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# Why is South Africa so rich in butterfly species, and why are so many of them endemic?

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**Abstract:** South Africa has a higher level of biodiversity in the Papilionoidea (butterflies) than might be expected from its relatively high latitude. In order to understand this phenomenon we consider the impact of continental drift on oceanic circulation, topographic changes wrought by persistent uplift, climatic consequences such as periodic cooling and aridification, and the resultant vegetational changes in Africa since the late Cretaceous period. This narrative is compared with evidence from dated phylogenies of southern African butterfly groups, such as the highly speciose lycaenid genera *Thestor, Chrysoritis* and *Lepidochrysops.* Certain satyrine genera are also considered such as *Bicyclus*, all genera of the tribe Dirini, and *Pseudonympha* of the subtribe Ypthimina of tribe Satyrini.

Particularly influential vegetation changes were the transitions from forest to grassland and savanna, and later to the karoo biomes and fynbos. This resulted in the plant heterogeneity seen today, and influenced the cladogenesis and speciation of the butterfly groups under review. Adaptations like the use of cold-adapted grasses as host plants in the Satyrinae and ant association (ultimately aphytophagy) in some aphnaeine and polyommatine lineages allowed such butterflies to occupy the large variety of ecological niches provided by the vegetational changes. This led to the current highly speciose and endemic characteristics of multiple South African butterfly genera.

**Key words:** *Bicyclus, Chrysoritis,* climate change, continental drift, Dirini, fynbos, grassland, karoo, *Lepidochrysops, Pseudonympha, Thestor*

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## INTRODUCTION

Western Europe is approximately 10 million square kilometres in area, with 482 species of butterfly (according to the latest eBMS figure). South Africa is 1.22 million square kilometres and has 674 butterfly species (806 if subspecies are counted). The butterfly species density in South Africa is therefore roughly 11 times as high as Europe, and almost 17 times as high as that in continental North America. Why is this so?

One reason might be that whilst western Europe has been regularly and extensively glaciated (wiping out most butterfly species), South Africa was not glaciated during the last 100 or so million years since butterflies evolved (Kawahara *et al.*, 2023). Might it be that the climatic cycles that led to extinction in Europe (and North America) could be driving speciation events in South Africa? And that these species do not die out during the cycles, but accumulate in number with speciation events outnumbering extinctions?

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An initial investigation into the work of Van Zinderen Bakker *et al.* (1957, 1989) on glacial cycles showed that vegetation shifts followed changes in climatic cycles, which are driven by the Milankovitch cycles of global solar energy influx (Campisano, 2012). Because butterflies are largely herbivores they would have perforce 'followed' the inevitable plant speciation events. However, fifty years ago there was little hard evidence to follow this line of reasoning. In fact, at that time, Cottrell (1985) investigated relationships between South African butterflies and our vegetation but found no evidence that they were linked, at least for the Capensis floral element.

In recent years there have been many studies reporting on southern African geological and climatological changes (Partridge, 1988; Cowling *et al.*, 2009; Stanley *et al.*, 2021). Since the late Cretaceous period (65 Mya), by which time most modern butterfly families and subfamilies, and many of their tribes, were already in place, Africa had undergone profound changes in topography and climate. These would have forced the adaptation and evolution of butterflies, driven by changes in their host plants or use of other food resources. In this paper we review the palaeo-environmental patterns of South Africa to provide insights regarding potential conditions that may have generated the relatively high diversity seen in several butterfly lineages.

## METHODS AND MATERIALS

The source material for this study came from works by various authors on the geomorphologic, geological, and climatologic history of Africa and Gondwana, including van Zinderen *et al.* (1986), Partridge & Maud (1987), Jansson & Dynesius (2002), McCarthy& Rubidge (2005), Gasse (2006), Scher & Martin (2006), Cowling *et al.* (2009), and Stanley *et al.* (2021), This was also informed by the extensive floristic studies reported in Mucina & Rutherford (2006) and Mucina *et al.* (2014), which referred to the works mentioned above, among others.

