lignites within the Weißelster basin (Brause et al., 1989; Fig. 2). It is interpreted as a fluvial-sand dominated unit deposited within a fully terrestrial setting (Eißmann, 1968). The unit thickness is variable across the basin, but may be greater than 10 m east of Gestewitz, and thins eastward and westward towards the edges of the basin. It is overlain by Quaternary sediments.

We have studied the Thierbach Schichten exposed in Tagebau Bockwitz, an abandoned open-cast mine east of Borna (Fig. 1). Here, the Thierbach Schichten is composed of two coarse-clastic fluviatile complexes (Fig. 2). The lower fluvial complex is in erosional contact with Oberflöz II; the upper fluvial complex is in erosional contact with a paleosol overlying the lower fluvial complex. It is within the upper fluvial complex that macrofloral assemblages are preserved within channel-fill sequences.

The upper fluvial complex is composed of several distinct lithofacies. Its basal contact is sharp and erosional, and the lithologies directly overlying the contact are variable along the strike of the exposure. These include coarse pebble conglomerates and fine to medium cross-bedded sand. The section fines upward from lenticular bodies of cross-bedded pebble-conglomerates and pebbly-sand to coarse sand. A sharp contact exists with overlying sandy- or silty-mud lithofacies, that are restricted within small channel-form structures. Three of these channel-forms are seen along the highwall (Fig. 2), the largest of which has a width of approximately 35 m.

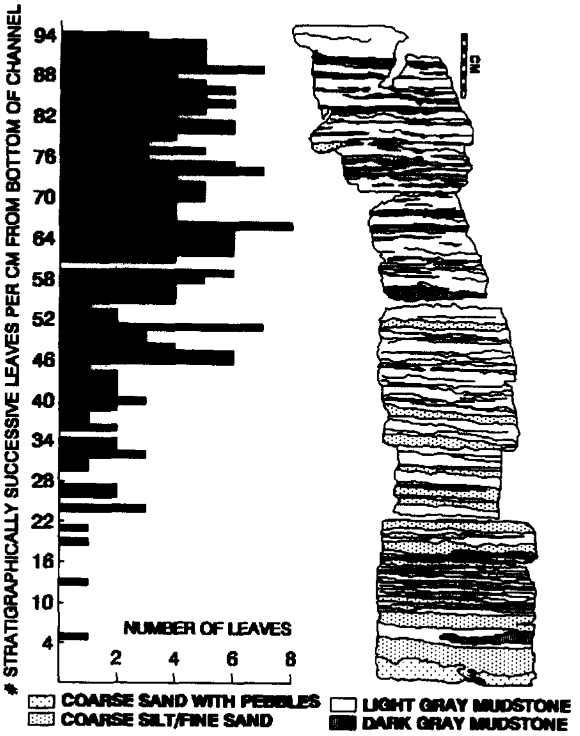

Fig. 3. Detailed lithological section of the abandoned channel-fill in Wasserriß am m36 depicting a fining-upwards sequence. Graph shows the number of leaves per vertical centimeter of section. Leaves occur in clusters of 3–5.

The channel-fill sequence within each of these scours fines upward (Fig. 3). The basal part of the fill is composed of a bed (up to 7 cm) of essentially fine sand which is poorly sorted. Isolated ripples and clasts of coarse-sand occur in a fine-sand matrix (Munsell color 5 Y 6/1). This fines upward into a fine-sand with isolated coarse sand clasts. In addition, small quartz pebbles may be dispersed throughout this bed. There is evidence of soft-sediment deformation as micro-flame structures are present. Overlying the basal bed are fining-upward, generally planar laminations of fine-sand and/or silt (Munsell color 5 Y 6/1) alternating with clay. Light (Munsell colors 5 Y 6/1 and N6) and dark (Munsel color N5) clay beds occur, with dark-colored beds concentrated near the top of the channel-fill. Fine lamination characterizes the clay fraction, whereas low amplitude ripple crests may be present at the contact between coarser and finer sediments. Horizontal and shallow vertical burrows filled with clean sand occur near the base of the channel-fill. The silt and clay fractions increase vertically, with fine sand found in isolated beds up to 0.5 cm thick or starved ripples. Higher in the section, starved ripples are composed of very fine sand and coarse silt. These may be slightly burrowed.

A basal lag of wood may be present above the scour contact. Vertical woody rooting structures penetrate the entire fill sequence. They cross-cut, but do not destroy, the adpression fossil flora that is preserved within the uppermost part of the preserved channel fill.

A thick mudstone, 10–15 m, overlies this channel complex and is heavily bioturbated by rooting. It is not possible to trace the edges of the channels into this overlying unit. Primary sedimentary structures are no longer visible, but secondary features, such as slickensides, are common. These deposits represent a thick paleosol formed within a reestablished alluvial plain setting.

### 3.1. *Phytoclast distribution*

Primary (those deposited contemporaneously with sediment) and secondary (those introduced afterwards) plant parts comprise the phytoclast component in the channel-fill sequence. The primary macrofloral elements include logs, branches, leaves, fruits, seeds, and rare flowers; secondary elements are vertical and subhorizontal woody roots, some of which penetrate to near the base of the channel-fill. The disposition of primary plant parts is only considered here.

Large (30 cm diameter) prostrate logs, where present, are restricted to the base of the sequence. These have not been found in any other part of the channel-fill, albeit there is limited available exposure. The wood component increases up section as smaller diameter (up to 3 cm) lignitized branches become more abundant near the top. Those that have been examined in the field are variously oriented and are not found to be concentrated on any single bedding surface or horizon. Overall, the wood component does not comprise a quantitatively significant proportion of the assemblage.

Leaves and taxodiaceous short shoots make up the vast majority of preserved specimens (> 15,000 leaves exposed on 21 m$^2$ surface area), but are not distributed evenly through the sequence (Fig. 3). Scattered leaf fragments are first seen where there is an increase in the proportion of clay-sized sediment. Leaves are virtually absent in the relatively coarser, basal channel fill. The first cluster of leaves, found 57 cm upsection from the base, is preserved within a thick (1.8 cm) homogenous light-gray claystone. These leaves are not directly overlying or associated with the coarser clastics. This disposition continues from here to the top of the section, with an increasing density of leaves per linear centimeter (Fig. 3). Rarely are leaves found within or draping coarser clastic ripples or coarser planar laminae, and they are not found to be more clustered in the darker-gray clay beds. Concentrated leaves occur within clusters up to as many as 8 leaves (generally clusters are comprised of 3–5 leaves), and appear in the form of overlapping individual leaves when bedding planes are exposed. Leaves comprise the greatest plant part component as assessed by individual numbers. Fruits and seeds are interspersed within the leaf assemblage and constitute only a small fraction of the total biomass (2500 specimens recovered from 200–300 kg washed sediment; Mai and Walther, 1991).

Although we do not have data to discuss the spatial resolution of leaves distributed laterally in the channel fill, due to limited exposure, it appears that there are taxonomic patterns in the collection. Some blocks are dominated by leaves that represent one or two taxa only. For example, there are large specimens on which only *Fraxinus saxonica*, *Populus germanica*, *P. zaddachii* or *Cyclocarya cyclocarpa* are preserved. These leaves are found to be individually concentrated on the exposed bedding surface by species, with few additional taxa mixed with them.

