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# Taphonomic considerations for plant evolutionary investigations

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Gastaldo RA 1992. Taphonomic considerations for plant evolutionary investigations. *Palaeobotanist* 41 : 211-223.

Taphonomic processes play the underlying role in the characteristics of fossil plant assemblages. Their influence on this data set, from which we interpret evolutionary trends within lineages and clades, often is not considered or taken into account. Examples are provided to illustrate the effects that plant life strategy, environments and ecological associations, original biochemical constituents, and the nature of depositional regimes have on plant part representation in subfossil and fossil assemblages. It is recommended that fossil assemblages be evaluated within depositional and sedimentological context before the data set is utilized for higher-order synthetic investigations.

**Key-words**—Taphonomy, Evolutionary trends, Palaeoenvironment.

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## सारांश

पौधों के विकासीय अन्वेषण हेतु जैवसाविकी का महत्व

रोबर्ट ए० गस्टाल्डो

अशिमत पादप समुच्चयों के लक्षणों में जैवसाविकीय प्रक्रियाओं की आधारभूत भूमिका रही है। आँकड़ों के समुच्चय पर इनके प्रभाव, जिनसे हम विकासीय प्रवृत्तियों का अन्वेषण करते हैं, पर कभी ध्यान नहीं रखा जाता। इसकी पुष्टी करने के लिए उपयुक्त उदाहरण भी प्रस्तुत किये गये हैं। यह प्रस्तावित किया गया है कि आँकड़ों का अन्वेषणात्मक संश्लेषण करने से पहले अशिमत समुच्चय का निक्षेपणीय एवं अवसादीय सन्दर्भ में मूल्यांकन करना आवश्यक है।

IN our attempt to develop testable hypotheses about evolutionary mechanisms and diversification patterns within vascular plants since their colonization of land, palaeobotanists often have regarded preserved macrofloras (taphocoenoses) as fully accurate portrayals of the vegetation existing at the time of accumulation. It was believed that non-vascular plants were rarely preserved due to the absence of "hard parts", in the sense of their not possessing vascular tissues. But, vascular plants that did possess "hard parts" were able to be fossilized if the conditions of the burial site were favorable. The emphasis for preservation was placed on the prevailing physical and chemical conditions within the depositional site. Few investigations in the early part of the 20th century (i.e., Potonié, 1910; Chaney, 1924) were conducted either to test these assumptions or to understand the possible

community contribution to any particular fossil plant assemblage. It is just within the past fifteen years that a major emphasis has been placed on actuopalaeontological investigations to examine these assumptions. Such studies have been designed to understand the origin of plant-bearing assemblages, the nature of that terrestrial record, and the underlying causes (biochemical and geochemical) that provide for their preservation. We can propose more accurate hypotheses to evaluate plant evolution only when these factors are integrated with the data subset. The purpose of this short contribution is to present an overview of plant taphonomic processes operating on the development of macrofossil assemblages in order to provide that basis.

### WHAT IS TAPHONOMY?

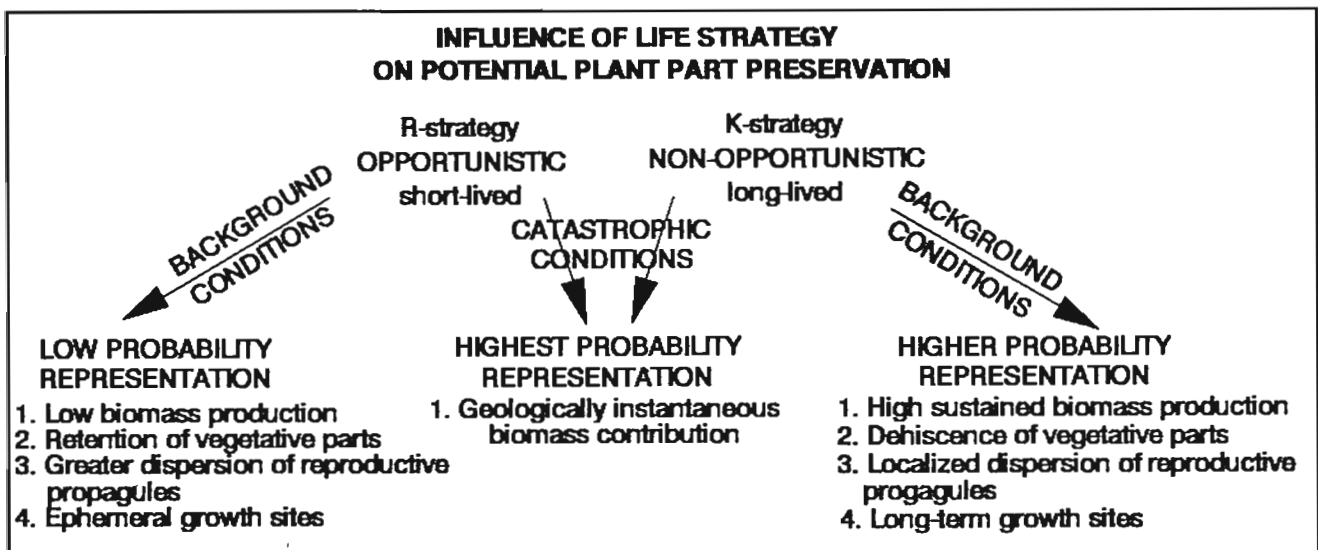
The term taphonomy was originally proposed by Efremov (1940) for the study of the principles that controlled the transferral of organic remains from the biosphere to the lithosphere. The definition and scope of these studies have been explained by several authors and the reader should consult other references for more detailed discussions (e.g., Behrensmeyer & Kidwell, 1985; Wilson, 1988; Gastaldo, 1988; Spicer, 1989; Allison & Briggs, 1991). It is agreed generally that the discipline encompasses the processes between 'death' of an organism and recovery at the outcrop. The former idea is certainly the case with vertebrates and most invertebrates. As I have discussed previously (Gastaldo, 1986, 1988), plant 'death' is not a prerequisite for the transferral of part of an organism (aerial or subterranean) or an entire organism (e.g., pollen and seeds) from the biotic to the abiotic realm. In most instances, a vast quantity of biomass is lost from a parent plant either through physiological (e.g., canopy part abscission, release of reproductive propagules) or traumatic (e.g., wind storms, hurricanes/cyclones, erosional bank failure, high-energy floods, volcanoclastic events, mud flows, etc.) mechanisms without necessarily causing its death. These plant parts include the majority of specimens that become our data base. Preservation of autochthonous (*in situ*) vegetation is a relatively rare phenomenon, and such assemblages make up a small proportion of the plant fossil record.