Further material was sourced from various publications on dated butterfly phylogenetic studies by Heath & Pringle (2004), Price *et al.* (2011), Talavera *et al.* (2020), Aduse-Poku *et al.* (2021), Quek *et al.* (2022), Espeland *et al.* (2023), Heath *et al.* (2023a; 2023b), Kawahara *et al.* (2023), Mathew (2003), and van Steenderen *et al.* (2023).

## RESULTS & DISCUSSION

Species Richness and Endemism

Before proceeding further, it is necessary to examine these two different concepts, and to attempt to place them into a global perspective. Species richness is about the diversity of butterfly taxa (both species and subspecies) within a region or country, whereas endemism concerns itself only with those taxa which are confined in their distribution to particular regions or countries. It is a well-known fact that tropical countries are richer in species per square kilometre than subtropical or temperate countries; there are National Parks in the forested areas of tropical Africa which are inhabited by more than 1000 different species. However, examples such as these in Africa pale in comparison with the tropical forests of South American countries such as Brazil and Colombia, which are home to roughly 40% of all known butterfly taxa on earth. The comparative richness of species in the tropics, and the Neotropics in particular, is one of the reasons why Kawahara *et al.* concluded that the Neotropical region was probably the birthplace of all global butterfly species. They also concluded that, over the course of evolution, butterfly speciation was substantially higher in the tropics than in the temperate zones, and that the tropics served as dispersal areas for many of the butterfly species known today. So, when comparing butterfly species richness in South Africa, it is therefore important that these comparisons be made with other countries from a similar temperate zone.

Endemism, on the other hand, is concerned only with those species which are confined to a limited geographical area within a country; here, political boundaries between countries play an important role, giving larger countries a higher probable degree of endemism than smaller ones. There is also little doubt that islands will have a higher proportion of endemism than continental countries, simply because of genetic isolation. However, within continents endemism is also caused by natural barriers such as mountain ranges or deserts which also inhibit the flow of genes between populations.

Looking at South Africa in the light of this, one notes that it is species rich in butterflies when compared to other countries within the temperate zones, even though it ranks only 25th in the world as regards its surface area size. For example, in comparison with the 806 taxa in South Africa, there are 650 taxa of the 48 contiguous states of the United States of America (i.e. excluding Alaska and Hawaii) (Edwards *et al*., 2025), and 646 taxa in Australia. It even compares very favourably with other African countries situated further north in the subtropical and tropical zones, such as Zambia (877 taxa) (Ackery *et al.*, 1995; Heath *et al*., 2002) and Kenya (883 taxa) (Larsen, 1991). This number is also markedly higher than in its neighbouring countries, with 490 taxa known from Zimbabwe, 240 from Namibia (Pringle *et al*., 1994), and 250 from Botswana (Collins *et al*., 2021).

The major difference between South Africa and its neighbours lies in its extraordinarily high rate of endemism, with 45% of its taxa (362 taxa) known to be endemics. This is markedly higher than in Namibia (4% of its taxa), Botswana (no known endemics) (Collins *et al.*, 2021), Zimbabwe (7% of its taxa) (Ackery *et al.*, 1995), Zambia (2,7% of its taxa) (Heath *et al.*, 2002) and Kenya (10% of its taxa) (Larsen, 1991). This rate of endemism in fact compares favourably with that of many islands or island chains: Mauritius has only 25% of its 40 known taxa as endemic (Lawrence & Williams, 2021), while the Comoros Islands (ibid.) are marginally higher than South Africa at 46%, as is Australia at 47% (217 endemic taxa). Australia is, of course, an island continent. The highest rate of endemism on earth appears to occur on the island of Madagascar (ibid.), where 79% of its 313 butterfly taxa are endemic; this is, however, quite exceptional.

Looking at its fauna and flora, this data shows that South Africa could, in fact, be regarded as an island within a continent. Let us then proceed to examine how this has happened.