### 3.2. *Leaf size distribution*

These results are based on observations from both curated large slabs and individual specimens because of the low number of entire leaves of any taxon preserved on either the large slabs or within the channel section. Two trends are seen when leaf length is plotted against leaf width for the eight most common taxa occurring on bedding surfaces (Figs. 4 and 5). Palmate leaves are plotted separately and their distribution reflects the influence of leaf morphology on the data set. Linear leaves (oblong–ovate–elliptical) plot along a gentle gradient. Both data sets illustrate a leaf size distribution from very small to large leaves. When leaf populations of individual taxa are plotted and regression analyses run on each data set, the same power trend ($y = ax^b$; $a > 0$) occurs (Fig. 5). When the $L$:$W$ relationships of each data set are normalized, it is evident that the leaves in the assemblage are not normally distributed (Fig. 6). This is con-

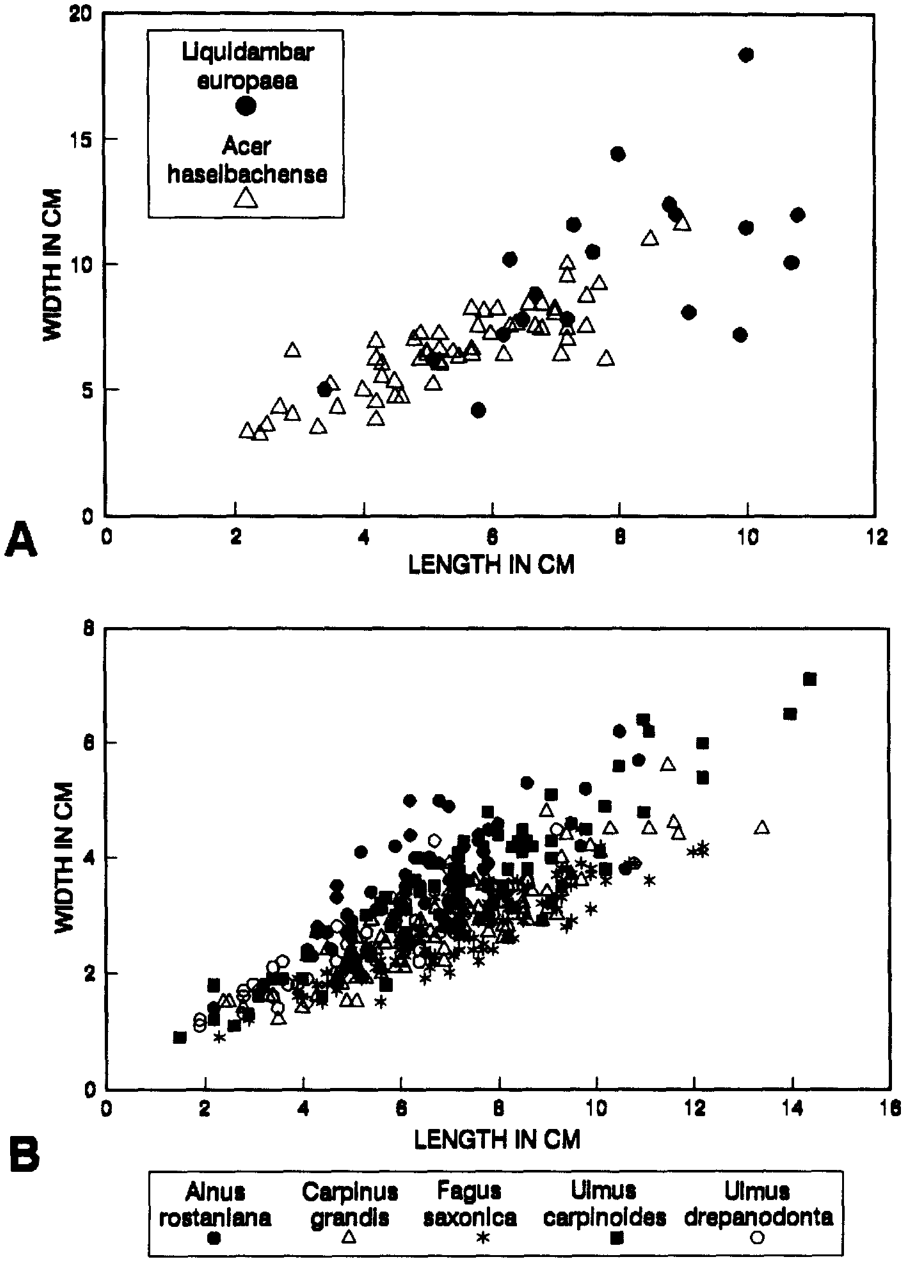

Fig. 4. (A) Length vs. width plot for palmate leaves of *Liquidambar europaea*, *Acer haselbachense* curated in the Dresden collections. (B) Length vs. width plot for all linear–ovate–elliptical leaves of *Alnus rostaniana*, *Carpinus grandis*, *Fagus saxonica*, *Ulmus carpinoides*, and *U. drepanodonta* curated in the Dresden collections.

firmed by using the Komolgorov-Smirnov nonparametric analysis to test for congruence with a gaussian curve. Both palmate and linear leaves are found to reflect a log normal distribution, with leaves of intermediate ratios most common.

### *3.3. Leaf orientation*

The orientation of taxodiaceous shoots and angiosperm leaves identifiable to taxon, as well as leaf fragments of uncertain affinity, were assessed

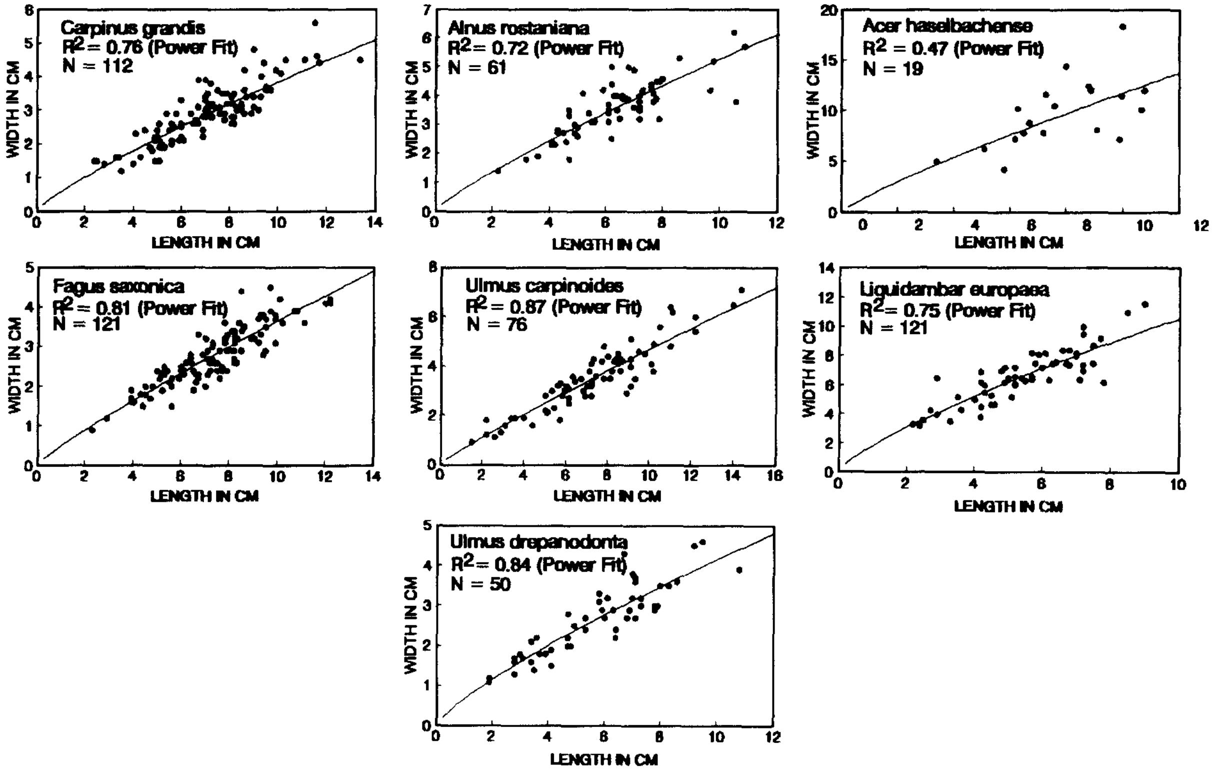

Fig. 5. Length vs. width plots of each dominant taxon found in the Dresden collections. Power fit regression lines are provided along with $R^2$ values.

for each curated slab. Because each slab was collected in the field unoriented relative to magnetic north, each leaf orientation data set must stand alone. Three slabs, each with greater than 60 specimens per bedding surface or leaf cluster, will be used as examples of the variability in plant part orientation. Angiosperm leaves predominate on specimens BOB2725 and BOB2251 : 4; taxodiaceous shoots predominate on specimen BOB2252 : 1. Data are presented in Appendix 1 for slabs on which there are fewer than 60 specimens per bedding surface or leaf cluster.

