Palaeogeography, Palaeoclimatology, Palaeoecology 262 (2008) 79–90

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Hot, dry, wet, cold or toxic? Revisiting the ecological significance of leaf and cuticular micromorphology

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ARTICLE INFO

Article history:
Received 14 September 2007
Received in revised form 18 January 2008
Accepted 3 February 2008

Keywords:
Xeromorphy
Plant cuticle
Papillae
Palaeobotany
Palaeoclimatology
Aridity
Pseudofrenelopsis

ABSTRACT

Fossil plant morphological traits have been used extensively as palaeoenvironment and palaeoclimate indicators. Xeromorphic features are considered to be structural adaptations that reduce water loss (e.g. thick cuticle, sunken stomata, epidermal papillae and trichomes, stomatal papillae and stomata arranged in sunken grooves), and their presence in fossil plants is often used to indicate palaeo-environmental aridity. However, in living plants, xeromorphic traits are not restricted to plants subjected to water stress and are commonly observed in plants growing in environments with high precipitation, humidity and water availability. These "xeromorphic" features often serve multiple functions such as water-repellence, defence and protection from excess light. The use of "xeromorphic" features as indicators of palaeo-environmental aridity therefore requires reinterpretation. Here we review the ecological functions of "xeromorphic" adaptations in extant plants and analyse the equivocal nature of these morphological features using the extinct Cretaceous conifer *Pseudofrenelopsis parceramosa* (Fontaine) Watson. We track the occurrence of stomatal papillae (waxy lobes over-hanging the stomatal pit) that are commonly considered to have an anti-transpirant function, in *P. parceramosa* through Valanginian–Barremian sediments deposited in a fresh water lowland environment at Worbarrow Bay, Dorset, southern England. The presence/absence of stomatal papillae in *P. parceramosa* does not display a pattern consistent with an anti-transpirant function. In the context of supporting sedimentological, geochemical and climate modelling evidence we hypothesise that the primary function of stomatal papillae may be to repel liquid water, in addition to other functions such as providing structural support, pathogen-defence and as a response to high atmospheric particulate content caused by localised volcanism. Our review presents a new palaeo-environmental interpretation of a widespread and important mid-Cretaceous conifer but also provides an updated synthesis of palaeo-environmental data that can be interpreted from "xeromorphic" features in fossil plants.

1. Introduction

The presence of "xeromorphic" features in fossil plants is often used to indicate palaeo-environmental aridity (e.g. Alvin, 1983; Watson and Alvin, 1996; Gomez et al., 2001; Axsmith and Jacobs, 2005). However, in extant plants these "xeromorphic" features are not restricted to plants growing in arid environments, but commonly occur in plants growing in both high precipitation and high water availability habitats (e.g. Brodribb and Hill, 1998; Waldhoff and Furch, 2002; Waldhoff, 2003; Burgess and Dawson, 2004). A xeromorphic adaptation is defined as a plant structural feature that reduces transpiration (Hill, 1998). Here, we will continue to use the term xeromorphic, however, not in its traditional sense, meaning "pertaining to a dry shape/form", rather as a descriptive term for the suite of plant features, outlined below, normally considered as being anti-transpirant in function (i.e. reducing water loss via plant evapotranspiration). We will review the numerous potential functions of cuticle features commonly classed as xeromorphic in extant plants, and relate this to interpretation of palaeo-environmental aridity using the extinct conifer *Pseudofrenelopsis parceramosa* (Fontaine) Watson. We outline the equivocal nature of the so called xeromorphic features in *P. parceramosa* as indicators of palaeo-environmental aridity and present new stratigraphical data tracking the temporal occurrence of one such "xeromorphic" feature, stomatal papillae, through the Early Cretaceous (Hauterivian–Aptian: 136–108 Ma) as a case example.

Supposedly xeromorphic plant features such as a thick cuticle, sunken stomata, trichomes, epidermal and stomatal papillae, have long been assumed in palaeobotanical research to equate to palaeo-environmental aridity (e.g. Seward, 1892; Watson, 1988; Srinivasan, 1995; Watson and Alvin, 1996; Watson and Alvin, 1999). Often these interpretations are speculative (Harris, 1956) and in some cases contradict co-occurring sedimentological climate indicators (e.g. Watson and Alvin, 1996; Gomez et al., 2001; Hesselbo et al., 2003).

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doi:10.1016/j.palaeo.2008.02.009

Features such as epidermal trichomes and papillae, sunken stomata and stomatal furrows are considered to be xeromorphic due to the resulting increase in boundary layer resistance (Fig. 1). The boundary layer is an area of still air at the leaf surface offering resistance to diffusion of water vapour. The boundary layer affects water vapour loss to a greater extent than CO_2 uptake due to the greater diffusion distance and resistances involved in CO_2 acquisition (Gaastra, 1959; Jones, 1992; Willmer and Fricker, 1996). Under field conditions the boundary layer resistance of crop species is at least an order of magnitude smaller than the minimum stomatal resistance (i.e. when stomata are fully open) (Long, 1985), illustrating the minimal importance of boundary layer resistance as an anti-transpirant mechanism in comparison to effective stomatal control. For example, the stomatal resistance to water vapour of *Salix herbacea*, a dwarf willow with extremely hairy leaves, is 11.7 ± 6.2 s cm^{-1}, whilst boundary layer resistance is 0.4 s cm^{-1} (Gauslaa, 1984).

"Xeromorphic" features have usually been assumed to indicate plant growth in an environment where photosynthesis is limited by water availability. This is because any increase in boundary layer resistance is considered to reduce water loss and also CO_2 uptake (Hill, 1998). In other words, it is assumed that "xeromorphic" traits should only occur where the benefit of reducing water loss via an increase in boundary layer resistance far outweighs the cost to the plant of reducing CO_2 uptake, which would lead to a decease in photosynthesis. This assumption is supported by stomata diffusion modelling studies that suggest that features such as sunken stomata and stomatal papillae reduce conductance of both CO_2 and water vapour (e.g. Roth-Nebelsick, 2007). These computer based diffusion studies, however, only simulate diffusion from the external environment to the base of the stomatal pore or substomatal chamber, and consequently overestimate the significance of boundary layer resistance in comparison to the overall resistance of the total diffusion pathway, particularly in terms of CO_2 uptake.

The impact of increasing boundary layer resistance on CO_2 uptake is not equivalent to that on water loss because CO_2 constitutes a relatively low proportion of the atmosphere. The gradient between the internal leaf and external atmosphere is relatively low (0.01–0.02 to 0.036%). CO_2 is a much larger molecule than water and diffuses more slowly. Additionally, CO_2 has a much longer diffusion pathway and, therefore, experiences vastly greater resistances than water vapour. Accordingly, resistance to CO_2 movement during its gaseous phase constitutes a far smaller proportion of the total resistance to CO_2 transport, and the impact of an increase in boundary layer resistance on CO_2 uptake will be minimal (Gaastra, 1959; Ehleringer et al., 1976; Ehleringer and Bjorkman, 1978; Ehleringer and Mooney, 1978; Willmer and Fricker, 1996). These arguments indicate that the possession of "xeromorphic" features will not always limit C-uptake and photosynthesis, and cannot, therefore, be assumed to uniquely indicate adaptation to growth in a water limited environment or represent a photosynthetic cost. As a case example, increased trichome cover in *Tillandsia* species enhances boundary layer resistance, yet does not significantly affect water vapour loss or CO_2 gas exchange (Ehleringer et al., 1976; Ehleringer and Bjorkman, 1978; Ehleringer and Mooney, 1978; Schmitt et al., 1989; Benz and Martin, 2006).