Continental drift and the uplift, cooling, and aridification of southern Africa

Since the mid-Cretaceous (~100 Mya) Africa has undergone many changes. By that time, it had begun to split from its Gondwanan neighbours Antarctica, India and South America as the proto-Atlantic, Indian, and Antarctic oceans opened. The continent drifted northwards (Smith *et al.*, 1994) and the central plateau uplifted in stages and underwent dramatic cycles of dry and wet climate since the early Eocene, around 60 Mya. The Great Escarpment began to form ~138 Mya (Ollier & Marker. 1985) because of the higher absolute elevation of the southern African portion of Gondwanaland. Isostasy uplifted southern Africa's great escarpment by 4–800 m during the mid-Cretaceous (Axelrod & Raven, 1978). Thereafter what had begun as a flat, moist, peneplained surface known as the African surface covered in forest changed and became floristically more heterogeneous as the continent uplifted, shifted, warped, tilted, and eroded during the Eocene and Miocene (McCarthy & Rubidge, 2005). It is thought that a savanna-like grassland may have been present in Africa during the Eocene. At that time, it was experiencing hot and arid conditions that could have led to the origin of one of the C4 grass lineages found there today (Handley *et al.*, 2012).

As the Southern Ocean opened in the mid-Eocene (Livermore *et al.*, 2005), aridification began because

Africa shifted northwards into warmer latitudes, and because of the growing influence of cold offshore currents to the west. This was particularly evident on the SW side of the continent (Coetzee *et al*., 1982; Cerling *et al*., 1997; Stanley *et al*., 2021). In the Miocene, temperate rainforests disappeared or retreated into niches. Grassy savanna spread across the high ground along the eastern escarpment and the Cape Fold (Cerling *et al*., 1997; Ehrlinger *et al*., 1997). More open grasslands – starting with savanna – evolved, around 40–35 Mya. Originally these grasses were of the ancestral $C_3$ photosynthesis type. Later, in the Oligocene, (24–35 Mya) $C_4$ grasses began to dominate as conditions favouring them (high aridity, low $CO_2$ levels, high summer temperatures) spread (Sage, 2004). In the Miocene-Pliocene, $C_3$ grasses were increasingly confined to moister, higher altitude habitats (Scott *et al*., 1997). Western coastal regions were taken over by a broad band of Cape sclerophyll vegetation; there is evidence that Mediterranean-type vegetation began to appear in southern Africa as early as 33 Mya (McCarthy & Rubidge, 2005).

By the late Oligocene (20 Mya) the mean altitude of southern Africa was still relatively low, and the moderating influence of the Indian Ocean maintained forests in areas close to the sea. There were warm periods roughly 14 & 19 Mya when subtropical palm-dominated savanna dominated the eastern side of the continent and aridity was lower than it is today (Thiergart *et al.*, 1962).

From the middle Miocene onwards, over the last 14 Mya, a combination of tectonic uplift, expanding polar ice caps, declining global temperatures, shrinkage of the Tethys Sea, and changing oceanic circulation has led to increasing climatic variability and aridification. Winter rainfall began in southern areas. Africa and South America continued moving north as the cold Antarctic Circumpolar and Benguela Currents developed (Livermore *et al.*, 2005; Partridge, 1997).

The growth of the Antarctic ice sheet has been attributed to reduced atmospheric $CO_2$ levels caused by the Himalayan uplift leading to a reduced 'greenhouse' effect (Zachos *et al.*, 2001). This reached its maximum during the middle to late Miocene 4.7–5.3 Mya, when subtropical elements in the Western Cape and proto-Nama-Karoo disappeared or retreated into refugia (Cerling *et al.*, 1997). Modern biomes began to develop in southern Africa; earlier tropical flora was lost due to the intensified aridification caused by strengthening of the Benguela Current. At about this time, the Namib Desert reached its current extent (Huntley, 2003).

By the mid-Pliocene, the tropical forests initially covering the landmass had retreated (Thiergart *et al*., 1962), and grasses became more widespread, leading to increased grazing and more frequent fires, further amplifying the aridification. By 8–3 Mya, this culminated with the establishment of the savanna and grassland biomes that now dominate much of the subcontinent (Deacon *et al.*, 1993). In the late Pliocene (2.5 Mya) there was a further 900–1000 m uplift of southern Africa accompanied by further global cooling. The Nama-Karoo eastern plateau experienced the greatest uplift (McCarthy & Rubidge, 2005). During these periods $C_3$ grasses reduced in the central plateau area and only occupied increasingly fragmented habitats in the mountains and winter rainfall southern coastal habitats.

