Plant part processing and community reconstruction

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ABSTRACT

The principles governing the dispersion of plant parts are explained. These are then applied to fossil assemblages to plot the position of the source vegetation. The importance of using autochthonous and parautochthonous assemblages in the initial stages is emphasized. Considering the scrappy nature of the material palaeobotanists have to deal with, careful analyses of plant fossils can yield a remarkable amount of detail about the former vegetation.

ZUSAMMENFASSUNG

Die Prinzipien, welche die Dispersion von Pflanzenteilen steuern, werden erklärt. Das Wissen um diese Prozesse wird auf fossile Pflanzenvergesellschaftungen angewandt, um die Ursprungsvegetation lokalisieren zu können. Die Wichtigkeit, zuerst die autochthonen, bzw. parautochthonen Vergesellschaftungen zu untersuchen, wird betont. In Anbetracht des durchaus unzusammenhängenden Materials, welches dann den Paläobotanikern zur Verfügung steht, ist es erstaunlich, wieviel Information man über die damalige Vegetation gewinnen kann.

1. Introduction

Most macroscopic plants are attached to a substrate. This sedentary mode of life has a number of consequences for their survival and reproductive strategies. Terrestrial plants generally require the mediation of wind, rain or animal vectors in order to reproduce sexually. In order to complete their life-cycles, spores or pollen have to be released from the mother plants. Unlike most animals, woody plants are also able to shed most of their non-reproductive (vegetative) organs (e.g. branches, leaves) without fatal results (Addicott 1982). As pollen dispersal, leaf abscission and fruit dissemination etc. are happening at different times of the year and under different weather conditions, the various organs from a given individual need not be found in the same horizon. On the other hand, depending on the life-span of the source plant, these processes can be spread over hundreds or even thousands of years. The presence of plant parts in sediments does not necessary mean that the source plant was dead. Subfossils may have been derived from a plant which is still very much alive! Because of this predisposition to shed plant parts, there is

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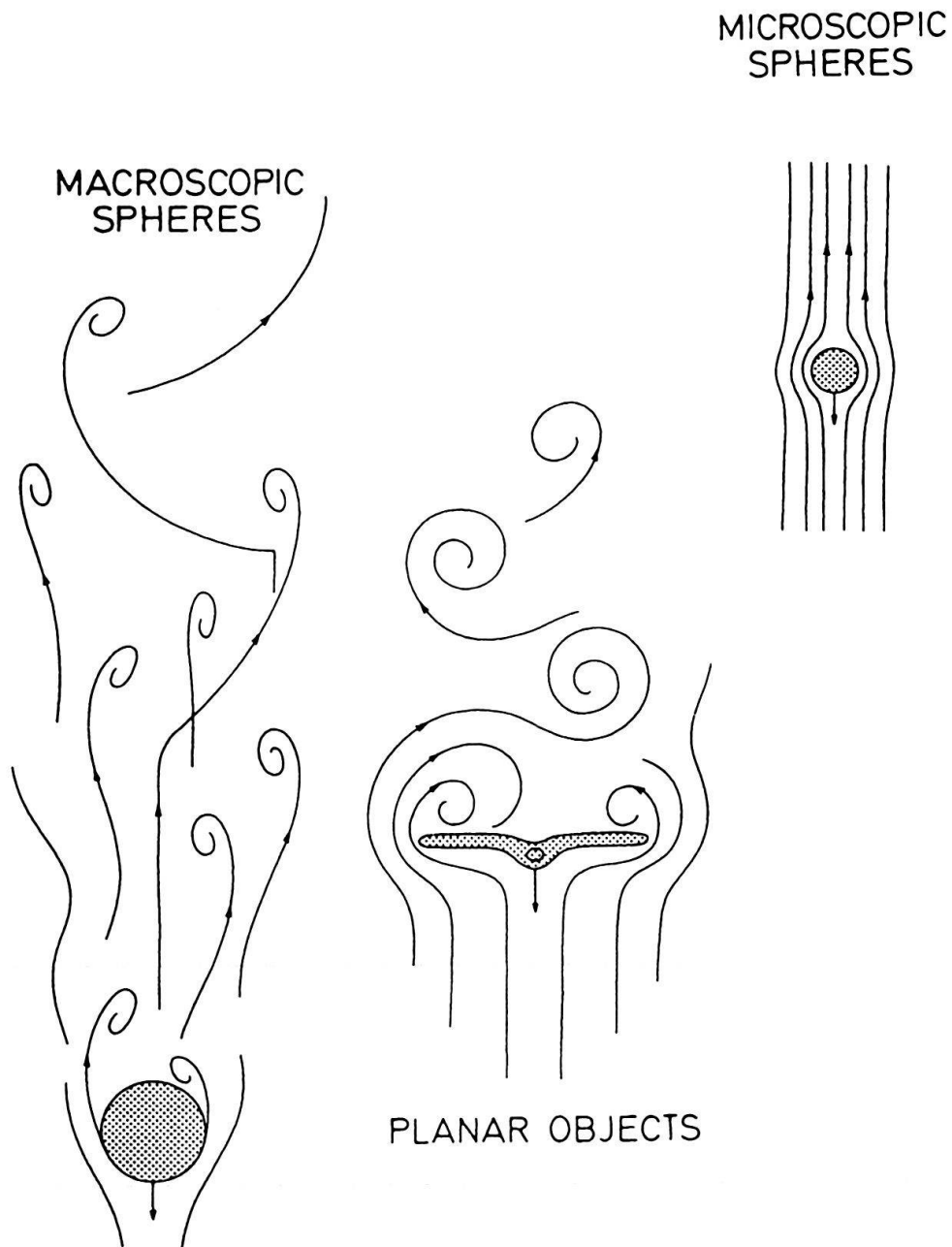
PLANAR OBJECTS

Fig. 1. The descent through air of macroscopic spheres (e.g. large diaspores), planar objects (e.g. leaves) and microscopic spheres (e.g. pollen grains). Note the eddies developing in the wake of the rapidly falling diaspores and slightly slower leaves. Because of their small size, the descent of the pollen grains is governed by the viscosity of the atmosphere. As a result of the low velocity, no eddies are produced.

little chance that more than a few organs will ever be found in organic connection. This explains why the reconstruction of fossil plants and the communities to which they belonged is no easy matter (Zhou 1992).