So called "xeromorphic" features that increase boundary layer resistance also occur in plants growing in high water availability environments, suggesting that they may serve numerous functions and not exclusively an anti-transpirant role. Sunken stomata, epidermal trichomes and papillae may also perform a self-cleaning function by removing liquid water and debris from the leaf surface (Barthlott and Neinhuis, 1997; Neinhuis and Barthlott, 1997), by protecting the leaf from herbivory and pathogens (Gloverï, 2000; Peeters, 2002), preventing entry of toxic gases (Sharma and Butler, 1975; Elkiey and Ormrod, 1979) and protecting the plant from photoinhibition by dissipating excessive light energy (Ehleringer et al., 1976; Jordan et al., 2005). It is probable therefore, that certain "xeromorphic" traits in some plants may initially have been favoured by selection pressures for a specific ecological function, such as anti-herbivory, but were subsequently co-opted for an alternative function, such as light-reflectance or water-repellence (Woodman and Fernandes, 1991; Valverde et al., 2001). "Xeromorphy" may also involve ecological "trade-offs". For example, anti-herbivory defences such as trichomes may also reduce incident light and consequently decrease photosynthetic rates (McGuire and Agrawal, 2005). In this paper we briefly review the numerous functions of "xeromorphic" leaf traits which have been documented for modern plants. We then assess the utility of such traits preserved on fossil leaf and dispersed cuticular material in the interpretation of palaeo-environmental conditions.

2. Ecological functions of "xeromorphic" cuticle features

2.1. Anti-transpirant

Features such as stomatal furrows, sunken stomata and epidermal trichomes are commonly viewed as adaptations to aridity, increasing boundary layer resistance and consequently limiting transpiration (Wuenscher, 1970; Schuepp, 1993; Rocas et al., 1997; Aronne and De Micco, 2001). An example of a modern species, where it may be assumed that "xeromorphic" features serve an anti-transpirant purpose, is the drought adapted conifer *Tetraclinis articulata*, which occurs in seasonally arid areas of Northern Africa and Southern Europe characterised by high temperatures and low precipitation (200–

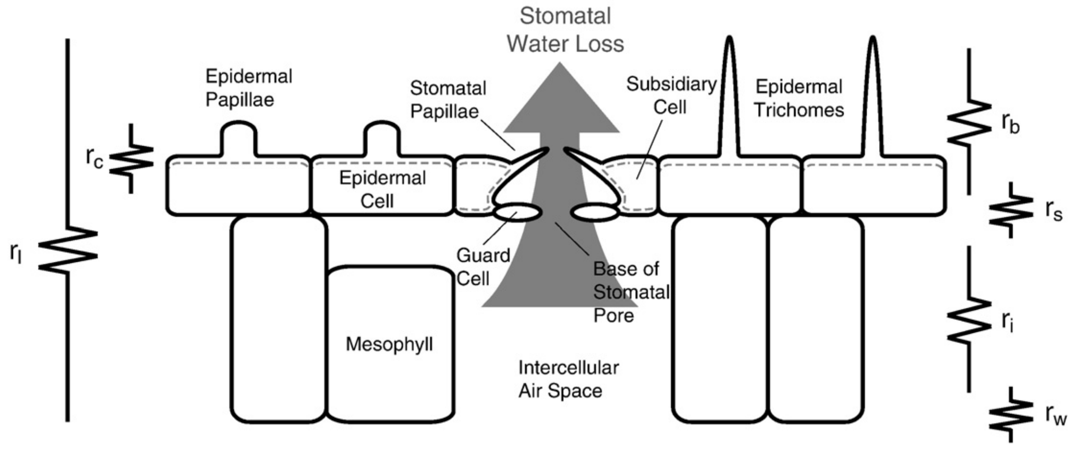

Fig. 1. Schematic figure illustrating water vapour diffusion resistances for cuticle features (epidermal trichomes, epidermal and stomatal papillae, sunken stomata) normally considered "xeromorphic" anti-transpirant adaptations due to an increase in boundary layer resistance. Resistances: boundary layer (r_b); cuticular (r_c); stomatal (r_s); intercellular space (r_i); wall (r_w); leaf (r_l). Redrawn from Jones (1992).

1000 mm p.a.) (Farjon, 2005). In *T. articulata* the stomata occur in papillate furrows between the leaves and are possibly indicative of selection for an increase in boundary layer resistance due to by growth in water limited habitats (Fig. 2).

Any anti-transpirant effect of "xeromorphy" has however to be balanced against the potential impacts of increased leaf temperature. Leaf temperature is closely coupled with stomatal conductance, as transpirational water loss is one of the main mechanisms of leaf energy dissipation, and is also affected by net radiation, air humidity, air temperature and boundary layer conductance (Jones, 1999; Grant et al., 2006). A large proportion of heat loss occurs as convection through transpiration, therefore, any increase in boundary layer resistance will cause plant leaf temperatures to rise, which can have deleterious effects in terms of photosynthetic physiology (Wuenscher, 1970; Pospisilova and Santrucek, 1994).

2.2. Effective cuticle

One of the most commonly assumed indicators of aridity in fossil plants is the presence of a thick cuticle, on the basis that a thicker cuticle is a more effective barrier to the diffusion of water (Alvin, 1982; Rocas et al., 1997). However, cuticle thickness in extant plants does not relate to its effectiveness as a barrier to water transport and thin cuticles are often most resistant to diffusion (Becker et al., 1986; Riederer and Schreiber, 1995; Kerstiens, 1996a,b; Riederer and Schreiber, 2001; Schreiber and Kerstiens, 2006). The crystalline wax layer of a cuticle (known as "the skin") is impervious to water transport, and in *Hordeum vulgare* is only 0.26 μm thick, at least an order of magnitude smaller than total cuticle thickness for extant and extinct plants (Alvin, 1982; Becker et al., 1986). The cuticles of evergreens tend to have lower permeability than deciduous species, possibly reflecting adaptation of species with long-lived foliage to conserve water during periods of reduced water availability (Kirsch et al., 1997; Gratani and Bombelli, 2000). The effectiveness of the cuticle is also dependant upon water availability, becoming more resistant to water movement as leaf turgor (Boyer et al., 1997), and atmospheric humidity decrease (Schreiber et al., 2001). Cuticular wax deposition is affected by light intensity and the relative humidity of the external environment, suggesting that the effectiveness of a cuticle as a barrier to water movement is influenced by environmental signals (Kerstiens, 1994; Richardson et al., 2005).

The cuticle acts not only as a barrier to water movement, but also as a physical barrier to infection. Cuticle thickness and physical strength may represent an adaptation to resist fungal invasion (Day et al., 1993; Taylor and Osborn, 1996; Gutschick, 1999; Bargel et al., 2004). The cuticle may also serve a physical function, providing external structural support to the leaf tissue, contributing to the maintenance of leaf physical integrity (Bargel et al., 2004). Cuticle thickness can also represent the light environment in which a leaf developed, with "sun" leaves displaying increased "xeromorphic" characteristics in comparison to "shade" leaves (Nobel and Hartsock, 1981; Kürschner, 1997).