In the Quaternary (the last 1.8 My) there have been extreme fluctuations in climate in southern Africa driven by the ~400/100 Ky Milankovitch cycle of mean insolation at 65°N (Campisano, 2012). These are regular repeated changes in the eccentricity of the Earth's orbit, the tilt (obliquity) of its axis, and the precession of that axis. These result in variations in solar radiation reaching the earth at different latitudes and times of the year. These variations have been occurring constantly through the geographic past and are not confined to recent times. However, changes in Africa's position and elevation during the Plio-Pleistocene since 3.7 Mya (Cohen *et al*., 2022) have made it more susceptible to these cycles, which have an exaggerated effect on local climate and vegetation.

These have been shown not to have had a significant effect on hominin evolution, whose average generation time is 26.9 years over the past 250 ky (Wang *et al*., 2023). However, the effect of these cycles would have been far greater on butterflies, whose average generation time is 0.2–1 generations per year depending on voltinism. Univoltine species like *Dira clytus* therefore have one generation per year, whereas bivoltine species like many temperate ones, two generations. Tropical species may be multivoltine with as many as four or five generations per year. It is therefore difficult to state an average generation length for butterflies, but it is in the region of 0.6 generations per year. Macgregor *et al.* (2019) have now shown that the phenology (flight periods) of butterflies can vary, as can voltinism, in response to climate change. This implies that butterflies have an approximately 50x higher probability of speciation than hominins, as seen in studies on the genus *Chrysoritis* (Quek *et al*., 2022; Heath *et al*., 2023a & 2023b).

## The origins of southern African butterflies and how they have changed over the past 100 My

For the early origins of butterflies, we rely heavily upon the work done by Kawahara *et al.* (2023), in their study of genetic data obtained from 2,300 butterfly species across the world. To date this is the most detailed and comprehensive work on the subject. They concluded that butterflies originated ~100 Mya in what is present-day Western North America or Central America, and were descendants of nocturnal, herbivorous moth ancestors. These early butterfly ancestors were Papilionidae, and they arose long after the origins of Angiosperms, ~200 Mya. All known butterfly families, excluding the tropical Hedylidae, diversified 10–30 Mya after the Cretaceous Thermal Maximum (90 Mya), and all were present except the Lycaenidae before the Cretaceous-Tertiary boundary (66 Mya). The evolutionary sequence, after the Papilionidae, appears to be: Hedylidae, Hesperiidae, Pieridae, Nymphalidae, Riodinidae and Lycaenidae. From about 60 Mya, the Neotropics served as an evolutionary cradle with high in situ butterfly speciation and many dispersal events. Seemingly the first dispersals were to the Nearctic region via Beringia roughly 75 Mya, although the majority of dispersal events between the Neotropics and the Nearctic took place after the Eocene-Oligocene boundary ~33 Mya. Butterflies were present on what are now all modern continental landmasses (excluding Antarctica) by the mid-

Eocene, roughly 45 Mya. Two lineages dispersed from the Eastern Palearctic around 17 Mya, and these appear to be the first colonisers of Europe.

Host plants

Kawahara *et al.* (2023) also surmised that the first host plants of butterflies were most likely to have been legumes (Fabaceae), whose common ancestor is from ~98 Mya They also found that more than two thirds of extant butterfly species feed on a single plant family, and that nearly all generalists (those feeding on two or more plant families) feed on plant families that are closely related. Butterflies feeding on grasses or legumes are often host specific. These two plant families are geographically widespread and abundant, and most lack potent defensive chemicals that restrict insect feeding. Both plant families occur in every vegetational system from forests to semi-desert; Fabaceae is the third largest plant family, and Poaceae the fifth largest.