2. Dispersion of plant parts

To make matters worse the various plant parts have different dispersal potentials in the atmosphere. This is related, among others, to the initial numbers of units available for dissemination, the height of the source above the ground and the terminal velocity of the plant parts as they fall through the atmosphere. While spherical objects greater than 4 mm in diameter all have the same fall velocity, those less than 100 μm in diamter are governed by Stokes' Law of Resistance (Ferguson 1993), i.e. the velocity is dependent on the diameter of the sphere (Fig. 1). This means that most diaspores (fruits and seeds) have a much higher terminal velocity than pollen grains and unless they take advantage of an animal vector (zoochory) are unlikely to be widely dispersed. Leaves and winged diaspores occupy an intermediate position between these two extremes. Luckily, empirical studies have shown that while the absolute distance covered may differ, the different plant parts display the same type of dilution away from their source (Wolfenbarger 1946, Ferguson 1985). The resulting distribution is leptokurtic, i.e. with a peak at the point of origin and an exponential decrease in numbers of plant parts away from the source (Fig. 2).

Numbers of plant parts

Distance from source

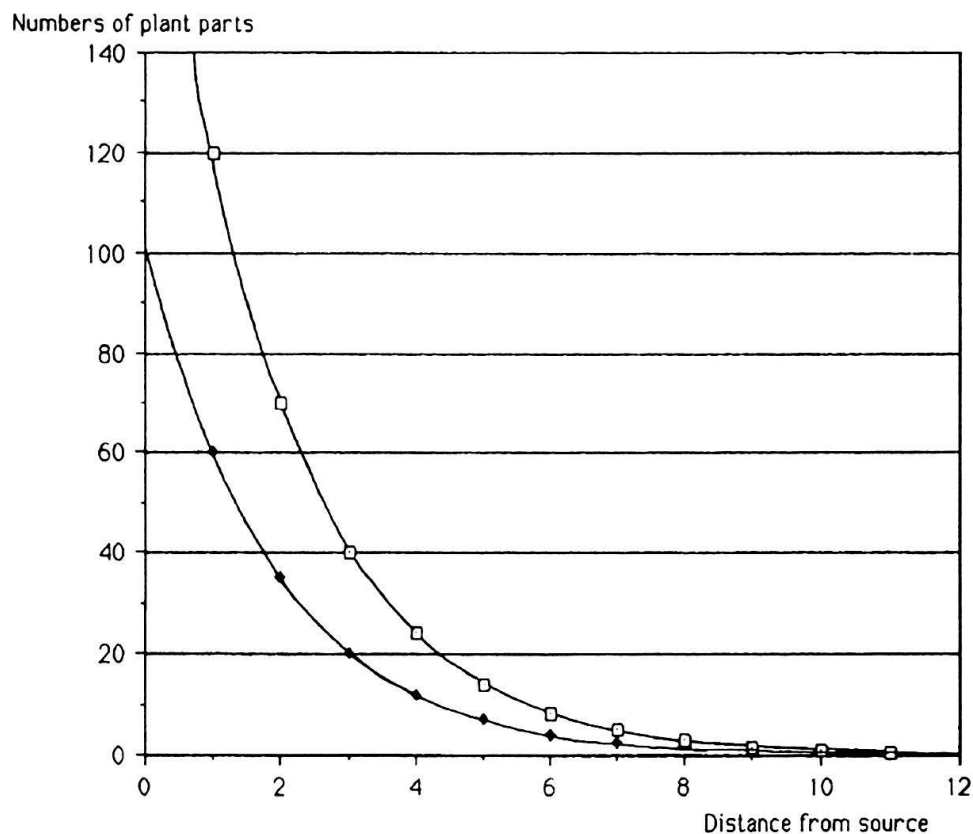Fig. 2. Graph illustrating the exponential dilution of detrital "rain" away from a source. Note that when twice as many plant parts are abscissed, the signal remains twice as clear even at some distance from the source. As a plant can produce millions more pollen grains than leaves (Ferguson, 1993), it is hardly surprising than the pollen signal remains loud and clear long after the leaves have become scarce.

3. Resolving the spatial pattern

In the case of recent vegetation, we use the source as a fixed point from which to follow the pattern of dilution. When dealing with fossils the outcrop becomes the fixed point from which we attempt to extrapolate back to the source. If this is to be successful, a number of preconditions must be fulfilled.

1. Undoubtedly the most important precondition is that little or no secondary transport should have occurred subsequent to initial wind dispersion. Hence it is imperative at the outset to investigate sites of closed forest vegetation, thereby reducing the risk of long-distance aerial transport, and those where little or no fluvial transport could have taken place, i.e. autochthonous or parautochthonous assemblages. These requirements severely limit the number of geological settings which are suitable in the initial stages of our research. A number of examples are given in Section 4.

2. Because they disclose different aspects of a single ecosystem, it is always advantageous to synthesize information from as many types of disseminules as possible. Combining evidence from both mega- and microfossils can give us an idea of the *distance* from the source plants. As pointed out in Section 2, the various plant parts have different dispersal potentials. Thus large fruits and seeds will tend to be found at their source, leaves up to 20–50 m from their point of release, and most winged disseminules within a radius of 100 m. Only plumed diaspores, spores and wind-dispersed pollen are likely to be found beyond these limits. This means that at or near their source a plant species would be expected to be represented by a range of different organs (Fig. 3). When only one or a few organs can be allocated to a particular taxonomic entity, this can mean a number of things. Either the fossil has been wrongly identified, or the remaining organs are not characteristic, do not fossilize well, or the plants grew outside the immediate area. When the first three possibilities can be ruled out, then an extra-local source seems likely.