2.3. Water repellence/self-cleaning

CO_2 diffuses 10,000 times slower in water than in air (Smith and McClean, 1989; Lide and Frederikse, 1996; Brewer and Smith, 1997). Many species therefore prevent a layer of water forming over the leaf surface; especially during the early morning when dew formation coincides with stomatal opening, and water status has improved overnight, and potential for carbon gain is greatest. In addition to an instantaneous suppression of photosynthesis, leaf "wetting" results in inhibition of photosynthesis subsequent to leaf drying, indicating prolonged impairment of photosynthetic physiology. Therefore, many leaf surfaces, especially stomatiferous ones, possess water-repellent properties (Smith and McClean, 1989; Brewer and Smith, 1995; Ishibashi and Terashima, 1995; Brewer and Smith, 1997). Such properties, will also contribute to the self-cleaning of the leaf surface, removing dust, particulates, epiphytes and pathogens (Barthlott and Neinhuis, 1997; Neinhuis and Barthlott, 1997). This "Lotus Effect" is achieved, in combination with a surface layer of hydrophobic wax crystals, by reducing the contact area between the leaf surface and the water droplet, encouraging the water to bead and slide off the leaf surface, while sunken and protected stomata may restrict water entering the stomatal pore (Brewer and Smith, 1995; Barthlott and Neinhuis, 1997; Neinhuis and Barthlott, 1997; Hill, 1998; Pierce et al., 2001). Water repellence is observed in *Taxus baccata* growing in high precipitation regions of north western Europe, where growth is not limited by water availability. The cuticle of *T. baccata* displays both epidermal and stomatal papillae (Fig. 2). Whilst sunken stomata are undoubtedly an anti-transpirant adaptation in many plants inhabiting arid environments, this is not a universal trait in water limited habitats and many taxa subject to drought do not possess this adaptation (e.g. *Arbutus andrachne*) and rely on stomatal regulation and physiological adaptation to low water availability instead.

Many conifers and angiosperms possess stomatal wax plugs made up of wax tubes that fill the stomatal pit. They form in young leaves above the guard cells, filling the stomatal pit and making stomata appear as white disks when the leaf surface is viewed under a microscope (Jeffree et al., 1971; Brodribb and Hill, 1997; Brodribb and Hill, 1998; Feild et al., 1998). Stomatal wax plugs have been interpreted as "xeromorphic" features, acting as anti-transpirant devices by reducing the area available for diffusion, and due to their complexity, increasing the diffusion distance (Jeffree et al., 1971). The occurrence of stomatal wax plugs in fossil plants has been used as an indicator of extreme xeromorphy, and consequently environmental aridity (Axsmith et al., 2004). The presence of stomatal wax plugs in living plants has indeed been demonstrated to reduce stomatal conductance (Jeffree et al., 1971; Brodribb and Hill, 1998), consistent with an anti-transpirant interpretation (Jeffree et al., 1971). However, their frequency, size and nature are not related to leaf conductance, and paradoxically stomatal wax plugs are found predominantly in species occupying environments with high precipitation levels. The Tasmanian montane conifers of the genus *Athrotaxis*, are a case in point having wax plugs in a high precipitation habitat (1600–4000 mm p.a.). They are absent however from species inhabiting arid environments, such as Australian *Callitris* species (Brodribb and Hill, 1997, 1998).

Feild et al. (1998) found that the stomatal plugs of *Drimys winteri*, a vesseless angiosperm tree found in forests of Central America with a high annual rainfall and atmospheric humidity, did not act as anti-transpirants but actually increased stomatal conductance preventing stomatal closure under conditions of water stress. This study suggests that the wax plugs maintain humidity at the guard cell allowing the stomatal pore to remain open. This differing effect of stomatal wax plugs on conductance may be the result of wax plug morphology; in conifers the wax tubes that form the plug are secreted by guard cells (Jeffree et al., 1971), yet in the Winteraceae the stomatal plugs form a layer above the guard cells from the overlying surrounding cells (Feild et al., 1998). In *D. winteri* the primary function of stomatal wax plugs appears to be water-repellent. Removal of the stomatal wax plugs allowed a layer of liquid water to develop over the leaf surface, impeding CO_2 uptake by the leaf and reducing photosynthetic rates by 40%, whereas misting of leaves had no effect on the photosynthetic rate in leaves with plugs (Feild et al., 1998). *Sequoia sempervirens* possesses typical "xeromorphic" features such as sunken stomata and stomatal wax plugs, yet occurs in habitats with high humidity and precipitation (Burgess and Dawson, 2004). This is another example where the so called xeromorphic traits act to repel water from the leaf surface during fog rather than reducing water loss.

It is likely that stomatal papillae may serve a similar water-repellent function. Such properties can be observed in Amazonian tropical floodplain forests (e.g. *Quiinia rhytidopus* and *Couepia*