Taphonomic studies have been subdivided into three subdisciplines: necrology, biostratinomy, and

diagenesis. As the name implies, necrological investigations are focused on the 'death' of the organism (although I would broaden the scope of the term as noted above). Biostratinomic processes effect the organic matter from the moment of 'loss' to the time of burial (including biochemical and biogeochemical interactions), whereas diagenetic investigations concentrate primarily on the geochemical processes that are responsible for the preservation of the organic matter. Plant biomass is subjected to a complex of inter-related processes (Gastaldo, in press). None of these mechanisms is separated from the life strategy of individual taxa, the environments and ecological associations in which the plants originally lived, the original biochemical constituents of the plants themselves, and the nature of the depositional regimes into which they may be placed. All of these factors affect the recoverable plant assemblages from which we evaluate evolutionary lineages. Large-scale geological processes operating regionally (intrabasinal) and/or globally (interbasinal) play a role in our perception of the timing of first appearances and/or evolutionary innovations. These factors ultimately govern our understanding of evolutionary rates. This latter issue will not be addressed here.

### LIFE STRATEGIES

The life strategy of taxa and the life span of individual plants within any taxon play a major role in biomass production and, hence, the amount of potential material that may be preserved under background conditions (Text-figure 1). Background



**Text-figure 1**—Generalized diagram depicting the bias that plant life strategy has on the potential for preservation of plant parts under background and catastrophic conditions.

conditions are herein defined as the day-to-day circumstances that occur throughout a year and not localized, catastrophic mass mortalities induced by infrequent events (the term anastrophic sensu Cadée, 1991 is not used because of confusion in its application [def. chemistry—a coming together of disparate elements to form a coherent connected whole]). Of course there are exceptions, but in a broad general sense, the aerial vegetative parts of “annual” herbaceous plants become non-functional after completing the reproductive phase. These are retained on the parent where they undergo degradation. Even when individuals are near to a site of deposition (see below), there is little chance for taxa to become fossilized. When such plants occasionally are found, they provide exceptional insight into stages of evolutionary advancement (e.g., Taylor & Hickey, 1990).

Other R-strategists behave similarly, although there is a wider variety of potential representation in modern subfossil assemblages and potential preservation depending upon growth habit. Two examples from coastal tropical zones will demonstrate this point. The first is taken from the lower delta plain of the Mahakam River delta and concerns the palm, *Nypa fruticans* (Gastaldo & Huc, in press). The present Mahakam River delta is approximately 50 km in “length”, as measured from the delta front to the hinterland, and is distributed along the coast for nearly 100 km. The subaerial delta plain is approximately 2,000 km<sup>2</sup> of wetlands that are crossed by river and tidal channels. The vast majority of swampy land is vegetated by a dense monoculture of *Nypa*. The shoot apex of the palm is at ground level. Large, erect leaves grow to heights of 8 meters. Although *Nypa* are relatively long-lived, aerial parts of these plants are not common subfossils within the (hydric) soils in which they live. Fibrous petioles are most commonly found in tidal channels adjacent to these monocultures; laminae are found rarely. The typical fate of laminae is degradation while still attached to the erect or semi-erect petiole after the leaf has become non-functional. Only after extensive aerial degradation, including decay of all parenchyma tissues, does the petiole break and fall over. Commonly, even when broken, the petiole remains above ground or water level while decay proceeds.

Reproductive parts are physiologically shed from the plant, although vegetative parts are not. In spite of this, *Nypa* pollen is difficult to recover from soils (J. Ward, pers. comm. 11/90) and seeds of the palm also are rarely found. Pollen is not dispersed aerially because pollination is insect driven. Seeds do not accumulate in the mud because they float out

of the swamp transported by daily tides. Based on the proliferation and success of this taxon, and the high proportion of resistant plant parts that could be potentially preserved, one would expect that the evolution of this Cenophytic group would be better known. Recognition of this taxon in the fossil record has been limited, and its occurrence is reported as sporadic throughout former tropical regimes of the Tertiary (e.g., Collinson, 1983; Biosca & Via, 1987). Its poor representation in the fossil record is most likely due to its life strategy.

The second example is based on the mangrove community. Although these plants expend considerable amounts of energy developing an architecture based on the production of wood, and hence might be considered K-strategists, the community in which they live, relative to the mixed hardwood forest in the Mahakam delta, is opportunistic. Therefore, they are considered here as R-strategists. Woody mangroves colonize approximately 80 per cent of the world's coastlines, demonstrating a varied tolerance to salinity (Chapman, 1976). In the Mahakam River delta *Avicennia*, *Rhizophora*, and *Sonneratia* occur as a vegetational zone fringing the seaward side of the *Nypa* swamp. These mangals may be found next to channels toward the interior of the delta where salinity gradients are maintained by tides. The release of plant parts to potential fossil assemblages is physiologically controlled. Their release, though, follows a distinct periodicity. Biomass production measured in a monospecific, banded *Avicennia marina* forest in Mexico, averaged 614.5 gms/m<sup>2</sup>/yr (Lopez-Portillo & Ezcurra, 1985). Leaves accounted for the largest weight percentage (83%), while branches (9%), aborted flowers and reproductive parts (6%), and propagules (2%) were responsible for significantly less biomass. These figures are similar to those reported by others (Pool *et al.*, 1975; Duke *et al.*, 1981). Although leaves are dehisced from the mangrove year round, there is not only a variation in timing and intensity of leaf fall (highest number between April and September during high water-stress periods) but also a correlation between the increased loss of plant parts and the plants' reproductive cycle. Flowering peaks in July to September and high numbers of flowers are lost during this period. Seedlings are shed 3-4 months later, peaking in December (when lower salinities occur). Branch dehiscence is related to the loss of leaves and flowers they subtend, with the highest quantity lost 45 days after propagule fall. This rhythm is altered in the southern hemisphere where flowering in *Rhizophora* occurs from April to June and the highest number of leaves are lost between

August and January (Thailand—Anderson & Christensen, 1978). Because these coastal communities are directly open to ocean influences, most litter is transported out by tides and may be deposited in offshore areas (Risk & Rhodes, 1985).