3. A reasonably large outcrop some hundreds of square metres in extent should be available, in order to lay out a series of quadrats along a given bedding plane. Because autochthonous megafossil assemblages can change radically within a matter of metres, the sampling sites should be closely spaced. If tree stumps are present, the transects should be chosen such that they intersect with as many trunks as possible. In this way it will not only be possible to obtain an idea of the major components of the woodland, but to establish how they were scattered within the forest. A "high" next a stump would tend to suggest that this tree was the source of the litter. When the wood anatomy is preserved, its identity can be verified by sectioning a piece of the stump. Should the trees be grouped into stands, the detritus will display a platykurtic distribution, i.e. with a broad maximum extending from one side of the stand to the other.

In the case of parautochthonous assemblages (see Section 4.2), it is much more difficult to pin-point the source of the detritus. Although this is theoretically possible when only one individual or a single stand was present within the area, the chances of finding such scarce elements is like looking for a needle in a haystack. Uncommon components are rarely represented in the detritus (Burnham 1994, Burnham et al. 1992). When, as is more likely, individuals of various ages were scattered throughout the vegetation, the individual contributions are masked by the overlapping of the different dispersion paths. As a result, a quantitative analysis of the quadrats will only show the direction from which the *majority* of plant parts of a given taxon were coming.
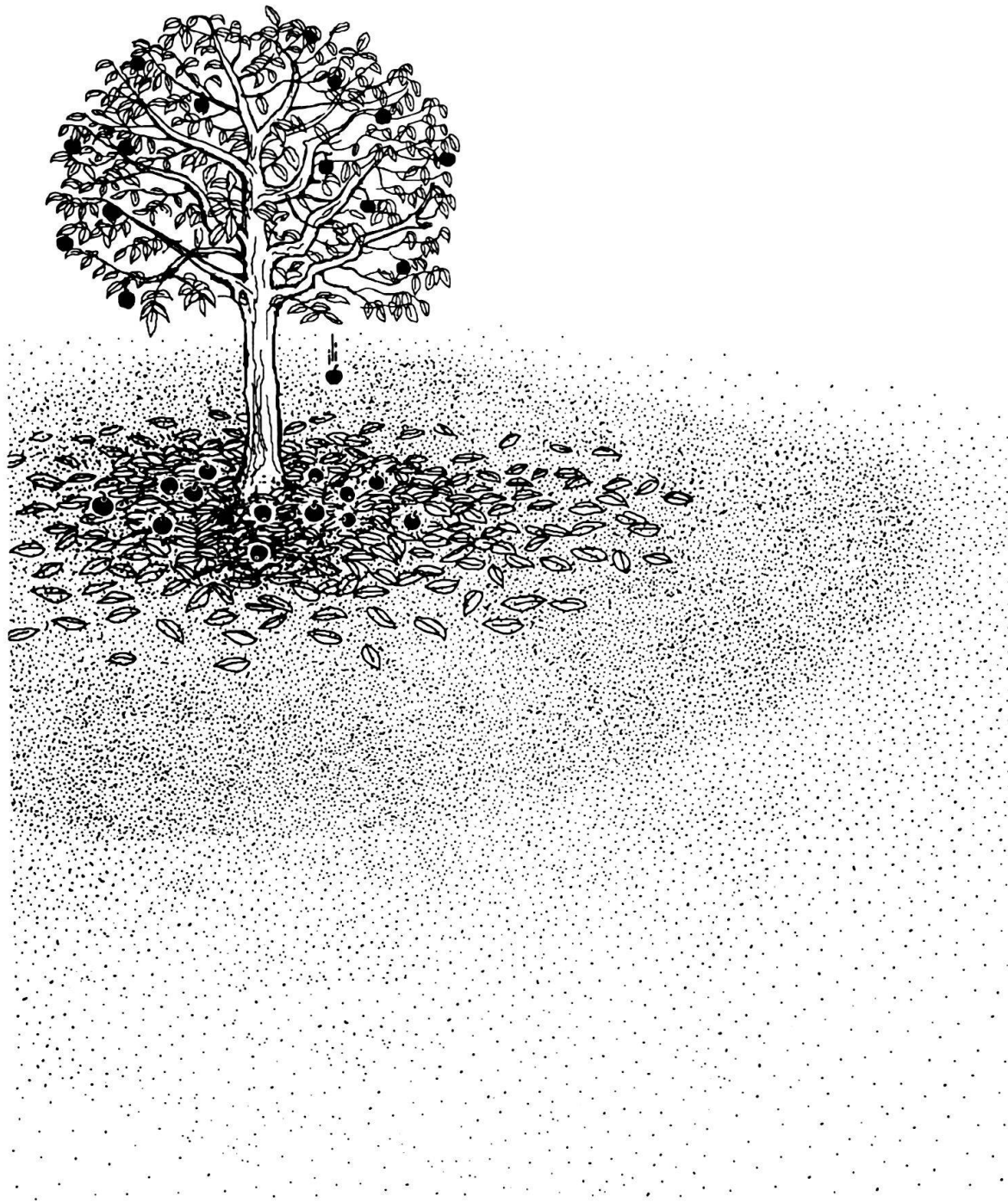
Fig. 3. Schematic diagram to illustrate the different dispersal potentials of fruits, leaves and pollen grains round a source tree.