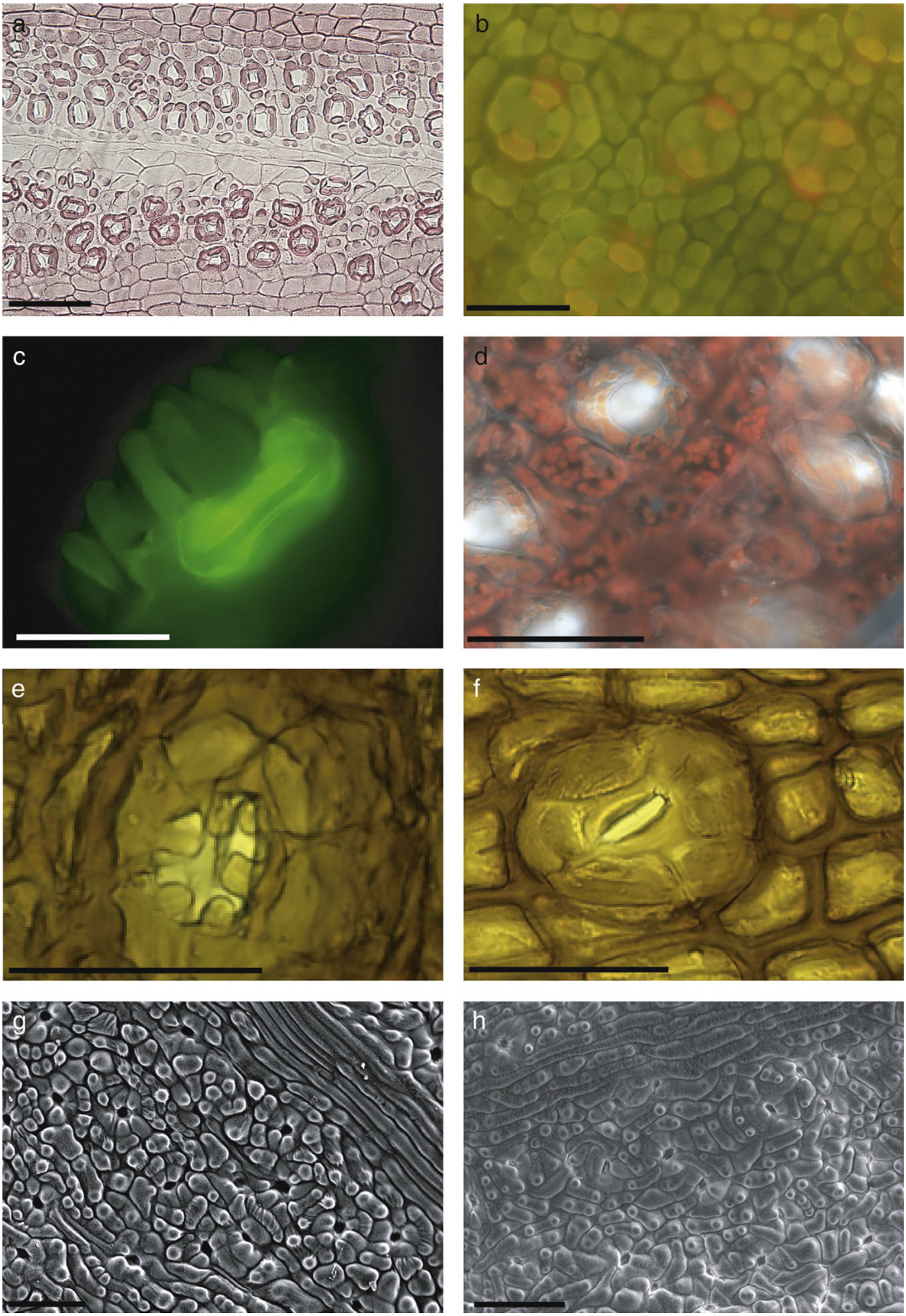

Fig. 2. a) Transmitted light image of *Tetraclinis articulata* cuticle displaying stomata arranged in papillate sunken furrow (scale = 100 μm); b) fluorescence image of abaxial surface of *Taxus baccata* displaying epidermal and stomatal papillae (scale = 20 μm); c) fluorescence image of the cross-section of stomata of *Sciadopitys verticillata* displaying overarching papillae (scale = 50 μm); d) fluorescence image of abaxial surface of *Wollemia nobilis* displaying stomatal wax plugs (scale = 50 μm); transmitted light images of papillate (e) and non-papillate (f) stomatal complexes of *Pseudofrenelopsis parceramosa* (scale = 50 μm); SEM images of sun (g) and shade (h) leaves of *Ginkgo biloba* (scale = 100 μm).

paraensis), where stomatal papillae allow the development of a pocket of air above the stomatal pore when the leaves are fully submerged during river spate (Waldhoff and Furch, 2002; Waldhoff, 2003). Many Mesozoic fossil plants such as the extinct conifer family Cheirolepidiaceae possess prominent overarching papillae, and these stomatal papillae have often been interpreted as having an anti-transpirant function (Alvin, 1982; Watson, 1988; Watson and Alvin, 1996; McElwain et al., 2004). It is noteworthy therefore, that the only extant conifer possessing such prominent overarching papillae is *Sciadopitys verticillata*, which occurs in cloud forest mountain regions of Japan (precipitation: >2000 mm. p.a.) (Farjon, 2005). The stomata of *S. verticillata* also occur in a sunken furrow beneath the fused leaves, another supposedly “xeromorphic” trait. In the case of *S. verticillata*, taken its high humidity, high precipitation habitat, furrows have developed in response to selection pressures favouring water-repellency, or represent a developmental legacy of leaf fusion (Fig. 2).

2.4. Defence

Epidermal cuticle ornamentations, such as trichomes, have been demonstrated to protect leaves from herbivores and pathogens by either causing physical/structural impediments to, or releasing defensive chemicals upon physical contact with, a possible herbivore (Levin, 1973; Gloverï, 2000; Krings et al., 2003). Evolutionary pressures should favour investment in chemical and structural cuticle defences in plant species with long-lived leaves inhabiting nutrient-poor environments, and in plants experiencing environmental stress (Grimes, 1977; Coley et al., 1985; Coley, 1988; Wilkens et al., 1996; Hoffland et al., 2000). Trichomatous plants have been shown to be more resistant to herbivory and experience lower levels of loss and damage to leaf material from herbivores. This is because herbivores spend greater amounts of time eating and digesting trichomous leaves and longer travelling between feeding sites in order to achieve the same level of nutrition, making them more vulnerable to predation (Woodman and Fernandes, 1991; Wilkens et al., 1996; Zvereva et al., 1998; Hoffland et al., 2000; Valverde et al., 2001; Peeters, 2002; Molina-Montenegro et al., 2006; Løe et al., 2007). Plants growing in calcareous environments (calcicoles), commonly use trichomes as sinks for excess calcium, so preventing disruption to stomatal function that would result from accumulation of calcium elsewhere (DeSilva et al., 1996).

Herbivory can increase trichome production in some species (Kivimaki et al., 2007), while other species do not possess the genetic flexibility to respond to herbivory by increasing trichome density (Dalin et al., 2004). Herbivory can stimulate production of defensive compounds such as terpenes from glandular trichomes (Bernasconi et al., 1998). Trichome density has been shown to decrease with leaf age in *Betula* species, suggesting a defensive purpose (Valkama et al., 2004), as mature leaves of *Betula*, with their higher concentrations of defensive compounds such as phenols and tannins, are less susceptible to insect herbivory and pathogen infection (Poteri et al., 2001; Haukioja et al., 2002). *Betula* can also alter the proportion of non-glandular to glandular trichomes, as the plant varies the allocation of resources between chemical and structural defences in response to herbivory (Rautio et al., 2002).

Liabum mandonii growing in humid tropical montane forests of Bolivia possesses non-glandular trichomous leaves (Molina-Montenegro et al., 2006). Trichome density in this taxon is positively correlated with light intensity and negatively correlated with the degree of damage by herbivory. This suggests that the trichomes may function to protect the leaf from excess light energy in addition to reducing the impact of herbivory, alongside insect herbivores general preference for more shaded humid environments (Molina-Montenegro et al., 2006).

Stomatal papillae and wax plugs may also act in defence against pathogens that enter the leaf through stomata. Fruit blotch bacteria infect *Citrus lanatus* via the stomatal pore; stomatal plugging increases with leaf age in *C. lanatus* and this coincides with increased resistance to infection (Giles-Frankle, 1993). In contrast, as leaf age increases in *S. sempervirens* stomatal wax plugs become degraded and incidence of fungal infection via the stomatal pore increases (Burgess and Dawson, 2004). The physical barrier to infection offered by stomatal wax plugs and stomatal papillae may be especially important acting in combination with leaf water-repellent properties (Feild et al., 1998), as pathogenic fungi and bacteria may be more active on surfaces covered in a thin layer of water (Lange, 1976; Bargel et al., 2004).

