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Comment on "Hot, dry, wet, cold or toxic? Revisiting the ecological significance of leaf cuticular micromorphology" by M. Haworth and J.C. McElwain [Palaeogeography, Palaeoclimatology, Palaeoecology 262 (2008) 79-90]

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1. Terminology

Haworth and McElwain (2008) reach the illogical conclusion that xeromorphic features of plants are not xeromorphic because of confusion between genetic and descriptive terminology. Descriptive terms for the suite of plant features including thick cuticles are scleromorph, sclerophyte, or sclerophyll (Greek σκληρον meaning "hard, harsh, rough, stiff"), not xeromorph, and descriptive redefinition of "xeromorph" by Haworth and McElwain (2008, *inter alia*) is confusing. Xeromorph is a form attributed to dry climate, and is thus unavoidably genetic: xeromorphic implies that scleromorphic features were induced by dry climate. Scleromorphy can also be produced by other environmental hardships, such as nutrient shortage (peinomorphy of Walter, 1973) and high salinity (halophyty, e.g. Rich et al., 2008: "halomorphic" is generally used for soils rather than plants, e.g. Mendoza et al., 2005). Haworth and McElwain's (2008) failure to mention halophytes is puzzling, because there are several published interpretations of their chosen example, *Pseudofrenelopis parceramosa*, as a mangrove or salt marsh plant (Retallack and Dilcher, 1986). Halophyty is a common explanation for the hard leaves and succulence of mangroves and glassworts (Walter, 1973). Peinomorphy is a common explanation for small stiff leaves of coastal heaths or pygmy forest in silica–iron soils (Spodosols) or on mineral-poor peats (Histosols: Walter, 1973; Jenny, 1980; Retallack, 1997). Peinomorphy may also be created by the acidic leaching environments of elevated atmospheric CO_2 and in areas of SO_2 gases from volcanic fumaroles, because both gases have the effect of acidifying substrates to make nutrient acquisition difficult (Retallack, 2001). A final possibility not mentioned by Haworth and McElwain (2008) is that scleromorphy may have no environmental significance in itself. Kräusel (1923) argued from the distribution of papillate stomata in fossil plants that this feature of *P. parceramosa* investigated by Haworth and McElwain (2008) was not of adaptive significance, but "primitive" (in cladistic terms, plesiomorphic) for gymnosperms.

2. Paleoenvironmental testing

Xeromorphy, peinomorphy, halophyty and the null hypothesis of plesiomorphy for scleromorphic features such as papillate cuticles are testable with independent evidence for environments of modern plants (Mendoza et al., 2005; Rich et al., 2008), or with paleoenvironment of fossil plants. The Early Cretaceous, Wessex Formation at Worbarrow Bay (Dorset, England) has evidence that the papillate sunken stomata of *Pseudofrenelopsis parceramosa* were adaptive, because the abundance of this feature varies with changes in paleoenvironment (Robinson et al.,

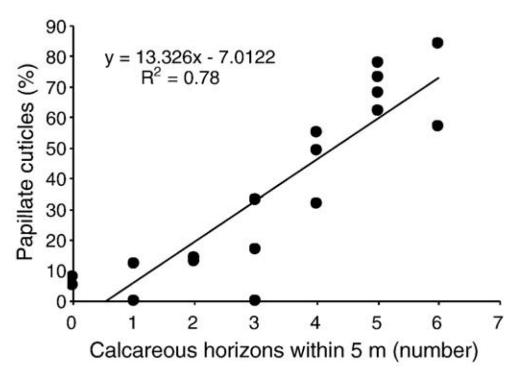

Fig. 1. Correlation between abundance of calcareous horizons within 5 m of stratigraphic level and proportion of papillate cuticles in *Pseudofrenelopsis parceramosa* at that level in the Wessex Formation (Early Cretaceous) of Worbarrow Bay (Dorset, England: data from Haworth and McElwain, 2008). The *t*-test probability of this relationship being due to chance is <0.0001.

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2002), although this is difficult to ascertain from the stratigraphic column of Haworth and McElwain (2008, Fig. 3), because it has no lithological key. The Wessex Formation includes dinoflagellates, and marine trace fossils and molluscs in the upper part where it passes conformably into the marine Greensand (Martill and Naish, 2001), but this uppermost part of the formation at Worbarrow Bay has the lowest proportion of papillate cuticles (Haworth and McElwain, 2008), so that halophyty is not supported. Nor is volcanogenic peinomorphy indicated, because there is no clear evidence of volcanic eruptions during deposition of the Wessex Formation. Paleosols of the Wessex Formation are clayey and calcareous (as in Alfisols and Aridisols), rather than coaly (as in Histosols) or ferric–quartzose (as in Spodosols) like soils and paleosols of coastal heaths or pygmy forests (Retallack, 1997). Moreover, peinomorphy would not have been induced by unusually acidic atmospheric gases: estimates of low atmospheric CO_2 come from the carbon isotopic values of pedogenic carbonate (Robinson et al., 2002), and low CO_2 and SO_2 (Tanner et al., 2007) from stomatal index of *P. parceramosa* (Haworth et al., 2005). Pedogenic carbonate in the Wessex Formation is evidence of a dry climate (<1000 mm mean annual precipitation) in which evaporation exceeds precipitation (Robinson et al., 2002), and it is striking how much more abundant are papillate cuticles in those parts of the Wessex Formation with the most carbonate nodular horizons. There is a highly significant correlation (Fig. 1) in data presented by Haworth and McElwain (2008) between the proportion of papillate cuticles versus the number of carbonate nodular horizons within the same stratigraphic interval (±5 m) in their lithological section. Better measures would be the depth of carbonate and its spread within the paleosols, as proxies for former mean annual rainfall and seasonality of rainfall (Retallack, 2005), or chemical composition of the paleosol B horizons as guides to nutrient status, paleoprecipitation, and paleotemperature (Sheldon et al., 2002). Nevertheless, the new analysis presented here (Fig. 1) is evidence that scleromorphic features such as the papillate cuticles of *P. parceramosa* were indeed xeromorphic, contrary to the conclusions of Haworth and McElwain (2008).

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