4. Useful settings for community reconstruction

4.1 Autochthonous deposits

4.1.1 Peat bogs and coal seams (Fig. 4)

Peat bogs grow under water-logged conditions. The moist surface acts as a trap for wind-dispersed plant parts. Although there is a certain amount of lateral and vertical water movement, this is not normally powerful enough to cause any redistribution of the dead organic matter. However, because of its porous nature prior to compaction, a certain amount of exchange of the finer detritus such as pollen and spores can be envisaged in the upper parts of the peat column. The direction of movement would be expected to be
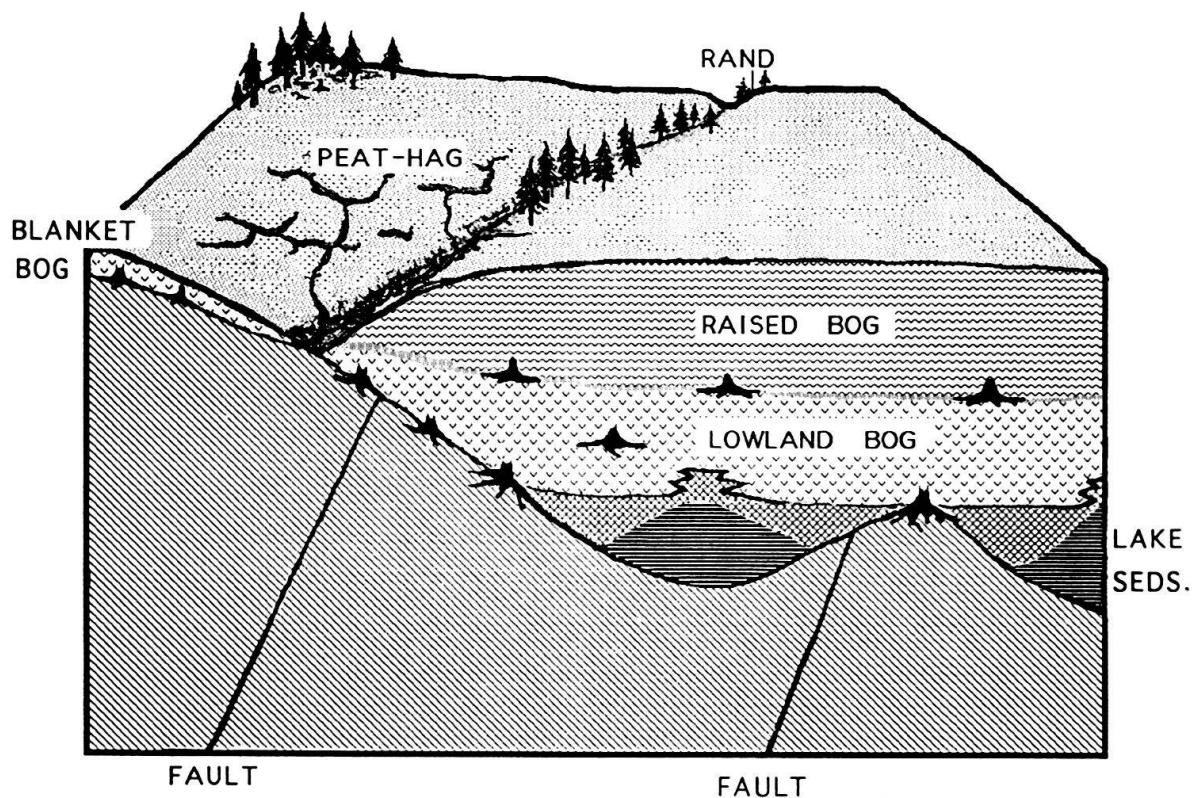
Fig. 4. A schematic representation of different types of peat bogs. Many peat bogs are formed by the terrestrialization of lakes. Once the substrate has become sufficiently stable, trees can colonize the peat. However for the perpetuation of lowland bog, subsidence and/or a rise in the water-table must keep pace with upward plant growth. Should peat growth outpace the rise in the water-table, a raised bog results. This is fed by meteoric water which drains down the sloping "rand", taking nutrients with it. Because of this and the better drainage, the "rand" offers a suitable site for trees. Under oceanic conditions, blanket bogs can develop. Should the blanket bog dry out irreversibly, gully erosion leads to the formation of peat-hags. Each of these bog types has a characteristic flora, which can be recognized in fossil assemblages.

governed by the hydrological situation. Thus during a period of persistent drought, evaporation of the superficial layers will cause an upwelling of water from below (Siegel et al. 1995). If this phase is prolonged it can cause irreversible desiccation of the peat, such that any rainfall will be repelled. In this case the precipitation drains away as surface run-off, thereby causing erosion and the formation of peat-hags. In less extreme cases the rainfall will be absorbed, leading to downward seepage. In this way pollen and spores could be flushed into deeper layers. While this possibility was raised in the early days of pollen analysis, it has proved to be of minor significance. Once trapped, pollen and spores are not easily released by the vegetation. They can even form such strong bonds with leaf cuticles, that it is impossible to separate them by mechanical or chemical means. This explains why it is possible to obtain distinct pollen spectra at different depths within a single moss cushion (Heim 1971). A greater danger as far as the fossil assemblage is concerned is that during a prolonged dry spell the superficial layers may become aerobic. This allows fungi, aerobic bacteria and soil invertebrates (e.g. Acari) to enter the peat. Between them they cause bioturbation and the destruction of the organic matter. This leads to an impoverishment of the megafossil assemblage and a less detailed picture of the one-time vegetation.

As compaction progresses the peat is coverted into lignite and finally high-grade coal. During this process the plant parts become increasingly difficult to recognize. In this case, the assemblage in the roof shales probably yields the best picture of the autochthonous peat swamp vegetation, although it is probable that the flood which swept over the area also carried some allochthonous plant parts with it.