2.5. Scleromorphy

Plant responses to water limitation and nutrient limitation, particularly in terms of phosphorous or nitrogen, are often very similar, both being characterised by development of small leaves with thick cuticle (Loveless, 1961, 1962; Beadle, 1966; Grubb, 1986; Turner, 1994; Hill, 1998). Sclerophylls often display high leaf structural carbohydrate-to-protein ratios (Loveless, 1961, 1962), and this scleromorphic response may reflect the protection of scarce nutrient investment in leaf material from herbivory and abiotic physical damage (Grimes, 1977; Grubb, 1986; Turner, 1994). Due to a lack of phosphate and nitrogen available for protein production, the thick cuticles of sclerophylls may effectively be a sink for excess photosynthate, as cutin, suberin and the waxes that make up the cuticle do not require phosphorus or nitrogen (Kerstiens, 1996a,b). Many nutrient limited environments are unable to support a dense canopy and consequently scleromorphic features may serve to protect the plant photosynthetic physiology from excess light energy either through reflection or interception of light (Jordan et al., 2005).

2.6. Light protection

Plant leaf structure is affected by the light intensity in which the leaf develops (Gutschick, 1999) with sun leaves displaying increased “xeromorphy” in comparison to shade leaves (Roth and Dilcher, 1973; Spicer, 1980; Masuch and Kettrup, 1989; Lee et al., 1990; Kürschner, 1997; Rocas et al., 1997). Many plant species reach light saturated rates of photosynthesis at levels of light intensity lower than mean midday levels of solar radiation. Selective pressures have thus led to the development of plant cuticles that reflect solar radiation, so preventing photoinhibition, reducing leaf temperatures and increasing water use efficiency (Smith and McClean, 1989; Smith et al., 1997; Turunen et al., 1999). The intensity of visible and UV light is positively correlated with cuticle thickness and integration of protective flavonoid compounds in the cuticle (Reed and Tukey, 1982; Day et al., 1993; Valkama et al., 2004). In some species, however, micromorphological adaptation of the leaf surface may serve to increase, rather than reduce, leaf temperature compared with the surrounding environment. Transparent trichomes may also increase plant temperature in comparison to the surrounding ambient temperature. For instance, the transparent trichomes of *Salix polaris*, allow sunlight to reach the plant surface, thereby offering resistance to heat loss via radiation from the plant surface, insulating the plant (Krog, 1955).

Plants with thick cuticles and trichomes display lower photosynthetic rates than non-trichomous plants, and those with thin cuticles (Benzing and Renfrow, 1971). The presence of trichomes in *Encelia* species does not affect the boundary layer resistance in comparison to non-trichomous species (Ehleringer et al., 1976). Trichomes occur in desert species of *Encelia*, yet are absent from those species growing in habitats with lower mean temperatures, suggesting that the ecological function of trichomes in this species is to reflect solar radiation, consequently reducing leaf temperature, damage of photosynthetic physiology and increasing water use efficiency (Ehleringer et al., 1976; Ehleringer and Bjorkman, 1978; Ehleringer and Mooney, 1978; Ehleringer, 1981).

Sun leaves of *Ginkgo biloba* tend to possess more epidermal and stomatal papillae than shade leaves (Denk and Velitzelos, 2002), suggesting that the stomatal papillae may be involved in reducing light penetration and photoinhibition (Fig. 2). As light intensity and UV radiation increase with altitude, an adaptation to protect the photosynthetic physiology from damage may be observed in the occurrence of increasing leaf trichome densities with altitude in many plant species (e.g. *Quercus kelloggii* and *Nothofagus solandri* var. *cliffortioides*) (Ehleringer, 1988; Kouwenberg et al., 2007).

In addition to performing a protective function, by intercepting and reflecting excess and harmful components of solar radiation, trichomes and papillae in some species may also increase photosynthetic efficiency when plant growth is limited by low light intensity of deeply shaded environments, by focusing solar radiation on to areas of the leaf where chloroplasts are concentrated (Lee, 1986; Melcher et al., 1994). The presence and type of "xeromorphic" epidermal features in shade leaves, such as epidermal papillae, to focus light on epidermal chloroplasts, may be dependent upon the type and angle of incident light reaching the leaf (Lee, 1986). Leaves of *Scindapsus picus* growing vertically on tree trunks reflect less light reaching the leaf at an oblique angle than leaves growing horizontally and understory plants dependant upon sun flecks (Bone et al., 1984; Lee, 1986).

2.7. Toxic atmospheric gases

Despite the fact that boundary layer resistance is proportionally smaller in comparison to stomatal resistance (Gaastra, 1959; Ehleringer et al., 1976; Ehleringer and Bjorkman, 1978; Ehleringer and Mooney, 1978; Willmer and Fricker, 1996)(Fig. 1), in extant plants, resistance to fumigation with toxic gases is often associated with an increase in the boundary layer resistance. This reduces entry of toxic gases into the leaf (Sharma and Butler, 1975; Elkiey and Ormrod, 1979). Visible injury to plants generally occurs initially at the leaf margins where the boundary layer resistance is smallest, rather than at the leaf centre where boundary layer resistance is greatest (Wellburn, 1994). *Metrosideros polymorpha* growing in the Kilauea crater region of the Island of Hawaii is resistant to persistent fumigation with toxic volcanic gases (SO_2, H_2S, HCl, HF) while other species (e.g. *Dodonaea eriocarpa*) growing in the same region display noticeable damage (Winner and Mooney, 1980). *M. polymorpha* from the Kilauea crater region display heavily trichomous abaxial surfaces, while those in neighbouring regions, that do not experience chronic fumigation, possess non-trichomous cuticles (Haworth, 2006). This pattern suggests that the development of trichomes in the Kilauea Crater region is an adaptation to increase boundary layer resistance, and consequently reduce entry of toxic gases into the leaf (Haworth, 2006).

Dust and particulates commonly co-occur with anthropogenic atmospheric pollution and volcanic activity, resulting in the partial occlusion of stomata, preventing full stomatal closure, and severely reduce plants regulation of transpiration and thereby preventing uptake of atmospheric pollution (Krajickova and Mejstrik, 1984; Farmer, 1993; Nanos and Ilias, 2007). The ecological function of stomatal wax plugs and over-arching stomatal papillae may therefore be to prevent occlusion of the stomatal pore by dust and debris, so maintaining stomatal function. The water-repellent properties of many "xeromorphic" leaf surfaces may be especially important in terms of atmospheric pollutants, where deposition and diffusion through the lipid phase of the cuticle, by a pollutant such as sulphur dioxide, increases on wet cuticles (Lendzian, 1984; Kersteins et al., 1992; Patrie and Berg, 1993; Turunen and Huttunen, 1997). Dust on the leaf surface causes leaf chlorophyll content, photosynthetic rate and plant productivity to decrease (Mandre and Tuulmets, 1997; Nanos and Ilias, 2007). Accumulation of dust on the leaf surface has been shown to increase leaf temperature through increased absorption of light (Eller, 1977). This in turn may lead to plant thermal stress in high temperature or high light intensity environments (Tobiessen and Kana, 1974; Ehleringer et al., 1976; Eller, 1977; Benzing et al., 1978; Pospisilova and Santrucek, 1994; Sawada et al., 2002). The eruption of Mount Saint Helens in 1980 resulted in release of 1.5 to 2.0 km^3 of ash into the atmosphere, resulting in loss of $1.4 billion in crops, as photosynthesis rates can be reduced by up to 90% by ash cover on vegetation (Cook et al., 1981). Therefore, selection pressures experienced by plants growing in volcanically active areas or periods in earth history should favour self-cleaning cuticle properties (cf. Barthlott and Neinhuis, 1997). This hypothesis is eminently testable using fossil plants deposited in high water availability environments.