It becomes clear that the preservation potential of any of these plant parts within the tidal flat environment in which they live, or the nearshore coastal zone, is related to several factors. The most obvious is their life habit which controls when the largest quantities of specific types of parts will be introduced to a depositional setting. Another factor relates to the coincidence of plant part loss and physical conditions (sedimentation rates, fluctuations in salinity related to freshwater discharge, etc.) associated with the hydrological regime that influences the site(s) of burial. Individual trees are relatively short-lived as small changes in edaphic and hydrological conditions cause community replacement in the developing hydrosere. Although woody mangals are a highly successful group of coastal vegetation, inadequacies exist in their fossil record. We lack true insight regarding the evolution of these plants. Again, the life strategy of the plant plays a role in the potential preservation of its various vegetative and reproductive parts.

Aerial parts of arborescent K-strategists have a higher potential of becoming fossilized because of the absolute numbers produced throughout the life history of an individual. A single mature deciduous arborescent angiosperm can abscise nearly 100,000 leaves in a single year (K. Johnson, pers. comm. 5/89). With a life expectancy of several centuries, the total number of leaves that could be contributed (under theoretical circumstances) to a depositional site would exceed several hundred million. Leaf loss can be temporally rhythmic, as demonstrated by Ebel *et al.* (1980). Short periods of high biomass shedding were noted to occur in evergreen angiosperms that related to the timing and production of new leaves. Although the patterns were observed for several evergreen angiosperms (e.g., *Magnolia grandiflora*, *Quercus ilex*) under artificial (greenhouse) conditions, biomass loss correlated well with data recorded previously under natural conditions. Not all arborescent plants act similarly; there are exceptions. For example, araucarians notably retain their leaf-bearing branches after the lateral system becomes non-functional.

Again, even in K-strategists, taxon life strategy will play a significant role as to the periodicity of plant part contribution to a subfossil assemblage. It is well known that many forest trees in the tropics

exhibit unique growth strategies. One such habit is displayed by members of the Dipterocarpaceae, but it is not restricted to this family. Mature trees may grow vegetatively for 2-7 years before suddenly undergoing a massive bloom. During these "mast" years, individuals of certain species flower in tight synchrony. It has been documented recently that closely related species of one taxon, *Shorea* (Section *Muticæ*), living within the same forest undergo sequential flowering over a period of several months (LaFrankie & Chan, 1991). Such behavior may influence the potential fossil assemblage. Flowers that are retained on the parent plant have a low probability entering a site of burial (presumed to be an adjacent depositional environment; see below). Flowers and their various vegetative and fertile parts that could be shed during the reproductive period may be absent because of an incompatibility between timing of reproduction and geochemical and/or sedimentological conditions in the depositional site. On the other hand, only certain taxa may be found "well"-preserved because of the coincidence of these abiotic factors in the site during the period in which this specific taxon sheds its parts. The life strategy of individual taxa, therefore, is one factor that is responsible for influencing biomass availability that might be forwarded to a fossil assemblage via physiological mechanisms.

Traumatic events may produce significant quantities of biomass instantaneously. These events may contribute a wide sampling of local and regional vegetation to a depositional system. Some plants may be undergoing a reproductive cycle at the moment catastrophe strikes, while others may be confined to a vegetative state. Even if a part of the community is fertile, the growth stature of individual plants may affect whether or not plant parts from those taxa have the potential of becoming part of the subfossil assemblage.

For example, when Hurricane Joan passed through the rain forests of southeastern Nicaragua in October 1988, more than 500,000 hectares of forest canopy were destroyed (Yih *et al.*, 1991). Nearly 80 per cent of canopy trees were either toppled or snapped during the passage of the storm (wind speeds exceeding 250 km/hr). Less than 27 per cent of the trees in the area remained standing, and only 18 per cent possessed leaves! Intermediate-sized trees were damaged the most, with the understory palms considerably less damaged. Minimal destruction and defoliation to understory vegetation is consistent with observations reported by Scheihing (1980) on the damage inflicted by Hurricane David that affected the eastern seaboard

of the United States, and Gastaldo (1990) reporting on the effect of cyclonic winds on forest vegetation. Parts of the canopy that are subjected to the full impact of the stress applied during passage of the storm front have the highest potential of being forwarded to a potentially preservable assemblage.

Not only will the stature and position of a plant within the community be a factor relating to the potential contribution of biomass to a fossil assemblage, but also the bauplan of individual taxa will govern what phytoclasts will be generated. When Hurricane Diana struck the coast of southern Florida in the early 1960's, damage to the coastal wetland vegetation in the Everglades was particularly concentrated. Up to 75 per cent of the mangrove population was defoliated. Not only were leaves stripped from the plants, but also woody branches and stems. Marsh grasses, on the other hand, remained virtually intact (Craighead, 1964; Craighead & Gilbert, 1962). Although some marsh grasses, such as *Spartina*, may grow to heights equivalent to mangroves, their histological construction allows for greater flexibility under changing stresses than does the mangrove architectural plan. Under such conditions, marsh grasses often are pushed over onto the soil's surface. These plants remain prostrate temporarily and commonly regain their erect stature.