4.1.2 Catastrophic burial (Fig. 5)

When a river bursts its banks or a volcano erupts, it is possible for a plant community to be preserved *in situ*. When this was a forest vegetation, the presence of stumps at the base of the sequence remains as a silent witness to the catastrophy. However, the presence of vertical tree trunks does not necessarily constitute proof of autochthony. Because of the great weight of the roots, stumps sometimes float vertically in water (Coffin 1983) or remain upright during transport in mud-slides (Spicer 1989). Thus the presence of an extensive root system in close apposition to a soil horizon requires to be demonstrated before autochthony can be confirmed. In the course of the catastrophy the finer detritus may have been blown or washed away. Thus it is not a foregone conclusion that any dispersed plant parts found along with the stumps were also autochthonous. They may well represent allochthonous elements transported into the area in the course of the catastrophic event, i.e. the assemblage is a mixocoenosis (Ochev 1993). Strong circumstantial evidence that the detritus was in fact autochthonous comes from leaves still attached to axes, a lack of preferential orientation of elongate plant parts and localized pockets of particular species within a given bedding plane (Christophel 1976; Wing et al. 1993).
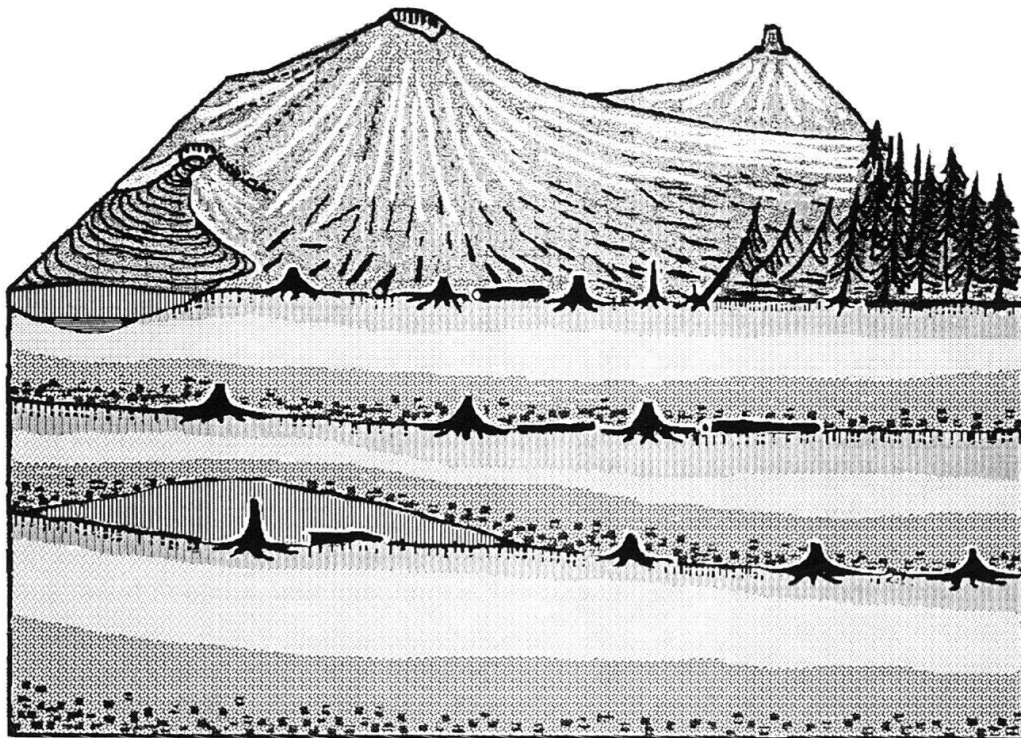
Fig. 5. A block diagram illustrating some of the plant taphonomic features of a volcanic terrain. When vulcan-
ism is of the effusive type, the vegetation can be overrun by lava flows. Due to the intense heat most of the or-
ganic matter is incinerated. Only a few charcoalified logs and tree stumps (lava trees) bear witness to the for-
mer presence of forest. When volcanic activity is of a more explosive nature, destruction is principally related to
the hurricane-force winds. Near the vent the vegetation is completely destroyed. A few kilometers away the
trees are snapped off close to their base and the trunks largely orientated in the direction taken by the blast
wave. At increasingly greater distances from the vent, the length of tree trunk left standing increases. However,
the trees are stripped of most or all of their branches. Near the perimeter of the blast zone, branches on the lee
side will be retained. Here a certain amount of windthrow can be seen. The nature of the air-fall tephra in
which the plant material is buried varies in time and space. Large pyroclasts, which are not ejected far into the
atmosphere, are found close to the vent and at the bottom of the sequence. The finer ashes, which take much
longer to settle out, are not only more widely distributed but cap the fall-out. Thus each eruptive event tends to
display a fining upwards sequence. As vulcanism is of a pulsatory nature, phases of activity are followed by
quiescent periods. During the latter, vegetation becomes reestablished, only to be destroyed in the next round
of volcanic activity. The nature of this vegetation is dependent on the length of time which elapses between suc-
cessive eruptions.

4.2 Parautochthonous deposits

These deposits in which only a minimum of transport could have taken place, are the
next best to autochthonous assemblages.

4.2.1 Crater lakes (Fig. 6)

Crater lakes are formed by the funneling of rain-water into extinct volcanic vents. Be-
cause they are not fed by any major rivers, the majority of the megafossils found in the
lake sediments can only have been derived by aerial transport from vegetation on the pe-
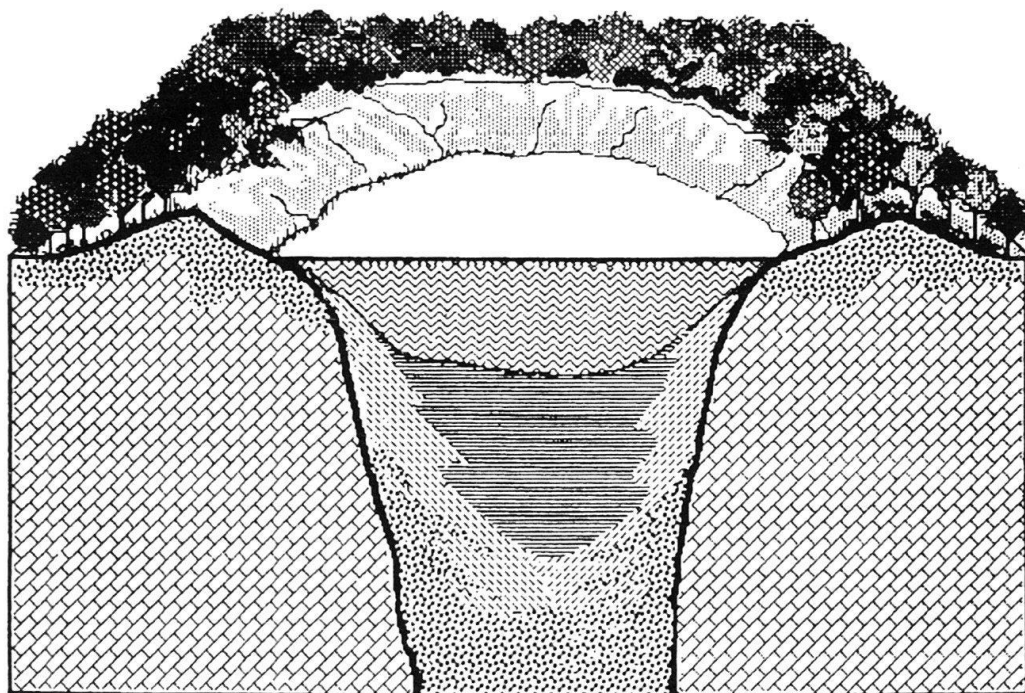
Fig. 6. Crater lake. Initially the steep-walled vent becomes infilled with unconsolidated coarse-grained pyroclasts. Only once the volcanic cone has been worn down and the crater rim stabilized by vegetation can finergrained sediments be deposited.