3. Taphonomy

The high proportion of plants displaying xeromorphic adaptations present in the fossil record may represent a preservational bias. Sun leaves tend to display more "xeromorphic" traits than shade leaves, such as greater cuticle thickness (Nobel and Hartsock, 1981; Kürschner, 1997; Robakowski et al., 2004). Plants with thicker "more robust" cuticles tend to possess greater preservation potential than those with thinner cuticles (Oldham, 1976; Kürschner, 1997). As leaf photosynthetic capacity is related to the hydraulic capacity of the supporting xylem tissue, leaf morphology is influenced by this hydraulic limitation (Ryan and Yoder, 1997; Brodribb and Hill, 1999; Brodribb and Field, 2000). This effect can be seen in leaves collected at different heights in *S. sempervirens*, with leaves displaying increasingly "xeromorphic" characteristics with increasing height (Koch et al., 2004). As sun leaves from higher in the canopy are preferentially preserved in the fossil record this could potentially lead to the false interpretation of environmental aridity, from fossil leaf deposits derived from high in the canopy in high water availability environments (Roth and Dilcher, 1973; Spicer, 1980; Kürschner, 1997). High canopy leaves are more likely than their low canopy counterparts to enter a depositional environment (Gastaldo, 2001) and sun leaves are preferentially preserved in the fossil record (Kürschner, 1997). These combined taphonomic biases would clearly lead to the incorrect interpretation of environmental aridity even in high water availability environments (Spicer, 1980).

4. Case study—*P. parceramosa* (Fontaine) Watson

The extinct Cretaceous cheirolepidiacean conifer *P. parceramosa* (Fontaine) Watson is used here to highlight the equivocal nature of many cuticle features as indicators of palaeo-environment and environmental aridity. *P. parceramosa* occurs as the dominant plant species in the Early Cretaceous Wealden Group (Valanginian–Aptian) in Southern England and Potomac Group (Aptian–Cenomanian) in Eastern USA (Oldham, 1976; Upchurch and Doyle, 1980).

4.1. Palaeo-environmental setting

In the English Wealden *P. parceramosa* is believed to have occupied a lowland habitat, growing on freshwater stream banks or low-lying areas dissected by braided streams, which dried out seasonally (Alvin, 1983; Watson and Alvin, 1996). The leaf morphology of *P. parceramosa* (thick cuticle, sunken stomata, severely reduced leaves with photosynthetic function transferred to the stem) has been interpreted to be indicative of xeromorphic adaptation in an arid habitat (Watson, 1977; Alvin, 1982, 1983; Watson, 1988; Watson and Alvin, 1996; Axsmith et al., 2004; Axsmith and Jacobs, 2005; Axsmith, 2006). This interpretation is supported by growth rings in the wood of *P. parceramosa* (*Protopodocarpoxylon*) (Alvin et al., 1981; Alvin, 1983), fossil charcoal indicating the occurrence of drought and forest fires in the Wealden Group environment (Alvin et al., 1981; Harris, 1981; Alvin, 1983; Collinson et al., 1999).

Sedimentological evidence however does not support the palaeobotanical interpretation of environmental aridity in the English Wealden. The Wealden Group is comprised of a varicoloured fluvial and lagoonal siliciclastic succession (e.g. Allen, 1981; Stewart, 1981). The depositional setting of the Wessex Formation, exposed at Worbarrow Bay, Dorest, is interpreted to have been a seasonal wetland, in which fine argillaceous sediments were deposited in floodplain environments cross-cut by meandering channels, carrying and depositing both coarse and fine sediments (Fig. 3). Deposition of the 350 m of sediments exposed at Worbarrow Bay occurred over a time period on the order of 10 Myr (Robinson and Hesselbo, 2004). The lack of evaporites, aeolian sediments and evidence of river drying, in addition to the volume of sediment being carried by the Wealden river channels draining a relatively small catchment area, all suggest relatively high levels of precipitation (Allen, 1975, 1981; Stewart, 1981, 1983; Allen et al., 1998; Wright et al., 2000; Robinson and Hesselbo, 2004). Furthermore, as charcoal develops in modern lowland tropical forests (e.g. Sanford et al., 1985) the occurrence of charcoal in the Wealden does not necessarily indicate aridity. This interpretation of high precipitation is supported by the limited area climate model of Haywood et al. (2004) that predicts high levels of precipitation but also high evaporative demand during the Barremian English Wealden. Both the Wealden and Potomac Groups occur within a "moist and tropical" climatic zone in global climate reconstructions (Beerling and Woodward, 2001), and isotopic evidence indicates the existence of an enhanced global hydrological cycle during the mid-Cretaceous, with much higher levels of precipitation occurring at mid and high latitudes than today (Ufnar et al., 2004). Together these data suggest that, although *P. parceramosa* may have experienced some seasonal aridity, the cuticular features previously considered "xeromorphic" might also be adaptations to growth in high precipitation humid habitats.

4.2. Water repellence/self-cleaning

In this envisaged high precipitation habitat, a likely function for the stomatal papillae of *P. parceramosa* can be drawn from comparison to stomatal wax plugs; acting as barriers to infection and preventing a film of liquid water forming across the leaf surface, that would stop gas exchange (Smith and McClean, 1989; Giles-Frankle, 1993; Barthlott and Neinhuis, 1997; Brodribb and Hill, 1997; Neinhuis and Barthlott, 1997; Feild et al., 1998; Hill, 1998; Bargel et al., 2004). In living plants, epidermal papillae are observed to reduce the contact area between water droplets and the epidermis, so preventing a film of water developing over the surface (Barthlott and Neinhuis, 1997; Neinhuis and Barthlott, 1997). Therefore, an alternative but equally plausible interpretation of the stomatal papillae of *P. parceramosa*, may be that they served to prevent a surface film of water developing on the leaf surface that would prevent gas exchange during periods of high rainfall throughout deposition of the Wealden.

4.3. Anti-transpirant

The stomatal papillae of *P. parceramosa* have been considered a xeromorphic feature serving an anti-transpirant function by occluding the stomatal pore (Upchurch, 1984; Watson, 1988; Watson and Alvin, 1996; McElwain et al., 2004). However, even when overarching papillae occlude the entrance to the stomatal pit, the cross-sectional area available for diffusion is much greater than the area of the stomatal pore (the main site of diffusive resistance for water vapour diffusing out of a leaf) (Fig. 2), suggesting that the impact of stomatal papillae upon water use efficiency will be minimal. The cross-sectional area of the stomatal pit of *P. parceramosa*, even when partially occluded by the papillae, is orders of magnitude greater than the minimum mean free path for diffusion of CO_2 in air (approximately 0.2 μm^2), at which point CO_2 diffusion would become reduced (Lide and Frederikse, 1996).