Biomass production is the first stage that affects the potential composition of a resultant fossil assemblage. The life strategy of any plant will affect the way(s) in which that plant keeps or sheds vegetative and reproductive parts. Under background conditions, their loss will be in response to the taxon's physiological shifts as changes occur in physical conditions of the growth site. This behaviour will influence the ultimate disposition of plant parts originating from that taxon. It is probable that the subfossil record accumulating under such conditions is composed primarily of K-strategists, plants capable of producing large quantities of biomass over long life spans. Traumatically-induced assemblages have a higher probability of including R-strategist taxa, although this is dependent upon the community composition and the environment which is preserved by the catastrophe.

### ENVIRONMENTAL CONSIDERATIONS

Actuopalaeontological investigations have demonstrated that the bias of any taxon potentially to become part of the fossil record is dependent upon the environment in which it lives. The closer a plant is to a depositional site, the greater the probability that the plant will be represented in a

subfossil assemblage. Those plants and plant communities next to, or living within, a depositional environment have the highest potential of being included into those sediments (Ferguson, 1985). As noted above, though, the growth strategy of any specific taxon will play a significant role in its capability to contribute phytoclasts, even when a plant is living in a depositional environment favorable for preservation (Scheiuing & Pfefferkorn, 1984; Gastaldo *et al.*, 1987). As the distance away from the margin of the depositional site increase (often less than 50 m; Ferguson, 1985), there is a decreasing probability that this vegetation will contribute phytoclasts to this site. This is in spite of the fact that individual plants may produce a large quantity of biomass over their expected life. Not all possible contributing taxa are capable of forwarding biomass to the potential fossil assemblage. This appears to hold true regardless of prevailing climatic conditions (arctic to tropics) and terrestrial depositional environment (again excluding catastrophic mass mortalities). Such circumstances have been shown to be the case in lakes (Spicer, 1978; Glaser, 1981; Spicer & Wolfe, 1987; Gastaldo *et al.*, 1989), rivers (Burnham, 1989; Thomasson, 1991), fluvio-deltaic (Scheiuing & Pfefferkorn, 1984; Gastaldo *et al.*, 1987; Gastaldo *et al.*, in press; Gastaldo & Huc, in press), and nearshore marine (Burnham, 1990; Smith *et al.*, 1990) settings. Based upon these investigations, it appears that the type of fossil plant assemblage (phytotaphocoenosis) that results from plant part accumulation appears to be tied to the depositional environment (see: Behrensmeyer & Hook, 1992; Table 1).

Two examples will serve to demonstrate this point. Gastaldo *et al.* (1987) evaluated the provenance of subfossil phytoclasts preserved within a crevasse splay of the lower Mobile-Tensaw River delta, Alabama. The crevasse splay is now thirty years old, originating in the early 1960's during a severe flood, and prograding into an estuarine bay. The lower delta is characterized by semi-emergent and emergent marshes (sedges, rushes, and grasses), with scattered shrubs and individual trees of limited diversity occurring in sites with slightly better drainage. Aquatic and semi-aquatic plants occupy the shallow waters of the bay. Phytoclasts recovered from detrital peat shoals and the sediment-water interface of the main crevasse channel originate from communities outside of the localized splay. Most elements are allochthonous, having originated from levee, swamp, or extrabasinal communities. When comparing the taxa that are recovered in these subfossil assemblages with the taxonomic diversity of the communities from which they probably

**Table 1—Phytoclast abundance and assemblage type(s) within environmental context**

Coastal settings	Fluvial and Deltaic
<i>Nearshore</i> : Present-locally common; Allochthonous	<i>Channel Lags &amp; Bars</i> : Common; Allochthonous
<i>Lagoon</i> : Present; Allochthonous	<i>Abandoned channel</i> : Very common; Parautochthonous & Autochthonous
<i>Estuary</i> : Common; Allochthonous +/- Autochthonous	<i>Levee</i> : Uncommon; Para- & Autochthonous
<i>Beach</i> : Rare; Allochthonous	<i>Floodplain Poorly Drained</i> : Very Common Autochthonous & Parautochthonous
<b>Lacustrine</b>	<i>Floodplain Well-drained</i> : Present Autochthonous & Parautochthonous
LOW OXYGEN	<i>Crevasse Splay</i> : Present; Allochthonous & Autochthonous
<i>Large, Deep</i> : Rare; Allochthonous	<i>Interdistributary Bay</i> : Common; Autochthonous & Parautochthonous
<i>Small, Deep</i> : Common; Allochthonous & Autochthonous	
<i>Small Shallow</i> : Common; Allochthonous & Autochthonous	<b>Volcanigenic</b>
OXYGENATED	<i>Explosive Events</i> : Present; Autochthonous & Parautochthonous
<i>Large</i> : Uncommon; Allochthonous & Autochthonous	<i>Primary Ashfall</i> : Common; Autochthonous
	<i>Lacustrine</i> : Common; Autochthonous & Parautochthonous
<i>Small</i> : Uncommon; Allochthonous & Autochthonous	
<b>Eolian</b>	
<i>Dune</i> : Very Rare; Autochthonous	
<i>Interdune</i> : Present; Autochthonous & Parautochthonous	
<i>Loess</i> : Rare; Autochthonous & Parautochthonous.	

(after : Behrensmeyer &amp; Hook, 1992)

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originated, it is evident that these riparian elements only represent a small percentage of plant diversity in these areas. Contribution from local vegetation was represented by less than 12 per cent of the recoverable leaves. Biomass from the marsh communities either decays in place, adding significant quantities of organic carbon to the sediments, or is transported out of the system (during periods of higher discharge and/or tides). Similar conditions have been observed in depositional sites of the Mahakam River delta (Gastaldo & Huc, in press). The fact that only a fraction of any plant community can be found in these subfossil assemblages leads to the next question. What proportion of the arborescent flora can we expect potentially to be contributed to any particular site?