rimeter of the lake or slope wash on the inner slopes of the caldera. Because of the steep slopes, littoral vegetation is restricted to a narrow zone, which means this is very ineffective at preventing plant detritus from entering the lake. Our picture of the local vegetation is therefore fairly complete. A great advantage of such crater lakes is that the pollen record is "clean", being initially free of reworked microspores (Follieri et al. 1993). These would have been destroyed ("sterilized") by the intense heat and/or pressure accompanying the eruption.

Preservation is often exquisite in crater lakes, and this for a number of reasons. First of all, the minute particle size of much volcanic ash, its thixotropic behaviour, and the neoformation of cryptocrystalline silica which ensures rapid and complete isolation of organic matter and fossils. These factors impede exchange between the pore water in the sediment and the overlying water body, thus protecting the organic matter against oxidation (Zimmerle 1993). Furthermore crater lakes are very deep to start with. This means that any changes in the water temperature and the related phenomenon of overturning will, with few exceptions, be confined to the top of the water column. As such they do not affect the organic matter which has settled onto the lake floor. As the dissolved oxygen is soon used up by the decay of the detritus, the bottom sediments quickly become anoxic and therefore free from the destructive influences of benthonic organisms. Finely laminated sediments, which offer an excellent time frame for palaeoecological studies, result. Even in the final stages of infilling a thermal stratification can be retained, should the area be subject to an equable climate.

4.2.2 Ox-bow lakes (Fig. 7)

Although young ox-bow lakes are not completely free from outside influences, and are liable to become inundated with allochthonous detritus during periods of severe flooding, the connection with the main channel is largely limited to the downstream side. It is from this point that most sediments enter the ox-bow. At their point of entry these are coarse-grained, but at the far end of the ox-bow lake the water is sufficiently stagnant to allow muds to settle out. The fine-grained sediments and the poor oxygenation of the water enable organic material falling into the ox-bow lake from the surrounding vegetation to be preserved. Abscissing leaves tend to fall with their lower leaf surface either upwards or downwards. This is related to the shape of the leaf blade in cross-section. When the upper surface is convex, this forms the leading surface as the leaves flutter down. Such leaves generally land on the water with their lower surface upwards. This orientation will tend to be retained as the leaves sink through the stagnant water. Leaves which have undergone little or no transport will therefore display a leaf-surface orientation in the sediments which deviates from a 50:50 ratio. This and the quasi-random orientation of the leaves and short shoots on the bedding planes are good evidence for a parautochthonous origin (Gastaldo et al. 1996). Moreover, by limiting the sampling to the fine-grained sediments, it is possible to keep the number of allochthonous elements to a minimum. Periods of flooding can be recognized by coarser intercalations. These contain more information about the vegetation further upstream.
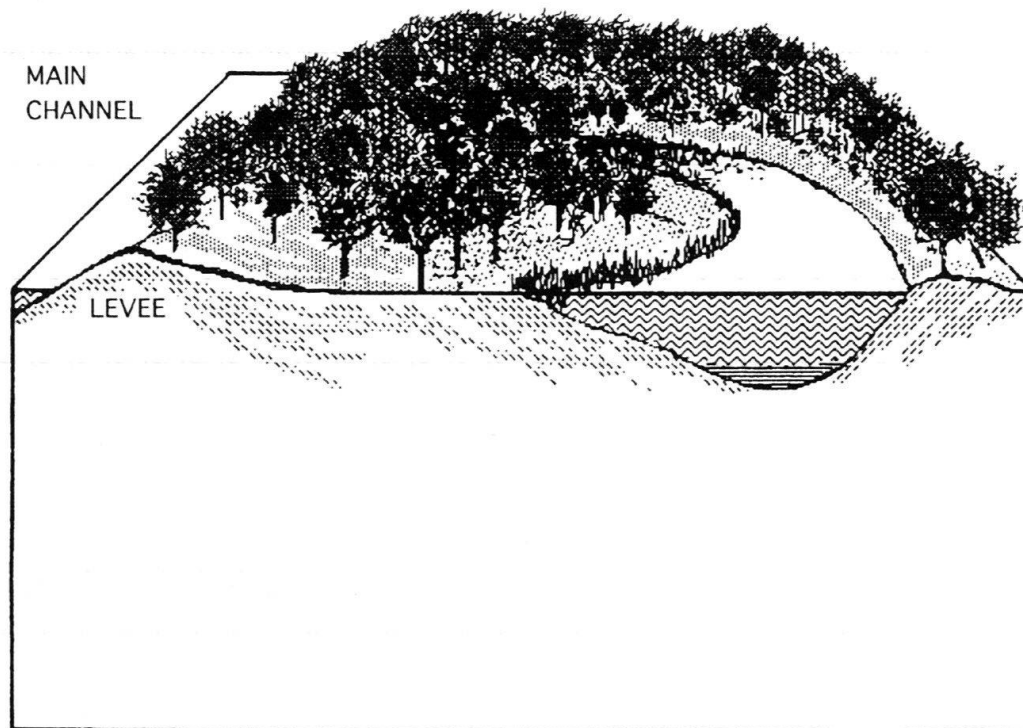

Fig. 7. Ox-bow lake, looking towards the shallow end, where the finegrained sediments are becoming colonized by riparian vegetation (helophytes).