It is difficult to envisage a scenario where the papillae of *P. parceramosa* would serve an anti-transpirant function. However, in order to investigate this possible function, the proportions of papillate and non-papillate cuticle fragments were analysed through the Wessex sediments of Worbarrow Bay, Dorset (Fig. 3). A total of 658 cuticle fragments were analysed with a size range of >0.5 to >2.0 mm^2, with the majority occurring in the 0.5 to 1.0 mm^2 size range and 10 papillate cuticle fragments exceeded 5 mm^2. We found no observable pattern in the occurrence of papillate and non-papillate cuticle fragments in relation to sedimentary indicators of water availability. For a plant that is considered to have experienced seasonal aridity, where water availability limited growth (Alvin et al., 1981; Alvin, 1983; Watson and Alvin, 1996; Watson et al., 2001), it would be expected that any feature that conferred an advantage in such an environment, where growth is restricted by an external environmental stress, would become universal in a population (cf. McNeilly, 1968), yet stomatal papillae are not found in all individuals of *P. parceramosa*. In addition, if stomatal papillae were an effective anti-transpirant device it would be reasonable to assume that they would be widespread in contemporary conifers, especially those inhabiting seasonally arid environments, such as *T. articulata* or *Callitris* species.

It may be possible that during times of drought, as plant water potentials decreased and leaf turgidity fell, then the papillae of *P. parceramosa* would collapse in on the stomatal pit, so blocking the stomatal pore and preventing further loss of water. However, the papillae of *P. parceramosa* are not large enough to occlude the stomatal pit in the event of turgor loss, if they did indeed possess active control. While blocking of the stomatal pit may sound superficially plausible, in reality it bears no relation to the behaviour of plants in drought situations. Contemporary plants experiencing drought, will attempt to maintain turgor through osmotic adjustment (i.e. increasing solute concentration in order to reduce plant water potentials), as during periods of drought it is not the osmotic adjustment that is lethal to plants but the reduction in leaf water content (Flower and Ludlow, 1986). It therefore seems highly unlikely that any drought-adapted plant's response to aridity would involve a deliberate reduction in cell turgor, as this would involve a reduction in relative water content. Members of the genus *Callitris* occur in areas experiencing some degree of aridity (Farjon, 2005). Of these, *Callitris columnaris* inhabits the most xeric environments, due to its ability to reduce leaf water potentials and increase leaf water content by closing the furrows in which its stomata are arranged (Attiwill and Clayton-Greene, 1984). This drought-adapted conifer demonstrates a high degree of osmotic adjustment and a unique adaptation to drought, and even during periods of low water availability can modify leaf water content in a manner contrary to the passive turgor role required in *P. parceramosa* to block the stomatal pit by actively controlled papillae.

4.4. Volcanism, OAEs and toxic gases

The influence of dust particles on plant growth can often be overlooked, but impact from air-borne particles can disrupt cuticular integrity, and is of major importance to long-lived conifer leaves (Jeffree et al., 1993). For a plant such as *P. parceramosa*, experiencing some degree of seasonal aridity, retaining stomatal function would be vital. The Cretaceous was a period of enhanced global volcanism (Larson and Erba, 1999; Weissert and Erba, 2004) and layers of bentonite occur within Lower Greensand (Ruffell et al., 2002) and Wealden sediments (pers. obsv.), demonstrating localised impacts of volcanic activity (Ruffell et al., 2002). Such volcanic activity would be associated with an increase in atmospheric aerosols, particulates and pollutants, likely making it important for *P. parceramosa* to protect its stomata in order to prevent entry of phytotoxic pollutants into the leaf and retain stomatal function. The potential influence of volcanism on the cuticular morphology is apparent in the Early Cretaceous Baquero Formation, Argentina, where *Pseudoctenis ornata*, whilst inhabiting a high water availability environment, may have developed "xeromorphic" morphological features (thick cuticle, stomata arranged in

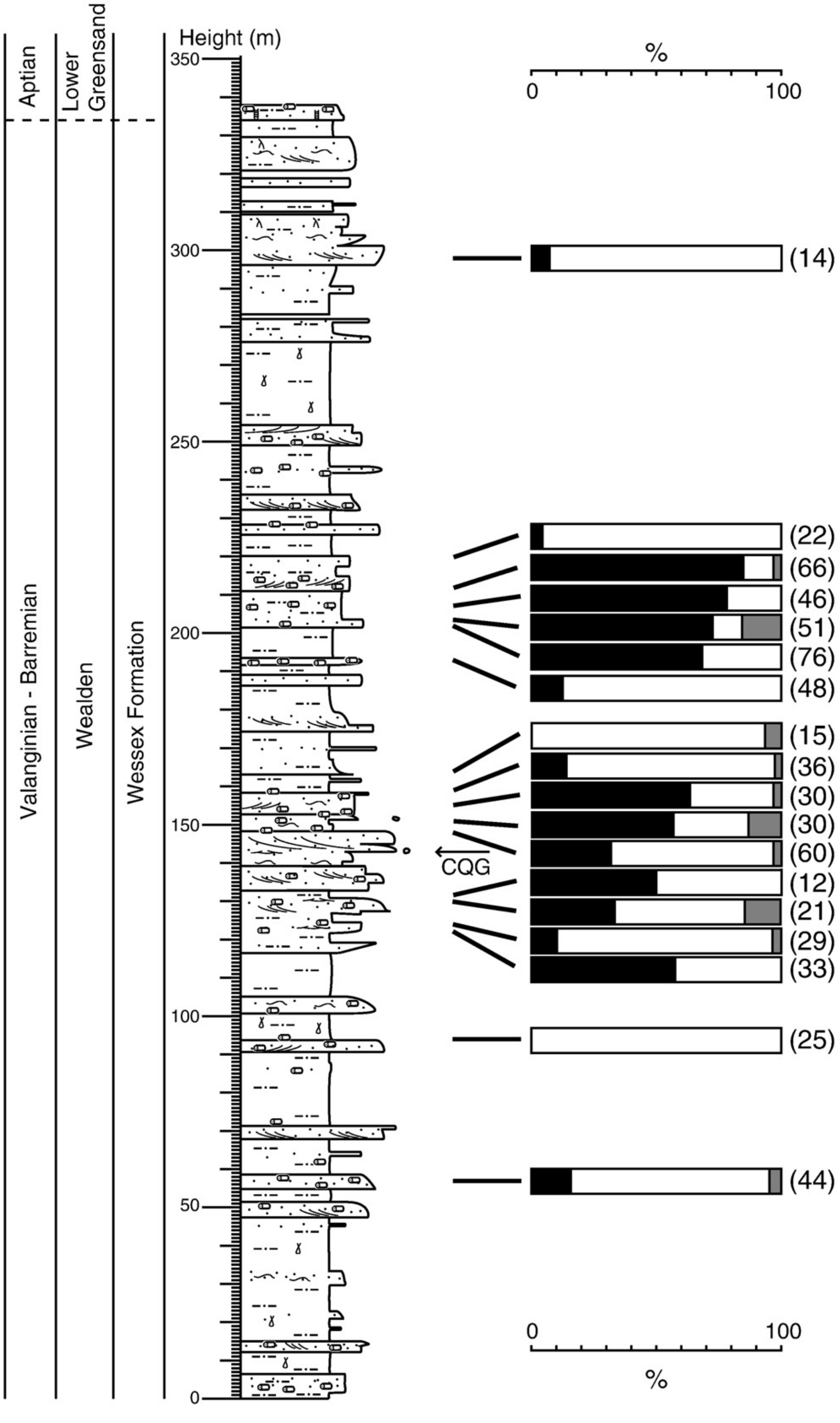

Fig. 3. Proportions of papillate (black) and non-papillate (white) fragments of fossil cuticle of *Pseudofrenelopsis parceramosa* from Worbarrow Bay, Dorset, South West England. Where poor preservation prevented analysis of the stomatal complex cuticles were classed as indeterminate (grey). CQG indicates base of Coarse Quartz Grit. Numbers in brackets indicate the total number of cuticle fragments analysed for each sample. Stratigraphy of Robinson and Hesselbo (2004).

rows and papillae and trichomes) in response to leaf loading with volcanic ash (Archangelsky et al., 1995).