Based on the rose diagram plot of all leaves and short shoots measurements for specimen BOB2725 it is obvious that there is no preferential alignment of plant parts (Fig. 7). When the rose diagram for *Taxodium* shoots is compared with that for angiosperm leaves, a similar dispersed pattern is seen. Visually there is a slight preferential orientation in the northeast quadrat of the *Taxodium* shoot plot, but there is no statistically significant bias towards any one quadrat ($\chi^2=2.4$; $P=0.05$; 3 d.f.). The same is true for the plot of only angiosperm leaves. It is difficult, in most instances, to describe anything meaningful concerning the orientation of leaves of individual taxa due to low numbers of specimens per taxon. In the case of *Carpinus grandis*, though, a sufficient number of specimens exist on this slab and their orientation reflects the random distribution of the population.

Specimen BOB2251 : 4 (Figs. 7 and 8) depicts the opposite extreme where the plot of all leaves demonstrates a non-random population orientation. There is a primary bias towards the southeast quadrat, and a secondary bias towards the northeast quadrat, caused mainly by the distribution of the *Taxodium* shoots within the population. It is true, though, that the angiosperm leaf data set, itself, exhibits a non-random orientation ($\chi^2=7.17$; $P=0.05$, 3 d.f.). Again, plots of individual

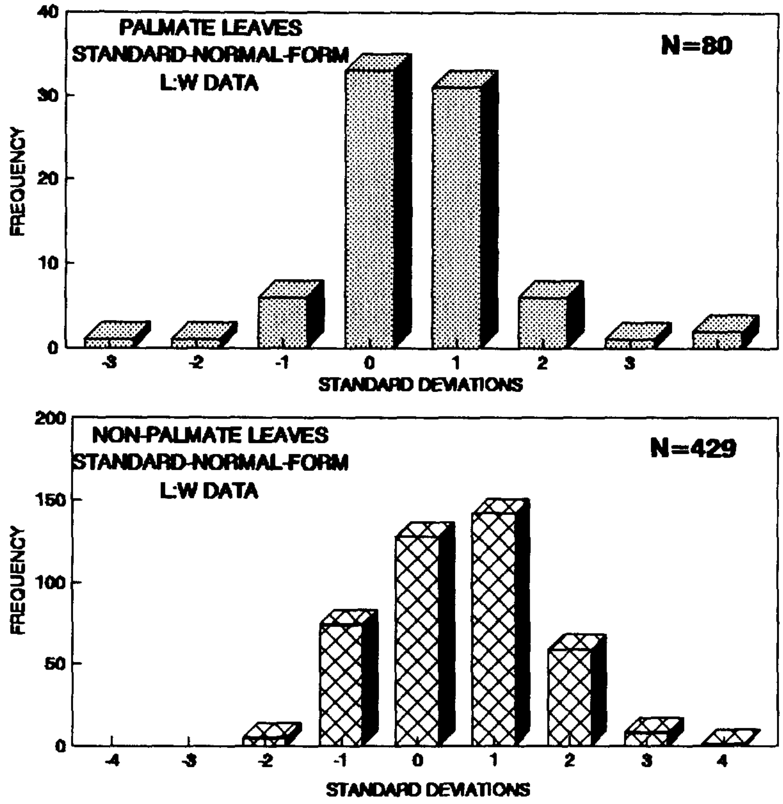

Fig. 6. Normalized length vs. width distributions of palmate and non-palmate leaves in the Dresden collections. Note that distributions are not gaussian.

taxa are not definitive with regard to spatial arrangement because of low specimen numbers per taxon.

The overall leaf population of specimen BOB2252:2 reflects a random orientation, the result of a high number of *Taxodium* shoots that show a non-preferential orientation (Fig. 7). The distribution of angiosperm leaves, alone, reveals a preferred distribution to the northeast and southeast quadrat (significant $\chi^2 = 7.5$; $P = 0.5$; 3 d.f.). Individual taxa, when plotted alone, show no distinctive preferential orientation. Again, the numbers of specimens per taxon are low.

The position of each angiosperm leaf relative to adaxial or abaxial side up was evaluated for each slab (Table 1). It is believed that slabs taken from the field in the 1980s were maintained in stratigraphic order and that split block surfaces reflect the original orientation of the rock. An oriented channel sample recovered in 1991 (Walther et al., 1992) was used as an independent check on leaf orientation. Results from this limited channel sample support this contention. It was found in all instances that the abaxial (lower) leaf surfaces were more prevelant in the population of any one slab than adaxial (upper) surfaces. Observed adaxial:abaxial ratios range from 1:1.28 to 1:4.25. Several specimens statistically conform to a theorectical 1:1 adaxial:abaxial ratio, but most samples conform better to a theorectical 1:1.7 adaxial:abaxial ratio (Table 1).

## 4. Modern analogs

### 4.1. *Abandoned channels*

The Macareo oxbow lake is an active system because the downriver end is open to the active

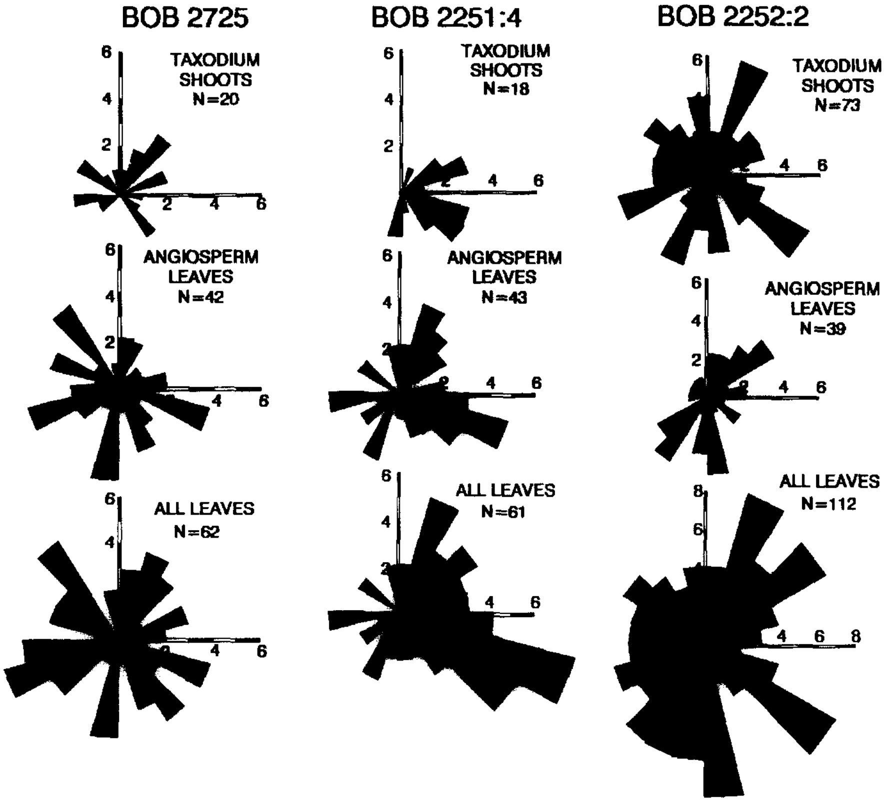

Fig. 7. Planar orientations (relative to arbitrary north) of *Taxodium* shoots and angiosperm leaves preserved either on a single bedding plane or within a single cluster of leaves for three slabs curated in the Dresden collections. Each slab preserves more than 60 leaves.

distributary (see Pfefferkorn et al., 1988). The channel cutoff has occurred within the past 35 years and, because of the recent abandonment, channel depth is variable. Depth at the downstream end is 7 m; the greatest depth is found near the channel center (13 m); and the channel shallows continuously from the central part of the channel to the closed end where it is vegetated. Floating plants are found along the channel margins in the quieter water areas, and in the closed portion of the channel these plants often cover the entire water surface. Sediments in the channel fill consist of fine sands near the downstream end, fining to clays at the closed end. An idealized channel fill consists of basal fine sands grading upwards to clay. Phytoclasts are uncommon in the sands, but increase in frequency in the clay. Stratified leaves and leaf parts were found throughout the length of the cores taken in shallow water. Leaves occurred in some grab samples where clay was encountered, and it is interpreted that these accumulations were localized in lenses (Rabold, 1990). Leaves represent contribution from the gallery forest adjacent to the channel rather than being allochthonous elements introduced from the Macareo river. This difference is easy to determine in the field. In general, parautochthonous leaves are found to be blackened, entire, with little degradation, allowing for their identification. Allochthonous leaves, on the other hand, are decomposed into small pieces which preclude their identification. Degradation occurs very rapidly in this tropical environment and this explains the absence of recognizable macroscopic floating vegetation in the sediments. These plants are buoyant, remaining at the water's surface where they

