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Review of Palaeobotany and Palynology 101 (1998) 3–6

REVIEW
OF
PALAEOBOTANY
AND
PALYNOLOGY

Reconstructing Tertiary plant communities: introductory remarks

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Received 10 February 1997; revised version received 14 August 1997; accepted 9 September 1997

Abstract

Many previous reconstructions of Cenophytic vegetation were based on solitary data sets (mostly leaves) without consideration of the geological context or sedimentological setting. The use of multidisciplinary data sets provides a more reliable framework on which to base reconstructions of Tertiary plant ecosystems. An explanation is given for tables found throughout manuscripts of this special volume that outline probable life forms, dispersal mechanisms, and physiognomic signatures of the plants that are encountered fossilized in these assemblages. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: depositional setting; dispersal mechanisms; life forms; paleobotany; paleosols; palynofacies; palynology; physiognomic signatures; taphonomic biases

1. Introduction

Beginning with the earliest workers, similarities in overall vegetation between the Quarternary and the Tertiary led paleobotanists to attempt reconstructions of post-Cretaceous vegetation. Traditionally, most paleobotanists have relied on a single data set (either megafloreal or microfloral) from which to reconstruct purported communities and regional vegetation patterns. Often this data set has been evaluated out of geological context, without an understanding of the depositional setting and the taphonomic factors controlling representation and preservation of the assemblage. Although vegetated landscapes have been envisioned and fabricated based on such solitary data sets, these are often more subjective than an

objective representation of information available in the fossil record. Such attempts are evidenced by the advances that have been made throughout the past century.

2. The first attempts

Reconstructions depicted by nineteenth century workers, such as Heer (1868), were based on the assumption that all fossils present in a single locality were representative of the entire local and/or regional flora. Concepts of autochthony (remains of an individual preserved at the death site or the site where the parts were discarded) and allochthony (remains that have been moved from the site of death and out of the original habitat; Behrensmeyer and Hook, 1992) were not foreseen. Biases were not accounted for between the original vegetation and

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that small fraction preserved in the fossil record, and the depositional site(s) in which the fossils were preserved was not identified. The resultant 'family portraits' usually were based on only one data set, that of macroscopic leaves, leaving the validity of such reconstructions suspect.

Early twentieth century reconstructions attempted to be more critical (e.g., the Paleogene reconstruction of Mägdefrau, 1956). Communities and ecosystems were reassembled by integrating data from a variety of paleontological disciplines, including vertebrate paleontology. The paleobotanical data from which the reconstructions were drawn were expanded to include plant parts other than leaves, particularly fruits and seeds. Unfortunately, there was little regard to the geological setting or the depositional context(s) of these fossil assemblages. Possible taphonomic biases went unaccounted. Such reconstructions, too, leaned more towards that of invention than on objective criteria.

3. Towards more robust reconstructions

Data sets used for late 20th Century reconstructions of Tertiary vegetation have recognized the need for the integration of some geological data, this being primarily sedimentological criteria for recognizing depositional settings. Multiple paleobotanical data sets have been used that combine information derived from wood anatomy, palynology, carpology, and macroscopic leaf remains (e.g., Mosbrugger et al., 1994) but, in most instances, taphonomic biases, inherent in the various floral assemblages used as the basis for reconstruction, have been overlooked. To overcome some of the biases imposed by these factors, multivariate statistical analyses have been applied to these data to provide a more robust result (e.g., Boulter et al., 1993). Such approaches have led to the incorporation in the final reconstruction of many untested assumptions. Nevertheless, these advances have led to the development of more accurate local and regional vegetation reconstructions placed within a generalized geological context (e.g., Bužek et al., 1985; Mosbrugger et al., 1994), although some appear as abstracted 'aerial views' that blur community and ecosystem distinctions (e.g., Retallack, 1983).

4. The present approach

Within the past decade it has become evident that it is necessary to integrate multiple data sets from a wide variety of geological and biological disciplines to obtain the most objective information from which to reconstruct past vegetation (Gastaldo et al., 1996). For example, it is imperative that detailed sedimentological investigations occur contemporaneously with the collection of the plant fossils in order to identify the paleosols and depositional environments in which the assemblage(s) is (are) preserved. Not only do these settings provide the spatial context for the flora, but they also provide insights into the general conditions of plant preservation. Three-dimensional vertical and horizontal lithofacies relationships provide the bases from which to construct ideas about the paleogeographic framework of the ancient depositional systems and basin evolution. Preserved plant-remains must not only be systematically identified, but also must be evaluated independently as clasts. The taphonomic characterization of assemblages within any basin provides a more accurate assessment of what the fossil assemblages actually represent. The analysis of independent floral assemblages (leaves, fruits and seeds, spores and pollen, woods, and roots), including multivariate mathematical manipulations (where feasible), provides an opportunity for evaluating complementary, contradictory, and amplifying data of local and regional origin. The use of advanced analytical techniques affords the possibility for the assessment of geochemical and biogeochemical features of the ancient abiotic and biotic realm. In addition, the search for biomarkers preserved within sedimentary units may provide insights into plant components that may not be macroscopically preserved.

Although the aim has been to integrate all the available evidence, this has not always proved possible for a number of reasons. Sometimes part of the data set has had to be omitted for lack of expertise or financial support. On the other hand, poor preservation may be the prime cause. For instance, plant and animal remains are only preserved together under exceptional circumstances. When this is the case, an attempt has been made to incorporate the paleozoological information into the account. However, even if no animal remains have been recovered,

it is still possible to gain some insight into the regional fauna from the morphology of the fruits and seeds, the systematic position of the plant-remains, and any ichnological evidence of feeding (agrichnia) or dwelling (domichnia) structures or a combination of both (fodichnia). Thus, the presence of a large number of plants, the fleshy fruits of which are today dispersed by animals will probably reflect the presence of a rich frugivorous fauna. This is one of the reasons for including a table of the probable life forms, dispersal mechanisms and physiognomic signatures based on the different plant parts encountered in the assemblage into each manuscript found within this special issue. In this way the reader, who might fail to see the forest for the trees, should be able to envisage the vegetation in which so many plants and animals coexisted.