Insights into quantitative estimates of the percentage of canopy vegetation that ultimately might constitute the fossil record in any specific site come from studies conducted in the paratropics of Central America (Burnham, 1989). Four riverine subenvironments were surveyed along a 20 km length of the Rio San Pedro in Tabasco, Mexico, to determine the effect of vegetational heterogeneity on accumulating leaf litter. Leaf litter collected within the channel, forebank, levee, and back levee environments varied with regard to the percentages of immediate (that within a radius of 4.5 m from the sample site), local (those species found within 100 m of the sample site), and regional (all taxa identified during the course of the investigation)

flora that were recovered. Burnham (1989) found that the percentage of species contributed from the immediate flora of any single site was only slightly higher than that of the local flora. The immediate flora was most accurately represented in the back levee sites (having a low preservation potential), with an average of 46 per cent of taxa found in the litter. Any single collection within the study area may have "preserved" 13 to 51 per cent (averaging 37 per cent representation) of the local species. The forebank and back levee sites most accurately reflected the local flora, accounting for 41 per cent of the source vegetation. The regional flora was best represented in the back levee (only 25 per cent representation). The combination of data from different sample sites increased regional floristic representation. Where data sets from two subenvironments were united, representation increased to nearly 52 per cent. When the data sets of all four subenvironments were combined, representation jumped to 70 per cent.

Although it has been stated elsewhere by several authors based upon various data sets (Spicer, 1981; Ferguson, 1985; Gastaldo *et al.*, 1987), it must be restated that the plant fossil record represents a selective and non-representative part of the original vegetation. Representation requires preservation in a neighbouring depositional (sediment-accumulating) environment. This is not to imply that plant-rich "erosional" environments are uncommonly found in the stratigraphic record. On the contrary, volcanoclastic terrains are well-documented

examples of such environs. But, their occurrence is the result of catastrophic depositional events. These strata do not constitute a large proportion of the plant-bearing sedimentological record. Investigations of subfossil assemblages reveal that the probability of any plant becoming part of the fossil record is less than 1:2 in any single depositional environment, and may be as low as 1:10. It becomes obvious that even before plant parts are introduced into a site of potential preservation, filters are operating within the biotic community.

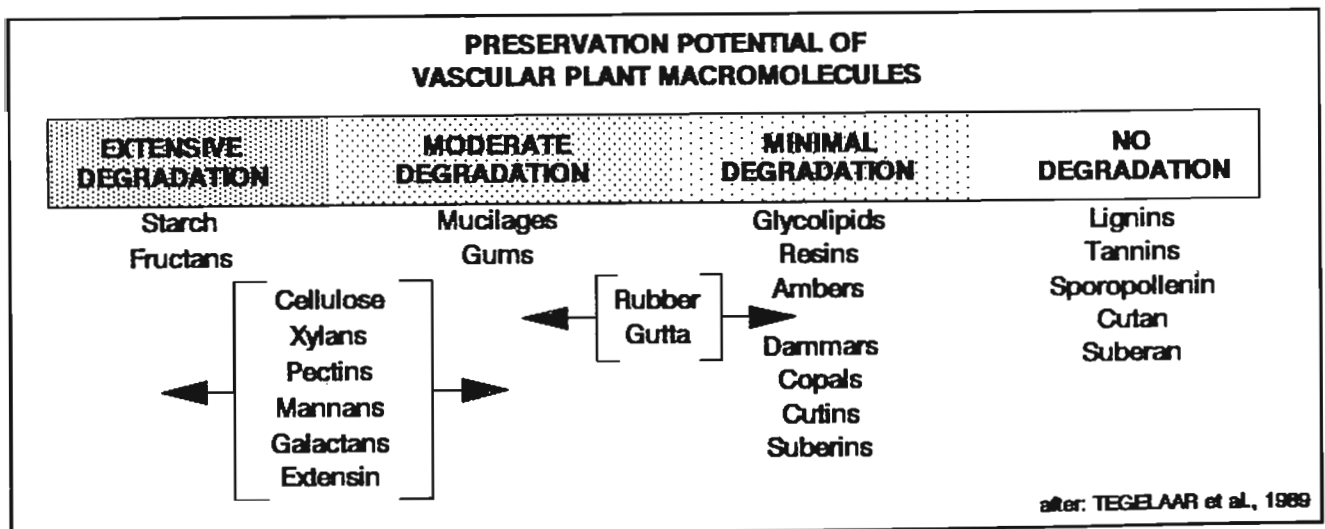
### BIOCHEMICAL CONSTRAINTS

It has been well documented that different rates of microbial and biochemical (catagenic) degradation affect the same plant part (e.g., leaves) from different taxa (see, for example, Spicer, 1981). This condition has often been referred to as 'palatability' (Gastaldo, in press), involving the energy content and nutritional value of the particular plant part. The physico-chemical attributes of different plant parts are responsible for the diverse rates of decomposition and what remains thereafter. It is becoming increasingly apparent that the underlying basis for these responses is biochemical.

Recent investigations have begun to explain the molecular complexity that selectively predisposes plants and plant parts to potential preservation. Those composed of labile and easily biodegradable biochemicals are consumed preferentially and rarely preserved, whereas the most resistant biopolymers and a variety of alteration products remain intact in the fossil record. Tegelaar *et al.* (1989) and De Leeuw and Largeau (in press) have inventoried

presently known biomacromolecules, their occurrence in living organisms, and their potential for survival in the molecular fossil record. Potential states of vascular plant macromolecule preservation range from extensive degradation (e.g., starch and fructans) to no degradation (e.g., lignins [Sigleo, 1978], suberan and cutan [Tegelaar *et al.*, 1989]) under any depositional condition. Other macromolecules also have a high preservation potential, a term that should be regarded as a relative concept that is dependent upon conditions within a particular depositional environment (Tegelaar *et al.*, 1989). These biochemicals include exudates (resins, ambers, and dammars), lipids, waxes, cutins (Tegelaar *et al.*, 1991), suberins, tannins (Wilson & Hatcher, 1988), and sporopollenin (Text-figure 2).