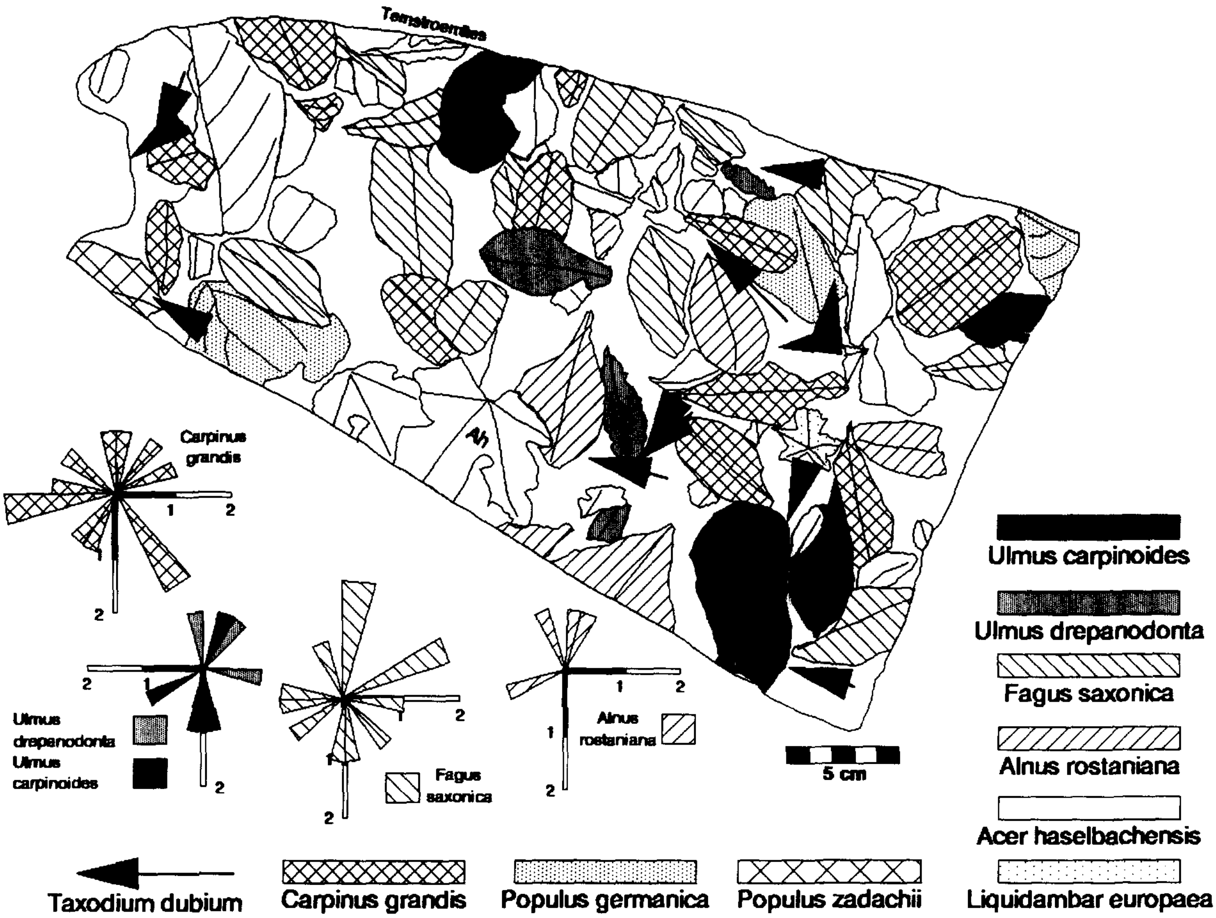

Fig. 8. Bedding surface of specimen BOB 2251:4 showing distribution of taxa. Planar orientations are provided for five principal taxa.

undergo decay. Only fibers that have been attributed to the decay products of these plants have been found in the sediments.

The stratigraphic distribution of leaves within abandoned channels is exemplified by x-radiographs from vibracores of False River, Louisiana (pers. observ. 3/87; Farrel, 1989). Leaves occur in accumulations or clusters composed of 3–5 parts, generally separated by a thin interval of fine clastics. These represent seasonal (autumnal/drought) leaf fall of riparian vegetation. Interspersed with leaves may be woody branches and twigs that show no predictive or climate-induced pattern.

An oriented core was recovered near the channel margin of Wash Branch at a depth of circa 90 cm. The package of leaves at the sediment–water interface consisted of 3–5 stacked (stratified) laminae interbedded with fine silt. These were the remains of previous autumnal–winter dehiscence (*Quercus* leaves are retained until mid–late winter before being shed). The recorded orientation of leaf (angiosperm) and shoot (taxodiaceous) apices were plotted in rose diagrams (Fig. 9) as individual and combined data sets. Angiosperm leaf orientation visually indicates a WNW and ESE direction, but a $\chi^2$ test indicates no significant quadrat preference in orientation ($\chi^2 = 2.42$; d.f. = 3; $P = 0.5$). This visually deceptive orientation does not conform with the course of the channel indicating little or no influence by water flow. Too few taxodiaceous shoots were found to evaluate their orientation

Table 1

Adaxial : abaxial ratios of angiospermous leaves preserved on large slabs evaluated in Dresden, Germany. Observed ratios are compared statistically to theorectically predicted 1 : 1 ratio and the 1 : 1.7 ratio observed in the forest floor litter of the Göttingerwald

| Borna Ost-Bockwitz sample number | Adaxial side up | Abaxial side up | ad : ab Ratio | $\chi^2$ 1 : 1 | $\chi^2$ 1 : 1.7 |
|---|---|---|---|---|---|
| BOB 2725 | 21 | 28 | 1 : 1.33 | 0.73 | 0.55 |
| BOB 2695 | 18 | 23 | 1 : 1.28 | $2.75^a$ | 0.66 |
| BOB 2121 | 3 | 11 | 1 : 3.60 | $3.50^a$ | 1.94 |
| BOB 2251.1 | 9 | 14 | 1 : 1.55 | 0.80 | 0.05 |
| BOB 2125 | 5 | 9 | 1 : 1.80 | 0.64 | 0.08 |
| BOB 2254.2 | 12 | 29 | 1 : 3.41 | $6.24^{a,b}$ | 1.29 |
| BOB 2187.1 | 7 | 10 | 1 : 1.43 | 0.24 | 0.06 |
| BOB 2376.1 | 7 | 10 | 1 : 1.43 | 0.24 | 0.06 |
| BOB 2726 | 6 | 10 | 1 : 1.66 | 0.56 | 0.07 |
| BOB 2252.2 | 12 | 37 | 1 : 3.08 | $11.76^{a,b}$ | $3.71^a$ |
| BOB 2251 | 6 | 11 | 1 : 1.83 | 0.94 | 0.06 |
| BOB 2251.4 | 8 | 34 | 1 : 4.25 | $14.88^{a,b}$ | $7.29^{a,b}$ |

[a] $\chi^2$ significant at $P=0.10$.
[b] $\chi^2$ significant at $P=0.05$.

reliably. Results of a $\chi^2$ analysis on the quadrat distribution of the combined data set showed that there is no statistical preferential orientation ($\chi^2=6.43$, d.f. = 3, $P=0.5$).

Abaxial : adaxial ratios were determined from leaves that had fallen into abandoned channels of the Danube River for three taxa of different shapes (*Salix alba* — lanceolate; *Populus alba* — palmate; *Quercus robur* — lobate; Table 2). In the case of *Salix*, the overall pattern has a statistically significant abaxial preference greater than 1 : 1 ratio (tested against a 1 : 1.7 ratio, the empirical ratio observed first in the Göttinger Wald). *Populus* and *Quercus* both statistically conform to a 1 : 1 ratio, but data for *Quercus* also statistically conform to a 1 : 1.7 ratio.

