

Floral ecostratigraphy in practice

GREG RETALLACK

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Fossil plant associations are best named by traditional phytosociological methods from genera or species prominent in a reference collection. The named association then has some stability during later palaeoecological interpretation and three-dimensional mapping in sedimentary basins. Biostratigraphic zones are best established from successions of events in similar associations within a specified area. Such events may not have occurred in other types of association, nor have been contemporaneous in separate areas. These events are most effectively correlated when the likely environment and ecology of the associations are also considered.

Greg Retallack, Geology Department, University of New England, Armidale, N.S.W. 2351, Australia; 21st March, 1977.

The growing eco-consciousness of stratigraphic palaeontologists is well exemplified in a recent article in this journal by Bruce Waterhouse (1976). At the time he was writing, I too was grappling with similar problems but decided on a slightly different solution, which I applied to megafossil floras of eastern Australia and New Zealand (Retallack, in press).

Traditionally, modern plant communities have been classified under a hierarchy largely devised by J. Braun-Blanquet (1932). Although widely superseded in modern ecologist's minds by the 'individualistic' and 'continuum' concepts, the Braun-Blanquet system can be productively applied to palaeobotany, as also intimated by Martinsson (in postscript to Waterhouse, 1976). The basic unit of the system is the association – a community of definite floristic composition and more or less uniform habitat. This may contain individual synusiae, such as the tree layers, lianes and herbs of tropical rain forest. There are also higher divisions into alliances, orders and classes.

Some of these units are preferable to the system proposed by Waterhouse (1976). Particularly advantageous is the method of forming association names from the root of the characteristic genus name by adding the suffix '-etum'. Several other ways of making more specific names are detailed by Braun-Blanquet (1932) and Daubenmire (1968). Association names are not italicized. Thus they are easily distinguished from species, stages and biostratigraphic zones. Hopefully, the reader will not be too confused about the Bringelly Shale containing *Dicroidium*

odontopteroides in a *Dicroidietum odontopteroides* of the *Dicroidium odontopteroides* zone during the Anisian (Fig. 1).

Poore (1956) has aptly pointed out that an association is best defined from a stand which is most distinct from others (a 'nodum'), than from where it intergrades. I have taken the nodum of a fossil plant association as a collection from a reference locality. Thus the association has an objective reality. Ideally the reference collection should be a subautochthonous, well preserved, diverse accumulation of plant material, including leaves, fruits and logs. This facilitates further identification of the association in the same way as a well preserved holotype of a fossil species. I found that if this grip on reality is not maintained, the system becomes very confused very quickly. The 'association' changes with every new interpretation of former ecology, depositional environment and bias in collecting and preservation, and may be critically affected by very tenuous evidence.

A major corollary of the concept of the nodum collection, is that my fossil plant associations are not purely a reconstruction of former plant communities, but merely a workable approximation. They are associations of fossils which are better explained by palaeoecology than biostratigraphy. The two examples following illustrate the difference.

A modern ecologist would have little hesitation in naming heath and forest vegetation as separate associations, even if their specific composition was more or less similar. Fortuitous association of palaeosols, exceptional preserva-

ASSOCIATION	OPPEL-ZONE	AGE
Johnstoneium Dicrodium xylopteroidium Phoenixopsetum Dicrodium odontopteroidium Linguifolietum Pachydermophylletum	<i>Yabeiella</i>	RHAETIAN
		NORIAN
		CARNIAN
Dicrodium zuberi xylopteroidium Taeniopteretum lentriculiformis Pleuromeietum Voltziopsetum Dicrodium zuberi Voltziopsetum 'Thinnfeldia' callipteroidium	<i>Dicrodium odontopteroides</i>	LADINIAN
		ANISIAN
	<i>Dicrodium zuberi</i>	SCYTHIAN
	'Thinnfeldia' callipteroides	LATE PERMIAN

Fig. 1. Associations and oppeI-zones of Triassic megafossil plants from eastern Australasia proposed by Retallack (in press). Stippled associations are mesophytic coastal plain communities. Associations to left are inland, those to right are coastal communities.

tion of some fossil woods, sedimentological analysis and intensive collecting suggest that my *Dicrodium zuberi* (Fig. 1) may have been a heath and a forest at different times and places. The evidence is inconclusive, valid for only a few places and the arguments for and against may range for centuries. In order to apply the association name to a workable biostratigraphy, it must cover both, or perhaps more, distinct types of vegetation.

A modern ecologist would regard a stand of trees with an understory of ferns as a single association containing two synusia - trees and ferns. Horsetails, ferns and lycophods are probably more prominent in the Triassic fossil

record than they ever were in life because they flourished near water and depositional environments. Thus, if a fossil plant association largely of pteridophytic remains has enough seed plant remains to recognize the seed plant association, it is better to regard the pteridophytes as a synusium of the seed plant association. Nevertheless, pteridophytic associations such as the *Pleuromeietum* have proved distinctive and stratigraphically useful. The interpretation of synusia will always be difficult.

Once one has grasped the ecological bull by the horns, it is very difficult to discern biostratigraphic zones anywhere in the complex interaction of migrating florules, soil types,

sedimentary environments and climates. For example, the floras immediately ancestral to, and examples of, the *Dicroidietum zuberi* are found in latest Permian to early Triassic rocks of the Indian part of Gondwanaland (Retallack, in press). How long did these, or the *Dicroidietum zuberi*, take to migrate around to the early Triassic coastal plains of eastern Australia? In the Sydney Basin, they seem to have made little headway against the *Voltziopsetum* coniferous forests until a regime of volcanogenic substrate and high water table changed to one of more quartzose, well drained soils. Thus the boundary between the *Dicroidium zuberi* and '*Thinnfeldia*' *callipteroides* Oppel-zones in the Sydney Basin is probably due to migration, but these zones can seldom be recognized within the *Voltziopsetum* in any case. The timing and nature of such migrations may be evaluated by concurrent sedimentological and palaeopedological studies, isotopic dating or the correlation of eustatic cycles, recently proposed by Vail & Mitchum (Gussow 1976).

Biostratigraphic zones do not have the magical power to truncate ecological patterns as shown by Waterhouse (1976, Fig. 1) and Krassilov (1974). For example, the *Linguifolietum* and *Pachydermophylletum* appear to have been specialized coastal communities of very low species diversity and lacking species diagnostic of other coeval plant associations. They persisted unchanged from the Late Anisian to Rhaetian regardless of an oppel-zone boundary.

Considering such difficulties, a boundary stratotype or 'golden spike' definition of biostratigraphic zones would seem most appropriate. However, terrestrial sediments are commonly composed of complexly interdigitating facies and are even more conspicuously riddled with diastems than marine rocks. In my experience, it

is simply not possible to collect fossil plants in a similar fashion to Kauffman's (1970) successive bivalve populations. The best approach to the boundary stratotype philosophy which I could manage, was to define oppel-zones from a single type of association from a single area; mesophytic communities of the eastern Australasian Triassic coastal plain. The boundaries of the four oppel-zones are delineated by five theoretical events in such communities: the arrival of '*Thinnfeldia*' *callipteroides*, the differentiation or arrival of *Dicroidium zuberi* and then of *D. odontopteroides*, the appearance of *Yabeiella* and the extinction of *Dicroidium*.

Once we have established the distribution of the associations in three dimensional sedimentary basins and in time (Fig. 1), then all associations convey some constraints for dating sedimentary formations, as well as palaeo-ecological information.

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