Although some of these macromolecules have a cosmopolitan distribution within the tracheophytes (for example, lignin in vascular cell walls), preliminary data indicate that there is a heterogeneous distribution of other biopolymers (Tegelaar *et al.*, 1991). Our best data, to date, concerns the macromolecules in cuticular matrices. Extant plant cuticles are either composed exclusively of cutin, cutan, or a mixture of both polymers (Nip *et al.*, 1986a, 1986b). Most extant cuticles examined are characterized by a mixture of biopolymers. Fossil cuticle is composed of either cutan or a mixed/modified-mix of polymers (Tegelaar *et al.*, 1991). This latter condition may be a function of geologic age. The mixed polymer cuticular matrix is reported from a Late Miocene taxodiaceous gymnosperm, whereas the modified-mixed cuticles are angiosperms of the Late



**Text-figure 2**—Diagrammatic illustration of preservation potentials of vascular plant biomacromolecules (after Tegelaar *et al.*, 1989).

Cretaceous to Late Eocene. All older cuticles analysed are composed exclusively of cutan. The presence of a mixed/modified-mix polymer also might be a function of systematic position, but the data set is presently too small to resolve this question. The fate of plant parts covered by cuticle, then, appears to be controlled by their original biochemistry.

The fossilization of cuticle is not a random occurrence. Cuticular matrices composed exclusively of cutin (e.g., *Lycopersicon esculentum*) have little chance of duripartic preservation, whereas those composed solely of cutan (e.g., *Beta vulgaris*) are most likely to be preserved (Tegelaar *et al.*, 1991). Cutin probably can not be diagenetically altered to cutan because it is found as a distinct monomer in extant plants. It is reported, though, that as biological maturation proceeds in the monocotyledonous angiosperms *Agave americana* and *Clivia miniata*, the cutin:cutan ratio changes (Tegelaar *et al.*, 1991). It appears likely that diagenetic enrichment of cutan, as a response to chemical alteration operating within mixed polymer cuticles, may provide the impetus for the duripartic preservation of all other cuticle-bearing plant parts. The presence or absence of these mixed-polymer cuticles will depend, of course, upon the original cutin:cutan ratio.

From the small data set available, it appears that neither systematic position nor physiological adaption to environmental conditions explains the distribution of the biopolymers. Within a single family there may be chemically diverse cuticular matrices. Cuticles of the two members of the Chenopodiaceae evaluated by Tegelaar *et al.* (1991), *Beta vulgaris* and *Salicornia europaea*, display both chemical extremes. Only cutan is found in the former, while cutin comprises the cuticle of the latter. Analyses of several taxa restricted to saline habitats exhibit the full spectrum of cuticular membrane types.

Hence, the preservational mode (*sensu* Schopf, 1975) of any particular taxon may be accounted for by taxon-specific biochemistry. Gastaldo *et al.* (1989) discussed the preservational mode of phytoclasts in a Recent oxbow of the Alabama River, Southeastern United States. We noted that whole leaves and/or leaf remains were not found when soft-sediment cores, recovered from the lake, were sieved. If a core was allowed to dry, though, leaf impressions could be recognized in the solidified sediment. Leaves occurred parallel to bedding. Distinctive venation patterns were found in relief on bedding surfaces, but cuticles were unrecoverable. At the time, the absence of tangible leaf remains was

thought to be due to geochemical processes operating in the depositional environment. It is quite possible that the absence of cuticle was the result of original biopolymer constraints, or a combination of both factors.

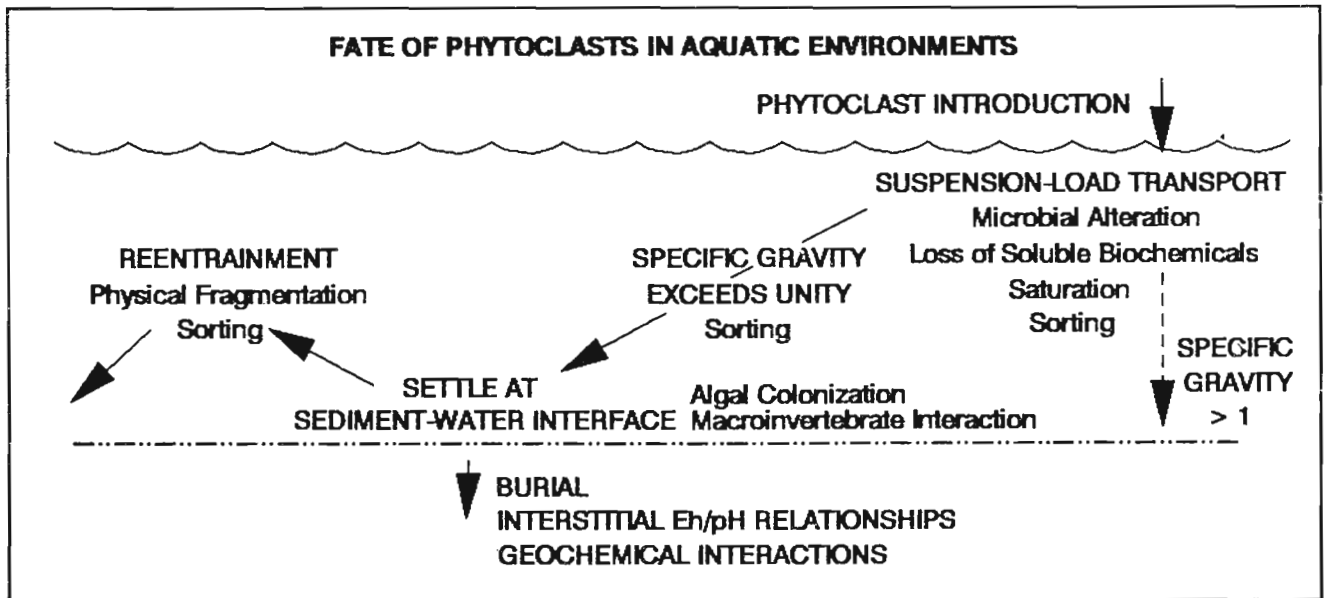
The role of molecular biochemistry has only recently been applied to palaeobotany. Its importance can not be overlooked. If the original biochemical composition of a taxon is found to be the controlling factor regulating its presence or absence in subfossil assemblages, the population of taxa that could potentially contribute to the plant fossil record would be greatly diminished. And, if such biochemical constraints are not systematically canalized, we may be evaluating a jig-saw puzzle and searching for more missing pieces than we now can imagine.