Angiosperm leaves found in shallow depressions and channels (maximum 1 ft depth) within the swamps of Maple Bayou do not conform to a 1 : 1 adaxial : abaxial ratio (Table 2). One data set of a random sample of leaves shows a preference to abaxial surface up, but in a ratio less than 1 : 1.7. When only leaves of *Q. laurifolia* were examined, a preference towards adaxial surface

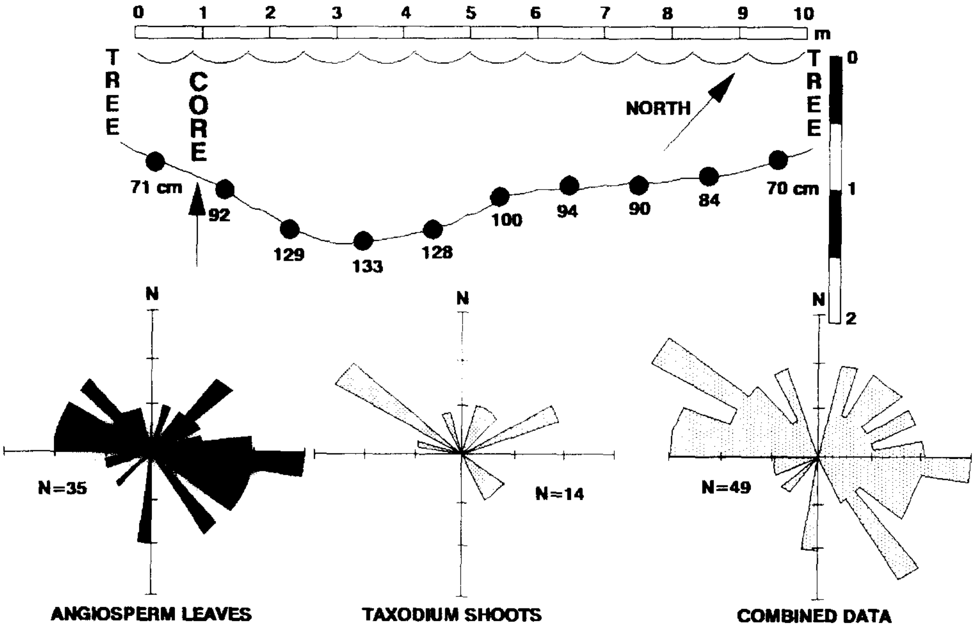

Fig. 9. Cross-section of Wash Branch, Dennis Lake, in the Mobile-Tensaw River delta, Alabama, indicating the position of the large-diameter core. Rose diagrams illustrating the planar distribution of *Taxodium* shoots and angiosperm leaves in the core.

Table 2

Adaxial : abaxial ratios of angiospermous leaves preserved in shallow waters of abandoned channel settings or alluvial swamps. Observed ratios are compared statistically to theorectically predicted 1 : 1 ratio, the 1 : 1.7 ratio observed in the forest floor litter of the Göttingerwald, and, in the case where adaxial surfaces predominate, a 1.7 : 1 ratio

| Sample site | Adaxial side up | Abaxial side up | ad : ab ratio | $\chi^2$ 1 : 1 | $\chi^2$ 1 : 1.7 | $\chi^2$ 1.7 : 1 |
|---|---|---|---|---|---|---|
| Maple Bayou, Mobile delta, AL | 101 | 137 | 1 : 1.36 | $5.15^{a,b}$ | $2.82^{a}$ | NA |
| *Quercus laurifolia* 1 | 81 | 32 | 2.53 : 1 | $20.34^{a,b}$ | $7.78^{a,b}$ | $2.76^{a}$ |
| *Quercus laurifolia* 2 | 67 | 33 | 2.03 : 1 | $10.89^{a,b}$ | NA | 0.55 |
| *Quercus laurifolia* 3 | 72 | 68 | 1.05 : 1 | 0.03 | $7.78^{a,b}$ | |
| Maple Bayou — all data sets | 321 | 270 | 1.18 : 1 | $4.22^{a,b}$ | | $19.27^{a,b}$ |
| Lobau, Austria, *Populus alba* 1 | 58 | 69 | 1 : 1.19 | 0.79 | $3.72^{a}$ | |
| *Populus alba* 2 | 83 | 55 | 1.51 : 1 | $5.28^{a,b}$ | | 0.36 |
| *Populus alba* total | 141 | 124 | 1.14 : 1 | 0.97 | | |
| *Salix alba* 1 | 13 | 90 | 1 : 6.92 | $56.08^{a,b}$ | $25.09^{a,b}$ | |
| *Salix alba* 2 | 93 | 123 | 1 : 1.32 | $3.89^{a,b}$ | $3.10^{a}$ | |
| *Salix alba* total | 106 | 213 | 1 : 2 | $35.12^{a,b}$ | 1.78 | |
| *Quercus robur* | 40 | 54 | 1 : 1.35 | 1.80 | 1.39 | |
| Lobau, Austria — all data sets | 287 | 391 | 1 : 1.36 | $15.64^{a,b}$ | $7.97^{a,b}$ | |

[a] $\chi^2$ significant at $P=0.10$.

[b] $\chi^2$ significant at $P=0.05$.

was found in most samples. The combined data set, biased by the *Q. laurifolia* data, indicates that there is a slight preference towards the adaxial surface up.

### 4.2. Forest litters

1.75 $m^2$ of surficial forest floor litter (489 angiosperm leaves, mostly *Fagus*) were evaluated in a mature stand in the Göttinger Wald to determine if there was any preferential adaxial or abaxial orientation in this setting (Table 3). An adaxial : abaxial ratio of 0.59 (1 : 1.7) exists in this population, and this ratio was used to test other forest floor litters collected and analyzed subsequently.

To evaluate the validity of the ratio observed in Göttingen, leaves in four 0.5 $m^2$ quadrats were investigated in Auburn (Table 3). All leaves are mesophylls. The total leaf population conforms to a 1 : 1 adaxial : abaxial ratio. Certain species, however, exhibit a <1 : 1 ratio (statistically tested against a 1 : 1.7 ratio). Additional data sets, collected from Neckargemünd and near Dresden, show that neither leaflets of *J. regia* nor leaves of *A. platanoides* conform to a 1 : 1 adaxial : abaxial ratio. Rather, leaflets of *Juglans* are biased towards a 1.8 : 1 ratio, and leaves of *Acer* are heavily biased towards a 3.8 : 1 ratio.

Two macrophyllous taxa in Sarawak show slight differences in their adaxial : abaxial preferred orientation. The large entire-margined leaves of Terentang (*Campnosperma coriaceum*) statistically conform to a 1 : 1 ratio, while the trilobate leaves of the Menua tree reflect a 1 : 1.7 ratio (Table 3). This latter condition may be a consequence of a low number of available leaves at the time of collection.

### 4.3. Experimental leaf fall

*Ligustrum vulgare* and *Ilex opaca* leaves dropped in free-fall from a height of 9.2 m both conform to a 1 : 1 abaxial : adaxial ratio (Table 4). Partially hydrated *Quercus laurifolia* leaves brought back from the alluvial swamp adjacent to Maple Bayou were dropped resulting in a preferential 1 : 1.7