It is unclear as to exactly when butterflies moved into Africa, but a study of the genus *Charaxes* (*sensu lato*) by Aduse-Poku *et al*. (2009) showed that the common ancestor of *Charaxes* diverged from the common ancestor of *Palla* in the mid-Eocene 45 Mya in central Africa and began diversifying to its extant members 15 million years later (i.e. 30 Mya). Most of the major diversifications occurred between the late Oligocene and early Miocene (25–20 Mya) when global climates were undergoing drastic fluctuations. Over much of this vast timespan, woodlands or tropical forest would have covered most of the continent. The *nichetes* group is the oldest lineage of *Charaxes*, appearing to have diverged from the common ancestor of the rest of *Charaxes* in the Oligocene roughly 30 Mya. Next came the common ancestor of the *Polyura-pleione/zoolina* clade, which appeared in the mid-Oligocene 27 Mya. The genera *Polyura* and *Euxanthe* are estimated to have branched off about 24 and 19 Mya, respectively, and the estimated time of divergence between the African and Asian species groups occurred between 17–13 Mya. The early Pliocene (5–3.5 Mya) is a significant diversification period as most of the extant *Charaxes* species were established during this period. In fact, the role of Pleistocene climatic oscillations in the diversification of taxa in African tropical rainforests was far more significant than was earlier supposed.

Nearly all of South Africa’s endemic butterfly species come from two families: Nymphalidae (subfamily Satyrinae,) and Lycaenidae (several subfamilies). Let us deal with each subfamily.

Satyrinae

These taxa are all dependent on grasses as foodplants, which originated about 125 Mya, with the currently accepted clades that exist in Africa diversifying 85–90 Mya (Gallaher *et al.*, 2022). At first, these would have survived within and around the fringes of the great forests, but they adapted quickly to progressive aridification, and grasslands become an established vegetation type by the Eocene (40 Mya).

McCarthy & Rubidge (2005) state that grassland had expanded enormously at the expense of dry woodland over the past 30 My. Initially grass competed with desert scrub but gradually its environmental range expanded, and it became the dominant vegetation type in intermediate rainfall areas. Like fynbos, it outcompetes other vegetation types by surviving fire.

Aduse-Poku *et al*. (2021) showed that *Bicyclus*, like *Charaxes*, also originated in the Congolian rainforests of central Africa, though more recently, at the Oligo-Miocene boundary ~25 Mya. In this instance, abrupt climatic fluctuations during the Miocene (at about 19–17 Mya) probably fragmented ancestral populations. Subsequently, a fluctuating Neogene climate, and uplift of the eastern African regions, produced one of the most spectacular radiations in Africa.

According to Price *et al.* (2011), the ancestral lineage of the Satyrine tribe Dirini probably also inhabited forested or wooded habitats, as is still the case with the Melanitini. *Paralethe* and the South American *Manataria* diverged from ancestral Dirini >40 Mya, and at some point *Manataria* (or its common ancestor with *Paralethe* and Dirini) crossed the Atlantic. This may have been via an archipelago of islands along the Walvis Ridge and the Rio Grande Rise, which has since become inundated (O’Connor & Duncan, 1990). A contributing factor could have been ‘rafting’ following flooding of the Karoo River during the early Tertiary, which drained the subcontinent at a more southerly position than the modern Orange River (Dingle & Hendey, 1984). This is the so-called ‘sweepstakes’ method of dispersal (Nathan, 2001), or the oceanic dispersal described by de Queiroz (2005).

*Paralethe* and the Dirini diverged ~ 29 Mya, when the first of the Dirini lineage appears to have adapted to more open habitats, such as grasslands. *Aeropetes* and *Tarsocera* appear to be the oldest lineage, followed by *Torynesis*, then *Dira* and finally *Dingana*. Most of this process took place between 18–12 Mya. Initially, during the Mid-Miocene Climatic Optimum (17–15 Mya) the climate was warmer and wetter, and the forests expanded. During this period, little diversification of the Dirini occurred. However, this changed at ~14 Mya with the upwelling of the Benguela current off the West Coast and a renewal of the aridification process (McCarthy & Rubidge, 2005). This was followed at ~5 Mya by an uplift of the Great Escarpment (by as much as 600 m to 900 m in the east and 200 to 300 m in the west), which created a rain shadow across the interior plateaux. This accelerated the expansion of the grassland biome, with expansion of the summer rainfall savanna and grassland areas with $C_4$ grasses. The $C_3$ grasses, better suited to cold and wet conditions, were driven by the increasing relief of the landscape (as the Pliocene uplift 2.5 Mya progressed) into isolated niches. Populations of the Dirini, whose larvae specialise in $C_3$ grasses, became fragmented and this likely led to their speciation. Most of the Dirini are only 3–5 My old, although some are double this age.

