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Invited review article

When did a Mediterranean-type climate originate in southwestern Australia?

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ABSTRACT

Knowing the environments under which biota have evolved is essential for understanding the functional traits that they possess. Here, we ask when a Mediterranean-type climate (MTC) originated in Western Australia that might help to explain some of its special plant adaptations to summer drought and heat, mild wet winters and intense summer fires. Periodic drought and fire can be traced back to the Cretaceous in southwestern Australia (SWA) but its seasonality is unknown. Previous estimates of the origin of the MTC in SWA have varied from 30 to 3 million years ago (Ma). An early proposal was that it originated in northwestern Australia 30 Ma and migrated south to its present location for which we find independent support. We collated 47 cases of what is currently known about the time of origin of adaptive responses to summer drought and heat, wet winters and periodic intense fire among flowering plants in SWA. About 15% arose in the 40–30-million-year (My) period, 32% in the 30–20-My period and 47% in the 20–10-My period, suggesting that a MTC may have been widespread in SWA by the mid-Miocene, but there may have been local appearances (proto-MTC) up to 20 My earlier. Uncertainties remain about the location of lineages at various times, the fitness benefits of apparent adaptive traits and their confinement to a MTC, and the significance of the origin versus the onset of diversification of traits. The current dearth of C4 grasses in SWA is consistent with other indications of the absence of a prior history of a summer-dominant rainfall, suggesting that the current MTC arose from a uniform-rainfall climate. Other lines of evidence that might refine these findings include the chemical composition of, and application of geochronometers to, laterites, carbonates and corals that have been used with success elsewhere. We conclude by noting that there may have been a mixture of climates for much of the time, indicated by the persistence of a few rainforest species up to 3 Ma, while there have been strong climatic oscillations about a MTC 'mean' over the last 5 My.

1. Introduction

There is increasing interest in the time of origin of the extant world's climates to explain unique traits of their current biotas, especially in the mediterranean regions (Rundel et al., 2016; Onstein and Linder, 2016). Thus, Cramer and Hoffman (2015) considered that special features of the floras of the Cape of South Africa and southwestern Australia (strong sclerophylly, small leaves, proteoid root clusters, on-plant seed storage) could be attributed to the leaching out of basic ions from the sandy soils under the cool wet winters of their mediterranean climates. The legitimacy of such a view depends on demonstrating a) that these traits are a function of such soil properties, and b) that these traits appeared after, or at least coincided with, the onset of a mediterranean climate. Here, we outline defining features of the Mediterranean-type climate (MTC) in southwestern Australia (SWA) and review previous estimates of the onset of a mediterranean climate there. We then describe the historical appearance of traits that we regard as indicative of mediterranean climates and thus can be used as a proxy for the advent of a MTC, and summarize their abundance in relation to geological time intervals in an attempt to identify the most likely period. Finally, we note approaches to determining past climates using proxy historical records for temperature and rainfall, including the onset of mediterranean climates, that have been used in other parts of the world and consider the scope for their implementation in southwestern Australia. The approaches we review hold promise for application to other mediterranean regions of the world.

2. Past records of seasonality and fire-proneness in SWA

SWA has a long history of periodic drought and fire-proneness either recorded among fossils or implied by indirect methods. Thus, fire-stimulated flowering and germination of soil-stored seeds can be traced to 90 million years ago (Ma) in the herbaceous family, Haemodoraceae, that probably originated in SWA (He et al., 2016; Lamont and He, 2017). On-plant seed storage and fire-stimulated seed release that precede wet-season germination in *Banksia* appears to have originated

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in SWA at least 62 Ma (He et al., 2011; Causley et al., 2016). In both cases, no details are available on the nature of the wet and dry periods that promoted the evolution of these traits, although Lamont et al. (2013) noted that seed storage of any kind is not favoured in summer-rainfall grasslands where fires may occur annually. Carpenter et al. (2015) obtained abundant charcoal ~70 Ma among fossil sclerophyll plants in central Australia that they compared favourably with the current fire-prone flora of SWA but made no comment on the likely seasonality at that time. It is clear that many traits, such as strong sclerophylly, resprouting and presence of essential oils, in the Australian flora may be traced back to the extremely wet but highly flammable Upper Cretaceous–mid-Paleogene, so that these must predate the onset of a MTC (Hill and Merrifield, 1993; Crisp et al., 2011; Carpenter et al., 2015).

What criteria should we look for in past records that would indicate a MTC in SWA? We consider three key but interacting features: a) a 3–8-month, summer-autumn drought (Beard, 1999; Groom and Lamont, 2015) with reliable winter rain of 300–900 mm pa (Cowling et al., 2005); b) warm/hot summer-autumn temperatures (daily temperatures may exceed 40 °C) with clear skies and low humidity (pan evaporation 1000–2500 mm pa, Lamont and Connell, 1996), and mild winters without snow; and c) intense crown fires at 10–20-year intervals promoted by the hot dry summers (Groom and Lamont, 2015; Rundel et al., 2016). As currently perceived, the mediterranean-climate region in SWA runs northwards along the west coast from the SW tip of Australia for ~1000 km and along the S coast for ~800 km and the triangle is completed inland by approximately following the 300-mm-pa isohyet (Fig. 1, Lamont and Connell, 1996; Rundel et al., 2016). This view includes the SE section otherwise allocated to an arid steppe hot climate in the Köppen-Geiger classification (Peel et al., 2007) that is no more elevated than the rest of the region (Byrne, 2008) and is included by J.S. Beard in the MTC region (Groom and Lamont, 2015).