Table 3
Adaxial : abaxial ratios of angiospermous leaves in forest floor litters

| Forest litter site | Adaxial side up | Abaxial side up | ad : ab ratio | $\chi^2$ 1 : 1 | $\chi^2$ 1 : 1.7 |
|---|---|---|---|---|---|
| Göttinger Wald 1, 0.5 $m^2$ quadrat | 39 | 56 | 1 : 1.43 | 2.69 | 0.55 |
| Göttinger Wald 2, 0.5 $m^2$ quadrat | 17 | 35 | 1 : 2.05 | $5.56^{a,b}$ | 0.18 |
| Göttinger Wald 3, 0.5 $m^2$ quadrat | 23 | 37 | 1 : 1.60 | $2.82^{a}$ | 0.02 |
| Göttinger Wald 4, 0.5 $m^2$ quadrat | 28 | 34 | 1 : 1.25 | 0.40 | 2.13 |
| Göttinger Wald 5, 0.5 $m^2$ quadrat | 24 | 45 | 1 : 1.87 | $5.80^{a,b}$ | 0.02 |
| Göttinger Wald 5, 0.5 $m^2$ quadrat | 11 | 51 | 1 : 4.63 | $24.53^{a,b}$ | $7.76^{a,b}$ |
| Göttinger Wald 7, 0.5 $m^2$ quadrat | 41 | 48 | 1 : 1.17 | 0.40 | $3.52^{a}$ |
| Göttinger Wald, total | 183 | 306 | 1 : 1.67 | | |
| Auburn, AL, 0.5 $m^2$ quadrat, *Quercus triloba* | 43 | 50 | 1 : 1.14 | 0.39 | |
| Auburn, AL, 0.5 $m^2$ quadrat, *Q. alba* | 29 | 43 | 1 : 1.48 | 2.35 | |
| Auburn, AL, 0.5 $m^2$ quadrat *Q. nigra* | 84 | 62 | 1.35 : 1 | $3.02^{a}$ | [1.71]<br>1.65 |
| Auburn, AL, 0.5 $m^2$ quadrat *Carpinus virginiana* | 25 | 46 | 1 : 1.84 | $5.63^{a,b}$ | 0.02 |
| Auburn, AL, all leaves in quadrats | 186 | 204 | 1 : 1.10 | 0.74 | |
| Neckargemünd, Germany, *Juglans regia* | 324 | 177 | 1.83 : 1 | $42.54^{a,b}$ | [1.7 : 1]<br>0.48 |
| Dresden, Germany, *Acer platanoides* | 130 | 35 | 3.8 : 1 | $53.23^{a,b}$ | $16.91^{a,b}$ |
| Peat swamp forest, Sarawak, *Campnosperma* spp. | 65 | 52 | 1.25 : 1 | 1.23 | |
| Sarawak, Menua tree, sp. unknown | 12 | 28 | 1 : 2.3 | $5.63^{a,b}$ | 0.57 |
| Sarawak, total macrophylls | 77 | 80 | 1 : 1.03 | 1.80 | |

[a] $\chi^2$ significant at $P=0.10$.
[b] $\chi^2$ significant at $P=0.05$.

abaxial orientation. Because the leaves were fully hydrated at the time of collection, partially dehydrated leaves were placed into swamp water and left for 24 h after which the experiment was repeated. Following rehydration, leaves conformed to a 1 : 1 ratio.

*Ulmus campestris* and *Populus alba* leaves were dropped in free-fall from a height of 5 m. Due to individual plant responses during the summer of 1994, *Ulmus* leaves were either adaxially convex or concave in cross-section as determined by looking at the upper surface of the leaf. Leaves of *Populus* were largely concave in cross-section. Convex leaves of *Ulmus* had a tendency to land with their lower surface upwards in a statistically significant 1 : 1.7 ratio (Table 4). Concave leaves of *Ulmus* had a strong bias to land with their upper surface upwards, also in a statistically significant 1 : 1.7 ratio. The concave leaves of *Populus*, however, showed a strong trend towards landing with their upper surface upwards in an observed ratio of 4 : 1.

## 5. Discussion

### 5.1. Phytoclast distribution

Modern and ancient oxbow lake sediments examined, to date, all share similar characters with respect to the distribution of leaves and other canopy parts. These plant parts are found to be

Table 4
Adaxial: abaxial ratios of angiospermous leaves obtained through experimental leaf fall

| Experimental leaf fall | Adaxial side up | Abaxial side up | ad:ab ratio | $\chi^2$ 1:1 | $\chi^2$ 1:1.7 |
|---|---|---|---|---|---|
| *Prunus americana* | 44 | 56 | 1:1.27 | 1.12 | 1.81 |
| *Ilex* sp. | 42 | 58 | 1:1.38 | 2.25 | 0.86 |
| Adaxial *Q. laurifolia* from Maple Bayou | 40 | 36 | 1.16:1 | 0.17 | |
| Adaxial *Q. laurifolia* after 24 h soaking | 34 | 37 | 1:1.09 | 0.06 | |
| *Ulmus campestris* convex leaves | 12 | 38 | 1:3.17 | $12.5^{a,b}$ | 2.62 |
| *Ulmus campestris* concave leaves | 38 | 12 | 3.17:1 | $12.5^{a,b}$ | [1.7:1]<br>2.62 |
| *Populus alba* concave leaves | 40 | 10 | 4:1 | $16.82^{a,b}$ | $4.88^{a,b}$ |

$^a\chi^2$ significant at $P=0.10$.
$^b\chi^2$ significant at $P=0.05$.

concentrated in the fine clastics that make up the passive infill phase. Leaves and woody elements are stratified, usually arranged into groups or clusters of several individual plant parts. These clusters in temperate climates are the taphonomic signature of cyclical (autumnal) leaf dehiscence. In the cases of False River, Louisiana (Farrell, 1989), and Boatyard Lake, Alabama (Gastaldo et al., 1989), the potential for preservation exists equally throughout the channel cutoff. Leaves may be found in clusters of 3–5. Individual leaves are generally overlain by <5 mm of mud. In the case of the Macareo oxbow, preservation potential is restricted to the closed, upstream end of the channel. Here, the leaves are concentrated in flat lenticular accumulations with a maximum thickness of approximately 10 cm (Rabold, 1990). In general, there is a low clay content in the organic accumulation. Although there is a high sedimentation rate in the downstream end of this oxbow, oxidation and decay of allochthonous leaves in the water column before emplacement onto the fine sands limit their potential preservation. In addition, oxygenated waters moving through the fine sands promote decomposition. Clusters of leaves are not expected to survive under these conditions.

Leaf concentration of a specific taxon along bedding planes may offer the possibility to reconstruct spatial resolution of the original channel margin vegetation if data are available along the strike of the channel. Burnham (1994) demonstrated that leaves dehisced from parental trees are found within a limited distance from the trunk, usually no further than the edge of the crown. Trees that live along channel margins often have crown branches that overhang the channel. Leaf loss from these plants would result in the contribution of more leaves in a localized area, directly beneath the tree. In the case of Bockwitz, it is common to find concentrations of leaves of certain taxa on sample slabs. This raises the possibility that the original parent trees were close to the site of deposition. We do not have spatially resolved data due to collecting limitations, but it should be emphasized that this type of resolution is possible with proper methodologies.

### 5.2. *Leaf size distribution*

To the best of our knowledge, few data sets exist that have presented the information either on *L*:*W* or area variation of leaves from living individual trees or extant populations. We realize that there has been concern on the part of some workers about the use of length:width data in systematic studies because of leaf response to environmental factors. Because we are evaluating the taphonomic character of an entire assemblage, such minor pertubations would affect all plants that had contributed to the deposit and would not essentially change the size distributional pattern.

From the limited data, it appears that both gaussian and log-normal distributions exist in nature. Burnham (1986) demonstrated that the *L*:*W* ratios of herbarium samples in three ulmaceous genera are normally distributed. The data presented by Ferguson (1974) for *Laurus*, also based upon herbarium samples, and unpublished data for *Ligustrum* spp. appear similar. Collections taken from tree litters appear to be either log-normal or gaussian in distribution. We are aware of the limitations in the use of the following data, but believe that it is germane. The *Fagus sylvatica* and *Alnus glutinosa* leaf area data that Spicer (1981) presented collected from stream traps near Silwood Lake appear to approximate a log-normal distribution. This does not appear to be the case for leaf length data published by Greenwood (1992) from forest litters of Australia. These data represent four sample collections of 224 leaves in each forest category. Histograms of leaf length data appear gaussian.

Taxa with similar leaf-size distributions have been found in the fossil record, for example, the *L*:*W* plots of Hantke (1954) and Ferguson (1971). If all *L*:*W* data for these assemblages were to be compiled, the same pattern would prevail. The distribution of *L*:*W* ratios for fossil assemblages may well be biased in several ways. First, there is a high probability that mainly leaves from the canopy top and forest margins will be introduced into the depositional environment (Roth and Dilcher, 1978; Ferguson, 1985). Secondly, there is a strong possibility that only the relatively small leaves with intact apices and bases are liable to be collected, uncovered complete and, therefore, measurable. Thirdly, there is always a possibility that anomalously large leaves may be introduced into the assemblage from regenerative juveniles, following death of the aerial stems of certain floodplain taxa (Sigafoos, 1980). To some yet unknown extent, these may influence the leaf size distribution in any assemblage.