### THE NATURE OF DEPOSITIONAL REGIMES

There exists an underlying assumption that all that is necessary for plant part preservation is transferral to, and/or burial within, a "favourable" depositional environment. For that fraction of the regional/local flora introduced into a depositional environment, the pre-burial physicochemical and biochemical diagenetic processes, contemporaneous mechanical processes, and post-burial geochemical interactions operating in that site will govern the character of the assemblage. Assemblages are best preserved where these degradational processes have been retarded or suspended for any one or various reasons. It is beyond the scope of this paper to discuss those processes that appear to control the features and preservational mode(s) of plants in all possible depositional environments. The reader is directed to Spicer (1989) and Gastaldo (in press) for some details concerning this topic.

It is important to understand that the properties of plant parts introduced into depositional sites will constrain their behaviour under transport (Text-figure 3). Plant part behaviour in a water setting will affect the overall composition of the final fossil assemblage. Once the specific gravity of any phytoclast exceeds unity, it will settle from the water column. The initial specific gravity of some plant parts (e.g., some wood) is already greater than 1, and these sink immediately when introduced into the water column. In other cases, floating plant fragments undergo progressive water uptake until saturated. For example, leaves suspended in the water column undergo physicochemical changes similar to those operating on the forest floor. Saturation is accompanied by loss of soluble





**Text-figure 3**—Generalized diagram illustrating the behaviour of phytoclasts in aquatic environments and post-settling interactions that may influence preservation.

biochemicals from inter- and intracellular sites. How fast saturation occurs is controlled by cuticle and epicuticular wax thickness, stomatal and glandular hair (e.g., hydathode) density, leaf anatomy, laminar or petiolar damage (prior to or post introduction), water temperature, and water chemistry (Spicer, 1981; Ferguson & De Bock, 1983; Ferguson, 1985). Progressive alteration, accompanied by microbial deterioration, results in "softening". It has been hypothesized that biochemical diagenesis (with specific reference to selected lipids) functions principally in the water column and not to the degree once believed to occur after shallow burial within the sediment (up to 80 cm depth; Wakeham & Ertel, 1987). Such diagenesis is believed to operate in both oxic and anoxic waters. This would imply that if a plant part were to be 'removed' from the pool of potential fossils, it would happen before burial. Some diagenetic alteration does proceed in the shallow subsurface following burial (see below), and these reactions may alter the characteristics of the final assemblage.

The loss of competency affects the suspension-load residence time of any particular leaf and, hence, influences transportability, settling velocities, and reentrainment. Floatation times may vary from several hours to several weeks; thinner leaves degrade quickly and saturate faster than thicker leaves. This is most likely due to the differences in histological architecture (Osborne & Taylor, 1990). Thin papery leaves tend to settle before thick coriaceous leaves. This may result in taxonomic

sorting along a hydrological gradient based on the degree of alteration and/or residency time in suspension-load. These factors may affect leaf distribution within a particular depositional site, presenting a biased assemblage at any outcrop or part thereof (Spicer, 1980; Boyd, 1991).

In addition, because these altered features play a role in the potential reintroduction of parts into the water column (reentrainment) from the sediment-water interface, small-scale fluctuations in the hydrological regime may also aid in taxonomic sorting. The first site in which a plant part may come to rest may not be its final burial site. Phytoclasts may be moved several times before being sediment covered. This is particularly true in shallow-water environments where continued physical interactions occur between abiotic processes and biotic components (Gastaldo *et al.*, 1987; Gastaldo *et al.*, in press). Variability in wind-generated wave-energy lowers wave base in near shore sites resulting in the movement of phytoclasts shoreward. Mechanical abrasion that occurs during bedload transport may result in fragmentation or rounding. Taxa with more resistant parts (either as a function of architecture or aquatic residency time) have a higher probability of withstanding physical disintegration than less-resistant ones. Physical alteration may account for selective transport of particular taxa within the regime.

Phytoclast burial does not necessarily prevent it from continued degradation or further alteration. In fact, localized geochemical conditions (particularly

Eh/pH relationships; Gastaldo and Huc, in press) within the depositional environment play a major role in plant part survival. Two examples are presented to demonstrate this point. The first concerns the introduction of oxygen to interclast pore spaces in a sand substrate. Rindsberg and Gastaldo (1989) observed in a coastal setting that leaf litter buried at a depth of less than 1 meter is quickly degraded (on the order of several months to a few years) where fluctuations occur in the water level. These oscillations develop in response to variations in discharge rates, prevailing wind patterns (strong directional winds may lower water levels particularly in protected bays), and tidal cyclicity. Changes in water level accelerate chemical and microbial degradation. Macroinvertebrate bioturbation does not appear to play a role in destruction of bedded litter. Oxygen is introduced to the litter layers when shallow water sand bodies are subaerially exposed. A subsequent rise in water level will facilitate flushing of the sand, accelerating the loss of soluble compounds. Where the sand is colonized by plants (aquatic and semi-aquatic), aerobic decomposition of buried leaf debris proceeds most effectively where aerenchymatous roots pump oxygen to the rhizosphere. This results in the formation of an amorphous organic-stained horizon in which the most resistant plant parts (e.g., tracheary elements and cuticles) can still be identified. Less than 0.5 km laterally, well-defined bedded litters are preserved in this environment. Contemporaneous localized conditions, then, affect the resultant quality of the subfossil assemblage.

