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The early evolution of the plant life of South-western Australia: comment

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In a recent presidential address, Beard (1989) suggested that "it was only with the coming of Angiosperms ..... that the entire surface of the earth could be colonized for the first time and a complete plant cover established." As Beard notes in his discussion of my work on reconstructing Triassic vegetation, there is no clear evidence for or against this proposition from fossil plants alone. Nor can there be. As is well known, fossil plants are seldom preserved in place in upland soils because they decay aerobically and are rarely buried in such environments (Retallack 1984). The critical evidence for Beard's hypothesis is not fossil plants, but the paleosols in which they grew. On these grounds, Beard's hypothesis is easily falsified. There are many published reports of red, highly oxidized Triassic paleosols of well drained and upland habitats, and many of these paleosols show abundant root traces and soil horizons typical for soils formed under woodland (Ortlam 1972, Retallack 1976, 1977, Kraus & Middleton 1987, Blodgett 1988, Martins & Pfefferkorn, 1988). It was the paleosols that were the basis for my reconstructions of vegetation and habitats during Triassic time, not the fragmentary remains of plants in local lowland deposits.

The problem of the advent through geological time of woodland and forest cover of well drained soils is only now beginning to be tackled from the perspective of paleosols. Root traces and soil horizons typical under woodlands are found in paleosols of alluvial bottomlands and semi-arid floodplains of Late Devonian age (Retallack 1985). Such stout root traces and thick horizons are found in nutrient-poor silica sands of deltas and in kaolinitic clays of karstified uplands no earlier than mid-Carboniferous (Retallack 1986). Thus there may be some merit to Beard's suggestion that woodland cover was at first in favourable habitats and later spread to habitats difficult because of excessive drainage or low nutrient levels, but all this happened long before angiosperms.

With regard to angiosperms, I can find no inkling that Hughes (1973) regarded them as mangroves during the Cretaceous, as stated by Beard. There were some mid-Cretaceous angiosperm mangroves (Retallack & Dilcher 1981a,b), but most of the early Cretaceous angiosperms were weedy coastal plants other than mangroves (Retallack & Dilcher 1986). In North America, mid-Cretaceous angiosperm megafossils are found in river, lake, swamp and coastal deposits and paleosols. However, associated deep marine and lacustrine deposits have pollen assemblages dominated by conifers. The abundant kaolinitic, nutrient-poor, densely-rooted paleosols of uplands probably were forested mainly by conifers (Retallack & Dilcher 1986). Thus the angiosperms were early successional colonizers of disturbed river banks and beach ridges, not stress-tolerant colonizers of barren uplands. Although one would expect angiosperms to have had a great effect on terrestrial weathering (Knoll & James 1987), Cretaceous paleosols now known are not discernibly different from those of Jurassic or early Tertiary age (Retallack 1986). Claims for the distinctiveness of angiosperms underestimate what is now known about the biological sophistication of seed ferns (Retallack & Dilcher 1988). The appearance of grassland paleosols, with their distinctive granular surface horizon, signals a new and important kind of angiospermous vegetation during the Oligocene and Miocene, but grasslands appear to have been interpolated between and displaced pre-existing wooded shrublands and dry woodlands (Retallack 1990). These and other hypotheses about where plants lived in the distant geological past should not be based entirely on paleobotanical evidence, but rely on increasingly sophisticated analyses of the ancient soils in which they grew.

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Reply by author J S Beard to comment by J Retallack

Dr Retallack's work on paleosols is well known and offers important contributions to our understanding of the plant life an habitats of earlier geological periods. I did not refer to it in my address because it did not seem to me, at the stage which it has reached, to give us significant evidence specifically on upland biota. The reason is this, that if a soil profile is to be preserved and not eroded away it must be buried by transported material of some kind. Almost always this comprises layers of sediment, and for these to be laid down the paleosol must have formed in a depositional sedimentary environment, and cannot have been a remote upland soil of the kind we are discussing. It is difficult to see how soils of the latter type could ever become buried by sediment; but they could of course be buried by aeolian deposits or volcanic eruptions, and if we are able to look for more evidence in this controversy, this surely is where our energies should be directed. If my theory is to be proved wrong we have to find a pre-Angiosperm flora growing on a dry inhospitable upland substrate.

Even then we shall not have reached a definite conclusion. While the existence of aeolian deposits is *prima facie* evidence for an arid climate, we would have to examine the fossil material for evidence of its xeromorphic character; in other words, was it really growing on a "dry inhospitable upland substrate". Numerous authors have commented on the lack of xeromorphy in Mesozoic gymnosperms and the evolution of such characters in gymnosperms later during the Tertiary.

I have seen a paleosol containing charcoal beneath a Pliocene lava flow in Victoria, and numerous examples of soil profiles buried by successive layers of volcanic ash in the Caribbean islands. These cases however are not of sufficient antiquity. Plumstead (1969) recorded in South Africa that a fossilized forest originally growing in the uppermost Cave Sandstone (Triassic) and buried by the basal Drakensberg lavas (Jurassic) could be traced over a distance of 2.4 km, but she identified no components. As this might very well be a case of a genuine upland palesol I endeavoured to obtain further information but without success. Material had been extracted and sent to Paris for examination but there the trail ended. This is Dr Retallack's field and I suggest he might like to arrange a visit to South Africa to locate the site.

I evidently gave the wrong reference to Hughes' halophyte theory, but in any case neither he nor I said that early Angiosperms were mangroves. The expression was that "mangrove environments were critical to their dispersal and succession as they moved to upland sites and disturbed areas along edges of stream valleys and coasts". This is essentially the same view as Retallack & Dilcher in their "Cretaceous Angiosperm Invasion of North America" (1986).

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