In addition to enhanced global volcanism, the Cretaceous is marked by oceanic anoxic events (OAEs). OAEs occur during periods of enhanced ocean burial of organic carbon; excursions in the carbon-isotope record of marine and terrestrial sediments occur during OAEs, suggesting significant perturbation of the global carbon cycle. OAEs are believed to be caused by the rapid release of large volumes of CO_2

into the atmosphere, either from release of methane from marine gas hydrates or volcanism (Jenkyns, 2003; McElwain et al., 2005). Ancient chemicals such as methyl isobutyl maleimide are found in OAE deposits, and indicate that ocean euxinia led to the growth of green sulphur bacteria and other anaerobic bacteria. These microorganisms will have generated toxic H_2S within the water column (a condition known as photic-zone euxinia), and also emitted H_2S into the atmosphere (Pancost et al., 2004; Kump et al., 2005).

Atmospheric pollutants produced by volcanic activity and OAEs, such as SO_2 and H_2S, are absorbed via the cuticle as well as the stomata. As outlined above, cuticular absorption of these phytotoxic gases is increased on wet leaf surfaces (Lendzian, 1984; Kersteins et al., 1992) and on leaves which have experienced physical abrasion (Jeffree et al., 1993; Turunen and Huttunen, 1997). This may account for the extremely thick cuticle of *P. parceramosa* (30 μm: Watson, 1977) and also support a multiple functional interpretation of cuticle features such as stomatal papillae.

4.5. Protective, structural and nutrient limitation responses

Physical wind damage, through repeated abrasion between leaves and impacts from air-born dust particles, disrupts cuticular integrity and increases cuticular conductance (Pitcairn et al., 1986; Jeffree et al., 1993). Once cuticular integrity is disrupted, nutrients begin to leach from the leaf making it more vulnerable to epiphyte growth and pathogenic fungi (Smith and Lytle, 1997). To maximise net photosynthesis, species with short leaf life-spans have relatively thin cuticles, while species where foliage has a longer life-span tend to possess relatively thicker/denser cuticles with a more robust leaf, protecting investment in photosynthetic apparatus (Reich, 1993; Kirsch et al., 1997). The thick cuticle of *P. parceramosa* may therefore be an adaptation to growth in a high energy windy environment, favouring investment in protecting photosynthetic apparatus and maintaining leaf integrity. Additionally, as a conifer with a single sheathing leaf surrounding a central stem (Watson, 1977; Srinivasan, 1995), the thick cuticle of *P. parceramosa* may provide structural support to the external leaf (cf. Bargel et al., 2004), due to the absence of structural support provided by the lateral edges of leaves in species with multiple sheathing leaves, such as *Frenelopsis* species. The remarkably thick cuticle and reduced leaves of *P. parceramosa* may also be indicative of growth in a nutrient-poor, rather than arid, environment (Loveless, 1961, 1962; Beadle, 1966; Grubb, 1986; Groom and Lamont, 1997; Hill, 1998). The thick cuticle of *P. parceramosa* may act as a sink for excess photosynthate caused by a lack of phosphate and nitrogen available for protein production (cf. Kerstiens, 1996b).

Modern conifer species with a similar leaf arrangement such as *Callitris* species and *T. articulata*, do not form dense canopies where light intensity becomes stratified. The thick cuticle of *P. parceramosa* may have protected it from excessive UV radiation, preventing photoinhibition (Day et al., 1993; Turunen et al., 1999). Watson (1977, p. 724) observes, as a "general rule" that short segments of *P. parceramosa* (less than 3 mm) have papillate subsidiary cells, whilst those with internodes of over 5 mm have non-papillate subsidiary cells. As sun leaves tend to be smaller than shade leaves (Lee et al., 1990; Kürschner, 1997; Rocas et al., 1997), this "general rule" may support interpretations of a protective function for stomatal papillae, whereby they prevent/limit damage to the leaf photosynthetic apparatus by excess light energy. However, this general rule of Watson (1977) is not observed in *P. parceramosa* in North America (Upchurch and Doyle, 1980; Srinivasan, 1995; Axsmith, 2006) and is not apparent in *P. parceramosa* from Worbarrow Bay.

As outlined above the "xeromorphic" features of *P. parceramosa* cannot be interpreted purely in terms of possible anti-transpirant properties. It is highly likely that features such as stomatal papillae, that have long been regarded as anti-transpirant in function, are adaptations to growth in high precipitation environments, serving a water-repellent role. Many of these "xeromorphic" features possibly served many functions and these properties acting in combination, such as water-repellence and resistance to toxic atmospheric gases and volcanic dust, may account for the development of a suite of "xeromorphic" traits observed in *P. parceramosa* and other Mesozoic taxa. The use of these "xeromorphic" characters as indicators of palaeo-environmental aridity in *P. parceramosa* and other Cheirolepidiaceae, therefore has to be made in the context of supporting sedimentology, geochemical analysis, climate modelling and examination of modern ecological analogues.

5. Summary—"a new interpretation of xeromorphy"

Leaf features considered to be "xeromorphic" occur in plants growing in arid and high water availability environments, suggesting that their ecological function may not be purely anti-transpirant. Selection pressures may initially favour the development of "xeromorphy" primarily for a specific ecological function in response to an environmental stress. However, a trait may then be co-opted for other adaptive functions, leading to the potential for varied ecological roles of epidermal traits usually referred to as "xeromorphic". As "xeromorphic" features often serve multiple functions, they cannot simply be regarded purely in an anti-transpirant capacity. The use of "xeromorphic" plant features in fossil plants as indicators of palaeoenvironmental aridity therefore has to be in the context of supporting sedimentological evidence. To this end, more ecological and growth experiment studies are required to fully elucidate the ecological function of "xeromorphic" features.

Acknowledgements

We thank the following for scientific discussion and technical assistance: O. Green, S. Harris (Oxford, UK), S. Heffernen (Mount Usher Gardens, Ireland), K. Bacon, P. Flood, L. Mander, B. Moran, C. Ng, G. Nolan, R. O'Hare (UCD, Ireland), M. Jebb (Glasnevin Botanic Gardens, Dublin), A. Farjon, S. Landrein (RBG, Kew), S. Jury (Reading, UK), M. Rondeau (University of Washington, USA) and K. Whittaker (Colby College, USA). The comments of S. Hesselbo (Oxford), G. Jordan (University of Tasmania), C. Belcher (UCD, Ireland) and two anonymous reviewers significantly improved the manuscript. We gratefully acknowledge funding from NERC, UK, and an EU Marie Curie Excellence Grant (MEXT-CT-2006-042531).

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