5. Synthesizing the fossil evidence

Each of these settings in itself only gives a partial picture of the vegetation. However, because they form a firm foundation on which to start mapping out past communities, the above environments represent the key to solving the palaeovegetational puzzle (Fig. 8). Once the composition of the autochthonous floral assemblages has been analyzed, it is possible to establish which elements had a local distribution and which were ubiquists. At this stage further gaps in our knowledge can be filled by examining coeval assemblages of allochthonous origin, e.g. the coarser-grained sediments in the ox-bow lakes. Such sudden changes in the sedimentary regime can be particularly enlightening because any differences in the detritus must be related to alterations in the source of the material rather than any longer term changes in the vegetation. Cross-bedding and heavy minerals can be used to discover where the plant parts came from.
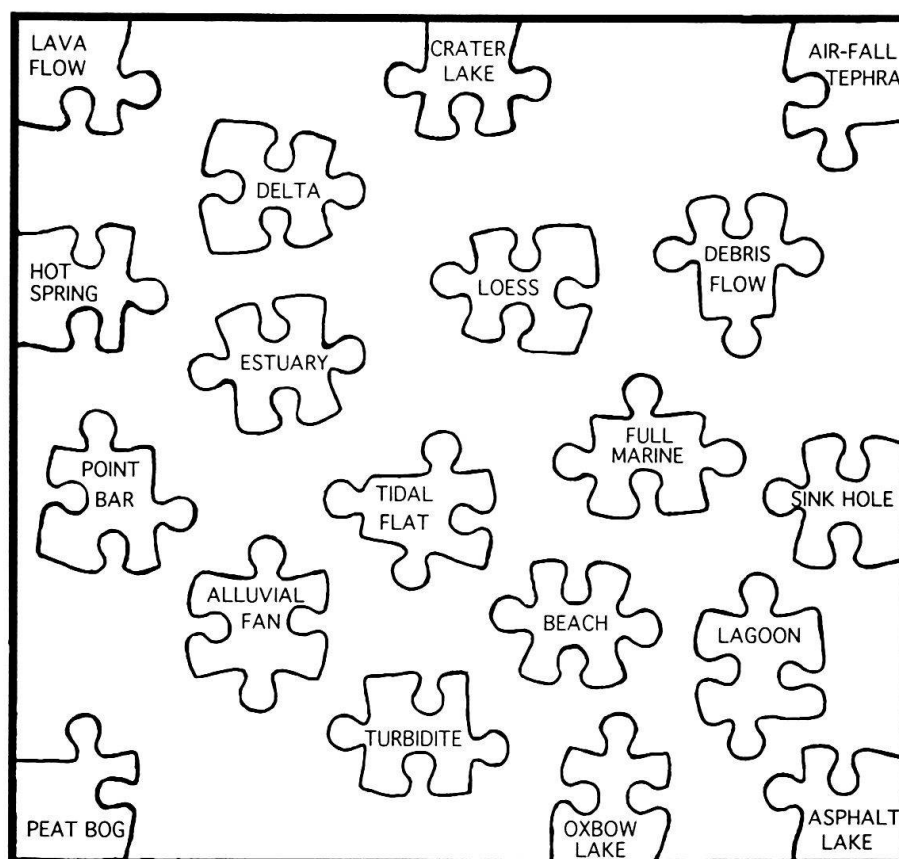

Fig. 8. Some depositional settings lend themselves better than others to the spatial resolution of past vegetation. In the process of synthesizing the evidence, autochthonous and parautochthonous deposits play a key role.

6. The stratification of the vegetation

Ever since mid Devonian times when the first trees appeared, tiered communities have clothed the landscape. Thus in any reconstruction of the vegetation, we should not only be concerned with resolving the spatial component, but in establishing the growth forms and stratification of the vegetation. Various approaches can be employed:

1. Assume the present habit of the nearest living relatives to have remained unchanged through time. In a recent paper on Neogene assemblages, Burgh (1994) distinguished canopy species, understorey species, shrubs and herbs. While this approach can probably be safely applied to Neogene and Quaternary assemblages, its application to older deposits is open to doubt.
2. Use certain physiognomic traits to identify those elements which probably belonged to the canopy and those which are more likely to have represented understorey plants (sciadophytes). For instance, polygonal adaxial epidermal cells normally represent sun-leaves characteristic of the canopy, while shade leaves of the same species have somewhat undulate epidermal cell walls. There again, in mummified leaves the presence of a hypodermis and/or more than one layer of palisade tissue is suggestive of canopy leaves.
3. Investigate the size and biomechanical properties of the stems in order to establish the maximum height to which the various taxa could have grown (Mosbrugger 1990, Mosbrugger et al. 1994, Niklas 1992, Speck 1994, Speck & Vogellehner 1992, 1994).
4. Study the sequence of leaf assemblages in volcaniclastic sediments in detail (Burnham & Spicer 1986, Spicer 1989, 1991). The ash will tend to coat the leaves of the canopy first. Because it cuts out the light, the leaves are no longer able to photosynthesize. This triggers the physiological processes leading to abscission (Addicott 1982). The shedding of the leaves (Fig. 9 B) may be aided by a new fall of ash, which covers the plants in the understorey. These in turn will loose their leaves (Fig. 9 C). The sequence of the abscissed leaves in volcaniclastic deposits will therefore tend to be inversely related to the stature of the plants from which they were derived.
5. When a bedding plane is exposed over a large area, it may prove possible to establish the height of individual plants from the lateral extent of their leaves. In recent woods the radius of the leaf shadow under a tree has been found to be roughly equivalent to the height of the specimen supplying the litter (Ferguson 1985, Burnham 1994).