Van Steenderen *et al.* (2023) analysed the large genus *Pseudonympha*, and concluded that this clade (which includes *Cassionympha, Stygionympha*, *Melampias* and *Neocoenyra*) split from its sister clade (now the *Ypthima* group) ~28 Mya and began differentiating about 23 Mya; this accelerated ~15 Mya, contemporaneously with Dirini. *Pseudonympha* originated in the Cape Fold Mountains ~5 Mya and spread eastwards and northwards along the Great

Escarpment during the aridification and uplift process (Partridge, 1997). As with *Dira*, most extant species are < 5 Mya. The Dirini and the *Pseudonympha* clade of the subtribe Ypthimini adapted by using hardy, wiry, cold- and drought-adapted grasses in the subfamilies Danthonioideae and Pooideae as host plants. These have a tussock-type growth system, and the butterfly larvae and pupae survive fires by burrowing into the tussocks. How they survive cold is a matter of conjecture, although Alpine and Arctic Satyrinae can survive frost (Vrba *et al*., 2022), so it is possible that the local species have the same adaptation.

Lycaenidae

Kaliszewska *et al*. (2015) found that the larvae of approximately three-quarters of species of this family associate with ants, as well as do a substantial proportion of the Riodinidae, an older family from which the Lycaenidae probably evolved. They state that the lycaenid subfamily Miletinae originated in Africa ~57 Mya, near the beginning of the Eocene when global temperatures were higher, and the Earth was covered by forests. In the mid-Eocene (40–33 Mya) there was significant cooling and a reduction in the prevalence of forests. During this period, specifically between 38–30 Mya, three clades of Miletinae dispersed out of Africa into Asia.

Polyommatinae

The evolutionary history of the Oboroniina subtribe (Grishin, 2023) of tribe Polyommatini (Swainson, 1827) is currently being researched by Espeland *et al.* (2023). According to these authors, the phytophagous genus *Euchrysops* originated ~22 Mya in the emerging Miombo woodlands of central southern Africa. The first major divergence from this line was genus *Orachrysops*, (also phytophagous) which split from *Euchrysops* >20 Mya. This was followed by *Thermoniphas* and *Oboronia* ~3 My later. The common ancestor of *Lepidochrysops* diverged at ~15 Mya, after which *Euchrysops* experienced elevated levels of extinction probably because of the aridification of Africa between 15–5 Mya. In contrast, the rapid radiation of the phyto-predaceous genus *Lepidochrysops* began at ~6.5 Mya, and two major clades developed in *Lepidochrysops*: one originating in the southern African montane grasslands and then dispersing from there into the Fynbos and Karoo biomes; while the other originated further north, in the Miombo woodlands, and spread from there throughout the Savanna and warmer Grassland biomes. The aridification process selected for a phyto-predaceous life history; ant nests providing caterpillars with a safe refuge from fire and a source of food when vegetation became scarce. Unlike *Lepidochrysops, Orachrysops* appears to have diversified ~5 Mya, more or less coincident with the origin of the cooler montane Grassland vegetation units. The larvae adopted rootstock feeding and an obligate relationship with *Camponotus* (Mayr, 1861) ants, enabling them to also have a safe refuge from fire in fynbos and grassland habitats (Edge & van Hamburg, 2008). It should nevertheless be noted that obligate dependency on ants is precarious, as can be seen from the lists of species with threatened conservation status; butterflies which rely on ants for their survival are dominant on these lists (Mecenero *et al*., 2013: 18–20).