However, before we can do this, it is necessary to be conversant with some of the assumptions and concepts employed. It is generally assumed that when a taxon is represented by different plant parts within a single fossil assemblage, autochthony/parautochthony is the mechanism responsible for their association. This is because of the fact that different plant parts have distinct transport potentials and hydrodynamics. This idea gains credibility when the various plant parts are equally well represented. However, in order to make such comparisons, it is necessary that the organ genera, such as frequently employed by xylotomists and palynologists, are converted into botanical taxa. This may require detailed examination of the micromorphology using SEM. Nonetheless, the older the deposits, the more equivocal this process becomes. This explains why the organ genera have been cited in full in the case of the papers dealing with older Paleogene sites.

When the identification of one or more of the plant parts is uncertain, this has been indicated in the appropriate column with a question mark. When only qualitative information is available, a reliable record is denoted by a cross (×). A number of authors have employed a semiquantitative scale with up to four crosses. When quantitative results were at hand, these were presented on a logarithmic scale in the following manner: one dot represents less than 0.31623% of the total assemblage (wood, leaves, flowers, sporomorphs and diaspores being counted separately); two dots 0.31623–1%; three

dots 1.0001–3.1622%; four dots 3.1623–10%; five dots 10.0001–31.6228%; and six dots more than 31.6228%. When more than one infrageneric or infrafamilial taxon is involved, this is indicated in brackets after the dots or crosses. In the case of families, the number of genera are expressed by adding a 'G' after the digit. When an extinct genus is involved a dagger (†) is employed.

The primary dispersal mechanism category refers to the means of dissemination of the fruits and/or seeds (diaspores) of the taxon, rather than that of the particular plant part(s) present in the assemblage. The aim is to give an idea about the original density of the vegetation (e.g., autochory and wind dispersal are better suited for open habitats) and the presence of frugivorous animals (see above). Animals may pick up the disseminules in their fur or feathers (exozoochory), feed on the diaspores and transport them internally (endozoochory), or collect and bury the fruits for later use (dyschory; Müller-Schneider, 1977). Those seeds with an oily elaiosome are often transported by ants (myrmecochory). Although most wind-dispersed diaspores are also dispersed by water (nautochory), this category has been reserved for those plants making more exclusive use of this means of dissemination.

Plant habit is an important criterion for interpreting the paleoenvironment. The presence of numerous woody plants (phanerophytes) and lianas is typical of subtropical to tropical conditions. As the habit of a woody plant is governed by phenetic and/or genetic influences and it is often difficult to pin-point the nearest living relative, no attempt has been made to differentiate between shrubs (nanophanerophytes) and trees/lianas (macrophanerophytes). The term chamaephyte herein refers to cushion-like plants no higher than 50 cm. The herbs have been separated into annuals (therophytes) and perennials with or without an underground rhizome/bulb (geophytes and hemicryptophytes, respectively). Fully aquatic plants are referred to as hydrophytes. In practice the limits between these last three categories are sometimes difficult to ascertain. When various life forms occur within a given taxon, the less common habit(s) beside the chief life form are cited between brackets.

Deciduousness can tell us something about unfavourable conditions (drought or cold) in the course of the year. Abscission patterns based on a compari-

son with recent taxa are presented within the tables, with 'D' standing for deciduous and 'E' representing evergreen. If deciduousness is rare, this is denoted by placing the symbol in brackets, i.e. (D)/E. As abscission does not occur in herbs, these plants are indicated by an H.

Ever since the classic paper of Bailey and Sinnott (1916), leaf margin analysis of the woody dicotyledons has been used as a proxy for paleoclimate (e.g., Spicer, 1989; Wolfe, 1995). One drawback of this method is that the climatic signal is largely based on the canopy species growing in or near the preservational site. In the following contributions we make use of the fossil data when available (this will explain certain discrepancies among the different tables). In the cases where data are available for wood, flowers, pollen and/or diaspores, but missing for leaves, we have included information on the leaf margin characteristics based upon extant genera. By expanding the data set in this way, it is hoped to arrive at a more holistic portrayal of the vegetation as a whole.

When information on angiosperm leaf size was readily available, this was added to the table. Although the size of the leaves entering a water body is subject to a number of taphonomic processes and does not always tally with information from other sources (see Mai, 1995, table 11), it should in principle tell us something about air humidity. The larger the leaf, in a broad generalization, the higher the water vapor content of the atmosphere. The Raunkiaer leaf size classes Raunkiaer (1934) as refined by Webb (1959) were employed. The different categories are defined as follows:

- nanophyll, 0.25–2.25 cm²;
- microphyll, 2.25–20.25 cm²;
- notophyll, 20.25–40.5 cm²;
- mesophyll, 40.5–182 cm²;
- macrophyll, 182–1640 cm²;
- megaphyll, >1640 cm².

Dr. Harald Walther has always been an advocate of such an integrative approach to paleobotany. Therefore, it is appropriate in this volume dedicated to him that we should employ this procedure in the reconstruction of a number of Tertiary localities

from Central Europe — Harald's stomping ground. Harald's influence is very much apparent as can be seen in most of the contributions to this volume.

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