Most reconstructions are still based on the first approach. However, one should be aware of the exaggerated role of arborescent plants inherent in this and the second method. Plant parts derived from tall trees are likely to be overrepresented in the assemblage for a number of reasons (Ferguson 1993):

1. More time elapses between abscission/dehiscence and their touch down, i.e. at a given windspeed these will travel further from their source.
2. Higher windspeeds are encountered at the top of the forest canopy than close to ground-level.
3. The organs meet with fewer obstacles on the way. Many of those disseminules originating from the understorey are taken out of circulation by impaction (Ferguson-Spicer Effect; Rabold 1990).

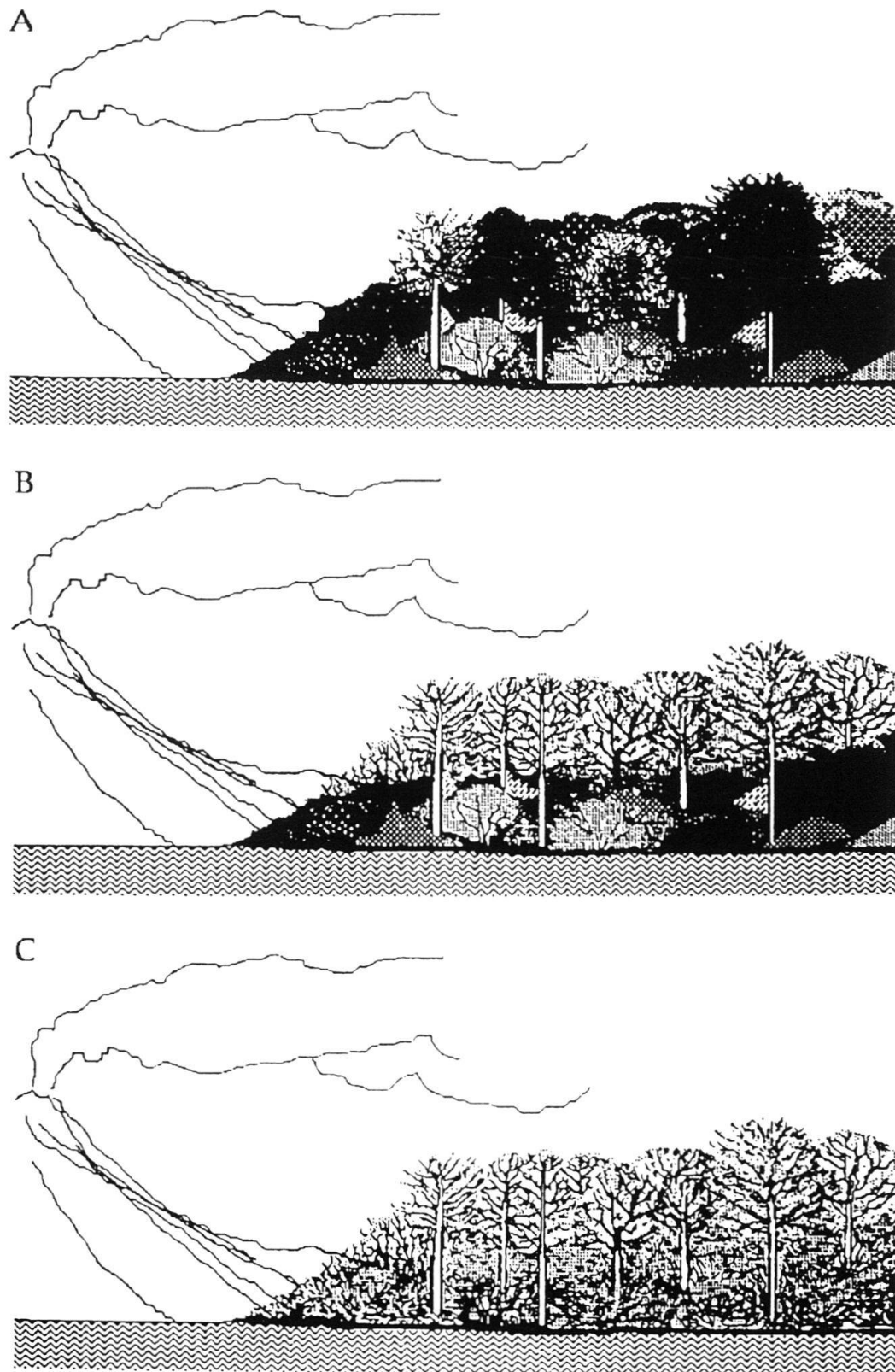Thus it is imperative that a combination of methods be applied whenever possible.

Fig. 9. The progressive loss of leaves in a forest as a consequence of volcanic activity. A. Situation at the start of a volcanic eruption – leaves of canopy and understorey still attached. B. Canopy species defoliated as a result of the coating of their leaves with volcanic ash. C. Leaves of the understorey dislodged by a subsequent ash fall.

7. Conclusions

1. As they are rooted to the substrate, terrestrial plants have to disperse their spores, pollen and diaspores if they are to be successful. This phenomenon and the fact that other plant parts are also shed in the course of life means that the palaeobotanical record is literally very scrappy.

2. Individual organs (e.g. wood, leaves, pollen, diaspores) only offer a very incomplete picture of past vegetation. By combining information from a variety of sources, a better approximation to reality is achieved.

3. Knowledge of the aerodynamic and hydrodynamic behaviour of individual plant parts is essential in order to estimate the distance from the source plants.

4. The plant-remains must be placed in their geological context and more attention paid to detail in the course of collecting. Badly preserved or fragmentary plant-remains should be noted as these can aid in the interpretation.

5. When different coeval depositional regimes are available, these ought to be studied as they can yield useful information on the spatial distribution of the vegetation. Sudden changes in the lithology can also be enlightening.

6. Considering the scrappy nature of the material palaeobotanists have to deal with, careful analyses of plant fossils can yield a remarkable amount of detail about the vegetation. As this data represents one of the primary sources of information on past climates (e.g. Wolfe 1993), it is imperative that it should be as accurate as possible.

Acknowledgements

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