### 5.3. Leaf orientation

Observations taken at Wash Branch and under forest canopies show that there is normally no preferential directionality to the leaves and shoots that have fallen onto the sediment–water interface or the forest floor, respectively. This is not surprising because it is a time-averaged accumulation that is affected by variable abiotic factors. In the case of an oxbow lake, small wind-generated currents might be expected to align the leaves as they sink through the upper part of the water column. Because winds are not always blowing in a prevailing direction, but change their bearing over the time of leaf fall, even this factor would not result in a preferential orientation of the leaves. This is what is exactly seen in forest floor litters that act as a proxy for what is observed at the sediment–water interface. In the case of the leaf accumulation in Wash Branch, there is no statistical evidence to indicate any preferential orientation. In most of the Bockwitz samples examined, the same is true. Where there is a slight preferential orientation in the Bockwitz material, this may be due to small sample area and/or the limitations of the bedding plane available for examination.

The leaf assemblages in Bockwitz have a preferential abaxial orientation that is reflected, in part, in the data from analog studies. There appear to be many variables responsible for the ultimate adaxial or abaxial orientation of any particular leaf or taxon. There is a tendency to think of a leaf-blade as a flat, two-dimensional object (Tanabe and Kaneko, 1994). This is an oversimplification because the nature of the lamina is governed by a combination of genetic factors (e.g. timing and degree of vascularization; [Maksymowych, 1973], petiolar support [Niklas, 1994], and support provided to the intercostal area) and environmental influences (e.g. drought). As a result, leaf cross-sectional shape can vary from strongly convex to strongly concave. Each end member and intermediate states provide a different aerodynamic response during descent.

### 5.4. Aerodynamics of falling leaves

The behavior of leaves in their descent following abscission is very complex, and only recently have researchers attempted to model their behavior (Tanabe and Kaneko, 1994). Assuming that the "leaf" is a two-dimensional case, Tanabe and Kaneko (1994) modelled the dynamics of a falling piece of paper in an $X$–$Y$ plane and found that increasing friction coefficients account for fall patterns. Five patterns have been identified: periodic rotation, chaotic rotation, chaotic fluttering, periodic fluttering, and simple perpendicular fall.

Natural leaves are more complex than simple pieces of paper. Differences in shape, size, weight distribution, petiole, etc. can independently or collectively influence their flight path in still air. As leaves start to fall the airstream parts at the windward side and is deflected around the object only to rejoin it on the lee side. This results in flow lines that are symmetrical. However, once the leaf starts to accelerate, orientation becomes of critical importance. Thus, although one might assume that a vertical orientation would allow the leaf blade to cleave through the air more effectively, the surface friction drag which then develops is such that a horizontal orientation is achieved. When the leaf blades are curled, the convex surface functions as the leading edge. Thus, the leaves offer less resistance to air flow. As the leaf sinks through the atmosphere, there is a build up of air pressure on the windward side leading to aerodynamic lift. This is accentuated by a pocket of reduced air pressure on the lee side. The low air pressure in the wake of the falling leaf has the effect of drawing in the air flowing around the leaf margins (Fig. 10). These inwardly spiralling vortices are, for some still unknown reason, shed alternately from the opposite edges (Von Kármán Vortex Street).

The heaviest leaves display the highest settling velocities (Spicer, 1981; Ferguson, 1985) and the laminae maintain a practically horizontal orientation throughout their descent. At most there will be a slight rocking motion (chaotic or periodic fluttering) induced by the Von Kármán Vortex Street. In lighter leaves, the leaf-blade shape begins to play a more important role (Fig. 10) related to the flow pattern of air. When the lamina is dissected, palmate, or badly insect-damaged, the air is able to pass through the sinuses (wounds) so that the turbulence developing on the upper surface is more or less evenly spread. In the cases where the weight of the petiole is not a major influence, this results in a high degree of stability such that these leaves fall more or less vertically in still air (simple perpendicular fall). In suborbicular leaves, the turbulence is concentrated at the edge. The Von Kármán Vortex Street effect, alone, results in the tilting of the blade. The skin-friction drag that builds up causes the laminae to rotate such that the leading surface faces into the wind. The leaf comes to a temporary halt and gravity causes the leaf to start an oblique trajectory in the reverse direction. These leaves follow a zig-zag course. Turbulence in lanceolate leaves is restricted initially to two bands on either side of the lamina. The Von Kármán Vortex Street soon disrupts the balance. The leaf, while remaining horizontal, is sent into a spin (periodic rotation) along the midrib resulting in a diagonal path to the ground. It should be clear that these lanceolate leaves theoretically should have a 50:50 chance of having the adaxial or abaxial surface facing upwards when they come into contact with the ground. The same should apply to flat leaf blades as well. However, most leaves show some convexity or concavity in cross-section. Theoretically these leaves should fall with a preferential side downwards. In the case of convex leaves, one would expect that the adaxial surface would be downwards (abaxial surface would face upwards). In concave leaves, one would expect that the abaxial surface would be downwards (adaxial surface would face upwards).

Nature does not always conform to theory. As the atmosphere is almost always in a turbulent state, eddies will interfere with the projected flight pattern. This means that in practice, the orientation of the leaves on the forest floor or lake surface can be expected to diverge from theorectical grounds. This is demonstrated in the experimental data sets from the Lobau and Auburn (Table 4). In the case of *Ulmus*, those leaves that were

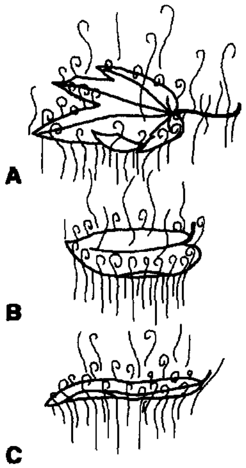

Fig. 10. Diagram illustrating the effects of air currents on falling leaves of various morphologies. As leaves sink through the air column, air pressure builds on the windward side resulting in a pocket of reduced pressure on the leeward side. The low air pressure in the wake of the fall draws in the air flowing around the leaf margins.

strongly convex in cross-sectional shape diverged from the theoretical pattern by 24% (ad:ab ratio 1:3.17). That is, even though one would expect to find all convex leaves with their abaxial surface facing upwards, nearly a quarter of the leaves ended up with their adaxial surface facing upwards. The concave leaves, *Ulmus* and *Populus*, showed a similar pattern of divergence from theory, with 24% (ad:ab ratio-3.17:1) and 20% (ad:ab ratio-4:1), respectively, abaxial surfaces facing upwards. In the cases of *Prunus americana* and *Ilex opaca*, both of which are convex in cross-section, the divergence from theory is more pronounced, with nearly half of the leaves (42–44%) ending up with the adaxial surface facing upwards. When tested with a $\chi^2$ statistic, though, these latter ratios proved not to be significant from a 1:1 ratio. Similar results are seen in the macrophyllous leaves from Sarawak and for all taxa, except *C. virginiana*, in the Auburn quadrats (Table 3). In this case, 32% more *Carpinus* leaves (ad:ab ratio 1:1.8) are found with abaxial surfaces facing upwards. The opposite is true for *Juglans* leaflets.

Leaves taken from the surface of shallow-water sites in the Lobau and Maple Bayou show variability in adaxial:abaxial leaf orientation (Table 2). *Salix alba* populations are statistically biased towards an abaxial surface upwards (1:2 ratio), while the *Quercus* and *Populus* ratios show no statistical difference from a 1:1 ratio for either data set. In the alluvial swamp adjacent to Maple Bayou, leaves of *Quercus laurifolia* show a statistically significant bias towards an abaxial surface upwards (statistically conform to a 1:1.7 ratio).

### 5.5. *Behavior in the water column*

Leaves that land on a body of water remain afloat for some time as a result of surface tension and the air-filled interstitial spaces. Leaf transfer to the sediment–water interface is governed, to a large extent, by the uptake of water via the stomates or other openings (sites of insect-damage) and cellular catabolysis (Gastaldo, 1994). Water replaces lost gases eventually causing waterlogging. However, before this has happened, the leaf may start to sink when density exceeds unity. Being only fractionally heavier than the medium, the orientation is likely to be influenced by the idiosyncrasies of the individual leaves (petiolar weight, heterogenous uptake of water, localized production and retention of gases). Individual leaves within a single species may behave quite differently in their descent. Petioles may affect the orientation within the water column. Sometimes the petiole leads the leaf downwards. In other cases, the petiole acts as a float or has no influence (unpubl. data).