In other instances, bacterial-induced alteration may occur where litters have been buried and isolated from oxygenating waters. This includes the formation of methane (Rindsberg & Gastaldo, 1989) or sulfur compounds (Kohnen *et al.*, 1992). Only a few sample sites within the Mahakam River delta have yielded shallow subsurface sediments that were sulfurous (less than 2 meter depth; Gastaldo & Huc, in press). The obvious byproduct of sulphur-reducing bacterial processes is the formation of pyrite, signaling biochemical (early diagenetic) activity. Framboidal pyrite has been found on or within several different plant parts recovered from a few vibracores in abandoned tidal channels of both the upper (freshwater) and lower (low to moderate salinities) delta plain (Gastaldo, in press; Gastaldo & Huc, in press). It occurs either on leaf surfaces or within parenchymatous leaf tissues that border insect-damaged areas, and also on wood clasts. The incomplete geometric character of recovered framboids indicates continued activity beneath the sediment-water interface. Such pre-lithification, site-

specific alteration can modify the final inventory of potential fossil data, predisposing some components to a higher preservation potential than others.

The way(s) in which abiotic processes interact with biotic components is the last stage for modification of the potential fossil accumulation. How close the final burial site is to the original contributing vegetation will be a controlling factor in the quality of the fossilized material. Parautochthonous and catastrophically-buried autochthonous litter generally result in better resolution and higher accuracy in the plant assemblages. On the other extreme, allochthonous accumulations have a higher probability of being altered physicochemically, mechanically, and/or diagenetically. The behaviour of individual plant parts of various taxa (based on differences in shape, size, density, residency time, etc.) may result in their sorting along a gradient. Burial by no means insures preservation, as short-term and long-term geochemical interactions may locally alter subfossil plants.

## DISCUSSION

Palaeobotanists have come to recognize that plant evolution differs in many aspects from that documented in the Animal Kingdom (Traverse, 1989). Evolution in the Plant Kingdom occurs as a mosaic. Vegetative and reproductive plant organs evolve at different rates within lineages. The data upon which we base our understanding of changes in discrete phenologies depends upon the quality and quantity of specimens available in any particular fossiliferous site. It has also been well documented that clades evolve at variable tempos. The rates at which we perceive these changes are conditional upon the distribution of fossil plants throughout lithostratigraphic Systems, Series, and Stages.

Diverse terrestrial depositional environments appear to preserve specific types of organic assemblages with a recurring pattern through time (Behrensmeyer & Hook, 1992). Although broad generalities (general 'laws') are beginning to be identified with regard to the development of plant-bearing strata, certain taphonomic processes seem to operate within specific genetically-related depositional environments. For example, fossil plant assemblages in volcanoclastic terrains (Burnham & Spicer, 1986; Spicer, 1989) differ from those generated in coastal settings (Gastaldo, 1989; Gastaldo *et al.*, 1989; Gastaldo & Huc, in press). But, even with this in mind, just as most vegetational communities are heterogenous with regard to the distributional pattern of taxa, the fossil assemblages

preserved within these depositional environments must also be appreciated as representing a mosaic. Their distribution and quality of preservation may be biased by taphonomic interactions operating prior to, during, and following burial.

The complex interaction of these factors plays a pivotal role in if, when, where, how and why plant parts may become part of the fossil record. And, it is only a small part of this record from which we obtain our data base for testing evolutionary hypotheses. I hope the foregoing illustrations have demonstrated that taphonomic processes bear considerably on the final fossil assemblage upon which our data base is built. It becomes evident, then, that fossil plants must be assessed within depositional context. It is essential that these conditions be recognized before that data base can be utilized effectively.

Various taphonomic factors may be responsible for the presence or absence of a taxon within a depositional site. The 'palatability' and/or biogeochemical constituents of the taxon may be ultimately the deciding factors influencing preservation. The maturity of any contributed plant part may be extremely important, as younger parts may be biased towards degradation due to a higher percentage of degradable biopolymers. Other factors include the proximity of a plant to a depositional environment in response to changing intracommunity relationships. Taxa living some distance from the margin of a depositional site only may be able to forward plant parts following a disturbance (perturbation) that allows them to rapidly colonise the newly created open space. The hydrological sorting of plant parts during transport, and the prolonged residency time in the water column, will bias plant part distribution and conditions of preservation. Microbial interactions and the presence of inhospitable geochemical conditions, either at the sediment-water interface or in the shallow subsurface, will effect the final assemblage composition.

The factors affecting representation within these sites may not only be taphonomic, but also ecologic in response to larger-scale processes. Taxonomic presence or absence at a particular stratigraphic horizon may not be necessarily a function of speciation or extinction locally, regionally, or globally. Rather, it may be due to a large-scale response involving the shifting of vegetational belts as there is a change in climate (amelioration or deterioration) and modifications of geological terrains associated with such a change (e.g., Cecil, 1990). As the range margin of a population advances, the plant population expands into sites providing the requisite conditions for growth. If these terrains

do not include potential preservational sites, or ephemeral depositional environments, the result will be data loss from the stratigraphic record. Although difficult to document, we must not overlook the possibility of changing physiological behaviour and requirements of individual taxa in response to climatic or edaphic fluctuations that, over time, 'remove' taxa (temporarily or permanently) from depositional sites of potential preservation. The reappearance of once-believed extinct taxa in younger strata (the Lazarus-effect; e.g., Mamay & Bateman, 1991) seems to provide evidence in support of such circumstances. Local shifts in environments, then, may be a reason for change rather than larger scale evolutionary trends. It is no longer reasonable to judge the plant fossil record at face value alone.

#### ACKNOWLEDGEMENTS

This manuscript was written by the author during a sabbatical leave at the Institut und Museum für Geologie und Paläontologie, der Georg-August-Universität, Göttingen under a Research Prize awarded by the Alexander von Humboldt-Stiftung, Bonn. Dr Harald Walther, Dresden, is thanked for a critical reading of the manuscript and making suggestions for improvements. Studies in the Mahakam River delta were supported by NSF-EAR 88030609 and ACS PRF 20829-AC8, studies in the Mobile River delta have been supported by ACS PRF 18141-B2. The support of the AvH-Stiftung and the hospitality of Professor Dr Walter Riegel are greatly appreciated.

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