Opinions as to when a MTC first arose in Western Australia vary from 30 to 3 Ma. The southern Australian climate changed from humid and nonseasonal in the Paleogene to drier and seasonal during the Neogene (Bowler, 1982; Kershaw et al., 1994). Martin (2006) noted that the paleochannels west of the Eucla Basin (in SWA) had ceased to flow by the mid-Miocene (15 Ma) and "this marked the first major step towards aridity [in Australia]". Stein and Robert (1986) postulated that aridification in Australia developed in the north and expanded southwards from the mid-late Miocene. The early stages of aridification may have been strongly seasonal with a dry period (Callan, 1977; Apthorpe, 1988). However, no comments have been made on whether this aridity was expressed as summer or winter drought, although seasonality would have existed at least at the level of intrannual temperature fluctuations with a warm summer. While world-wide temperatures trended downwards during the Cenozoic (Zachos et al., 2008), this was counteracted by Australia's drift towards the equator at this time (Hill, 2004).

Based on his models of xeric-mesic climates at present and in the Eocene, Oligocene and Miocene, Beard (1977) proposed that a MTC originated in northwestern Australia (NWA) 30 Ma, when Australia was 10° south of its current position, and then migrated south to SWA as Australia drifted north, but by 15 Ma it had only reached the northernmost tip of the current MTC corresponding to a 4° S drift by then (Fig. 1). In Beard's view, at no stage has the MTC in Western Australia on its eastern margin been surrounded by a summer-rainfall climate, only a uniform or 'bixeric' climate. Convinced of the region's long

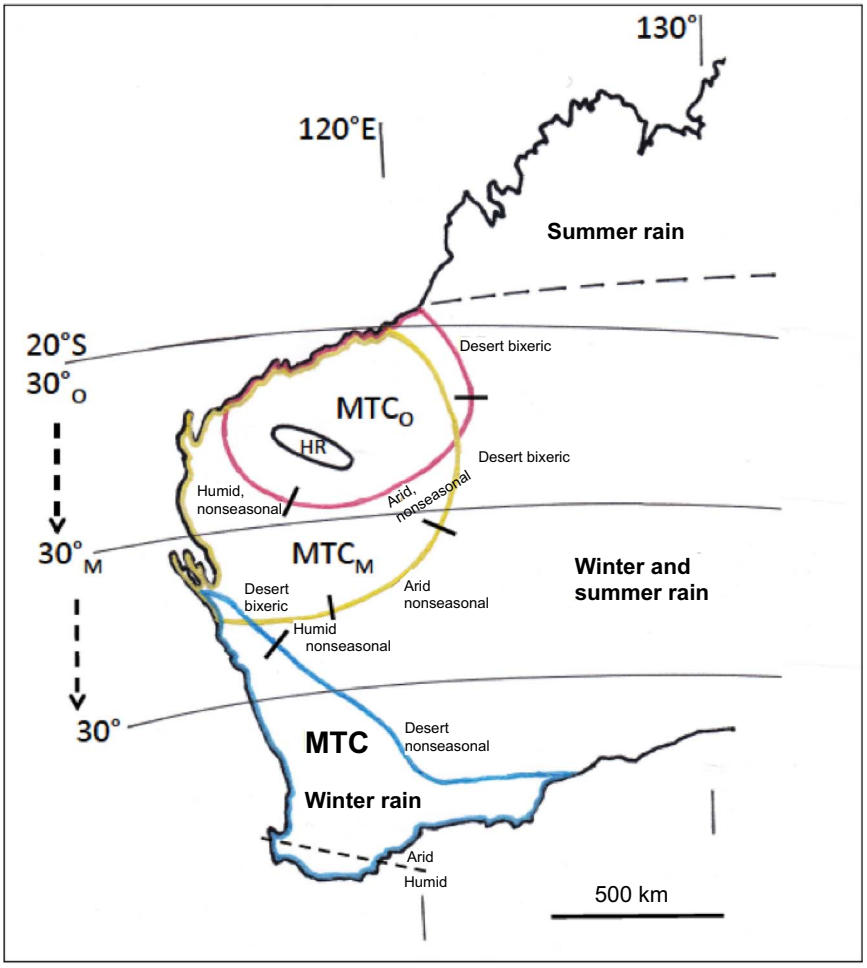

Fig. 1. Presence of a Mediterranean-type climate (MTC) in Western Australia over time (adapted from Beard, 1977). Current area bounded by blue, Oligocene (30 Ma) bounded by pink (MTC_O), Miocene (15 Ma) bounded by gold (MTC_M). 30°_O = projected position of 30° latitude line in the Oligocene, 30°_M = projected position of 30° in the Miocene, HR = Hamersley Range.