Once the vertically oriented leaves contact the sediment–water interface, they fall over on one side or the other. Thus, some of the preferential orientation visible at the water surface will be lost. This, of course, depends upon the proportion of leaves in a taxon that would descend vertically. To date, this aspect has not been investigated quantitatively. Depending upon the species and environmental controls such as water temperature and aeration, emplacement at the sediment–water interface may occur in a matter of hours or take weeks (Spicer, 1981; Ferguson, 1985).

### 5.6. *Comparison of actualistic data with Bockwitz*

Abandoned river channels may fluctuate between being essentially closed (Boatyard Lake; Gastaldo et al., 1989) or partially open systems (Macareo River; Pfefferkorn et al., 1988; Rabold, 1990) with regard to the phytoclasts that are introduced to the sediment–water interface. This interplay is in response to the flooding periodicity and intensity operating in the alluvial plain, as well as the maturation stage of channel-cutoff. During the latter phases of channel fill, more organics are added to the fine clastics, resulting in their stratification. This accumulation normally represents a short time interval ($<10^2$–$10^3$ yr; Behrensmeyer and Hook, 1992), and stratification reflects cyclical or periodic introduction of debris (a taphonomic signature of leaf fall). Hydrosere evolution results in the development of semi-aquatic and finally terrestrial vegetation that may alter the underlying sediments through root penetration. The upper part of the channel fill may be converted to an incipient or well-developed soil over time (Retallack, 1990). This is certainly the case in Bockwitz, with large woody roots distributed vertically through the upper part of the sequence. Although bioturbation affected the upper part of the channel fill, its effects were not significant in the lowest portion of the channels. The distribution of phytoclasts and evidence of hydrosere community development in Bockwitz conforms to the actualistic scenario. This situation commonly has been encountered in other lenticular clay accumulations in the stratigraphic record (e.g. Wing, 1984; Burnham, 1990; Greenwood, 1991).

The presence of a leaf assemblage that shows a log-normal size distribution would indicate that there has been no abiotic influence during its accumulation. There has been no size sorting by fluvial processes. The assemblage is neither biased towards unusually small or large leaves. Rather, there is a more representative sample of foliage. It has been demonstrated by Roth and Dilcher (1978) that in open lake systems there is a bias towards smaller leaves the further the sample is taken away from the shoreline. This is directly related to an overrepresentation of the sun leaves from the top of the canopy. This is not the case in Bockwitz which would indicate that there is an equal probability that sun and shade leaves are present.

The planar orientation of leaves in the Bockwitz assemblage is, for the most part, randomly distributed. There are several specimen blocks that show a particular bias in the leaf orientation, but this may be due to either the size of the sample or its original position within the channel. In recent oxbow lakes, more marginal, shallow water sites are affected by winds generated on the surface of the lake and may cause some preferential reorientation of the phytoclasts due to wave oscillation (pers. observ.). This would not affect the phytoclasts in deeper water settings because wave base is limited to one-half of the wave height. Waves in channel cutoffs are generally of low amplitude. Random leaf and shoot orientation as found in Wash Branch confirms the pattern observed in Bockwitz.

There is a bias in the fossil assemblage towards the abaxial surface (bottom side up) facing upwards in the deposit. The computed figure for the adaxial : abaxial relationship fits a ratio that approximates 1 : 1.6 as has been found in some modern analog cases. Some recent taxa show a 1 : 1 ratio, while others exhibit a preferential adaxial or abaxial statistical dominance. The divergence from a 1 : 1 expected ratio may be solely a function of leaf cross-sectional shape. In those leaves that have a convex cross-section, there is a strong tendency towards landing with their bottom-side up. Because the leaf-blades of many taxa are convex in shape, the preference towards an assemblage with abaxial-dominated leaves is explicable. The descent through the water column of such leaves is less likely to be of significance in their final orientation at the sediment–water interface. Experiments conducted to date (Spicer and Greer, 1986) have focused on the rate of descent rather than the ultimate disposition of the leaves on the bottom. Empirical data in natural systems would be useful in resolving the preferential abaxial leaf orientation in our locality. As of this time, we believe that an abaxial preference in a fossil assemblage is one criterion, which when used in conjunction with the other evidence, establishes parautochthony.

## 6. Summary

The identification and differentiation of parautochthonous assemblages in channel-fill sequences has been a subjective exercise. Taphocoenoses of bedded leaves preserved in apparently homogenous siltstone or mudstone have been considered, a priori, to represent contribution from local vegetation. Fluvial channels may experience complex sedimentological histories, and the phytoclasts preserved within these channel fills may be autochthonous, parautochthonous, or allochthonous. Using the fossil assemblage preserved in an abandoned channel-fill in Tagebau Bockwitz, as an example, in combination with modern analog studies, several criteria have been identified that can be used in conjunction with sedimentology to differentiate parautochthonous floras. Modern analogs included abandoned channels in the Mobile-Tensaw River and Mississippi River deltas, southeastern USA, and the Orinoco delta, Venezuela. Forest litters from several temperate and one tropical setting were used to assess whether or not fallen leaves display similar orientations to those found in the fossil example. Experimental data supplemented the forest litters to determine physical factors that may influence the adaxial : abaxial orientation of fallen leaves.

Several criteria have been identified as useful in differentiating parautochthonous assemblages. There is an increasing density upsection in the number of leaves found on a bedding surface or cluster per centimeter. The clustering of leaves in the stratigraphic succession is a taphonomic signature that indicates a cyclical (autumnal leaf fall in temperate climates) contribution. The diversity of the assemblage generally reflects hydrosere evolution and may result in bioturbation by rooting after complete infill, the establishment of arborescent vegetation, and soil development. Angiospermous leaves in the fossil assemblage display a log-normal distribution in size, and this parameter appears to be consistent with data from modern settings. The leaves and short shoots show no bias in directional orientation within the deposit. That is, the apices of these plant parts on any bedding surface are equally distributed throughout 360 degrees. There is no preferential strike to the assemblage members. This is confirmed from a limited data set in a modern channel cutoff. Angiospermous leaves display a preferential abaxial orientation. That is, more leaves are preserved with their lower surface upwards in the assemblage. The preference towards abaxial surface up is related to the original convex cross-sectional shape of most leaves, as has been observed under experimental conditions.

## Acknowledgements

K. Farrell is thanked for her assistance in vibracoring abandoned channels in the Mississippi River delta. B. Meller, T. Denk, A. Hager, S. Ferguson and J. Ferguson are acknowledged for their assistance in the Lobau; and L. Kunzmann, M. Röthel, and R. Schmidt for field work in Bockwitz. D. Dilcher, V. Wilde and R. Burnham are acknowledged for their assistance in manuscript reviews. The senior author conducted research in the Weißelster basin as a Forschungpreisträger, awarded by the Alexander von Humboldt-Stiftung, Bonn, during 1991–1992. The research in Bockwitz was benefitted by support from Deutsche Forschungsemeinschaft Scha 178/9-1 and Wa 757/1-1. The NATO Cooperative Scientific Exchange program is acknowledged for financial support that allowed for the actualistic studies to be conducted during 1992–1994. NSF-EAR 9111842 supported research in the Rajang River delta, Sarawak, East Malaysia. Data collected in the Orinoco delta was part of project DFG-Pf 98/3-1 awarded to H.W. Pfefferkorn.

Appendix 1

| Specimen | Quadrant 1 | Quadrant 2 | Quadrant 3 | Quadrant 4 |
|---|---|---|---|---|
| BOB 2726 | 9 | 2 | 2 | 3 |
| BOB 2252:2 | 38 | 28 | 30 | 27 |
| BOB 2077 | 8 | 4 | 1 | 7 |
| BOB 2251:2 | 7 | 4 | 13 | 16 |
| BOB 2251:4 | 20 | 21 | 12 | 4 |
| BOB 2725 | 16 | 15 | 18 | 14 |
| BOB 2695 | 10 | 14 | 14 | 10 |
| BOB 2121 | 7 | 3 | 2 | 2 |
| BOB 2251 | 6 | 10 | 6 | 6 |
| BOB 2125 | 5 | 3 | 5 | 6 |
| BOB 2254:2 | 20 | 8 | 17 | 20 |
| BOB 2187:1 | 7 | 7 | 9 | 7 |
| BOB 2376:1 | 7 | 10 | 1 | 8 |
| BOB 2187:2 | 6 | 6 | 6 | 6 |

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