Aphnaeinae

Boyle *et al*. (2014) proposed that the Aphnaeinae probably originated in southern Africa but did not exclude the possibility that this may have happened further north in Africa. They appear to have radiated out of Africa into Asia only once, through the Oriental genus *Cigaritis.* However, no timelines were given for this process.

The common ancestor of *Chrysoritis* diverged from its sister groups about 32 Mya (Talavera *et al*., 2020; Quek *et al.*, 2022; Heath *et al*., 2023a & b;) and split into Western and Eastern lineages (the *chrysaor* clade vs the rest) ~17 Mya. The colonisation of the fynbos region in the west began ~ 9 Mya, with rapid radiation after ~2 Mya.

Zhao *et al*. (2020) in their article on Tent Tortoises, pointed out that climatic oscillations in the Plio-Pleistocene Epochs (2.6–0.01 Mya) proved to be a fundamental driver that shaped distributional patterns and cladogenesis in many organisms and therefore facilitated their genetic divergence and speciation. During the cold periods, glaciations resulted in migrations and the shrinking of populations, thus functioning as major drivers in subdividing populations. During warm periods, recolonisation, dispersal and population expansion occurred.

This is also apparent in many of the South African butterfly species groups, where large-scale speciation has taken place within the past 2 My: the *thysbe* group of *Chrysoritis*; the *methymna* and *ortygia* groups of *Lepidochrysops*; the *brachycerus* group of *Thestor*; and the *thyra* group of *Aloeides* all fit this scenario.

To understand this, it is necessary to comprehend the forces which gave rise to the fynbos and the Western Cape winter rainfall area, together with the arid Karoo areas. About 38 Mya continental shifts gave rise to the start of the Antarctic deep-water circulation; this only intensified about 10 Mya, when the Antarctic ice sheets began to expand rapidly. By the end of the Miocene 6 Mya, the forests of the Western Cape had become increasingly fragmented through invasive fynbos elements (and accompanying fire), and by ~3 Mya both polar regions had become permanently glaciated, with atmospheric circulation approximating its present patterns. This resulted in the summer dry climates and extensive winter rainfall areas in the Western Cape. Simultaneously, it would have intensified the aridity of the Karoo and Namib regions. From this time the fynbos rapidly diversified through an explosion of speciation. This explosion would have been assisted by the Cape Fold Mountain geography, which encourages isolation on mountain aspects, and by the fact that, as Kruger & Taylor suggested (1979), climatic change in the region has not been on such a scale as to cause extinction rates to exceed speciation rates since it has not been accompanied by glaciation. Sea levels here would also have fluctuated over time; two and a half million years ago, for example, the coastal plain south of the present Breede River Mouth widened from 50–200 km when the sea level dropped about 120m below present levels (Klein, 1977). This would have increased the fynbos region lowlands to three times their present size.

These were some of the forces that have confronted southern African butterflies, particularly over the past 3

My. The Lycaenidae were likely able to survive the effects of aridification on host plants and the threats of fire in fynbos and grasslands by placing greater reliance upon underground nesting ants for their survival. This type of specialisation does, however, have the effect of localising colonies to small select areas. In turn, this would lead to increased fragmentation and diversification, depending on climatic conditions. It is probable that, during periods of fluctuating climates, the size of their colonies would also have expanded or contracted, enabling some to reintegrate and others to disintegrate. Reintegration would mean resumed gene flow between populations, which would recombine differences between them caused by genetic isolation. Both processes have undoubtedly occurred in the past, which is why the taxonomy of these species groups is so problematic. Even genetic analysis has not been able to resolve taxonomic issues, as is evident from the *Chrysoritis*, where several "hybrids" were encountered (Heath *et al*., 2023a). One needs to keep in mind that many of these isolated colonies appear to have been separated very recently.

Recent advances in nuclear DNA sequencing, DNA mutation rate calibration (mitochondria in animals and chloroplasts in plants) have allowed the construction and comparison of dated phylogenies. At the same time, our understanding of geology, paleoclimatology and the consequences of plate tectonics has improved considerably. It is now possible to look back into deep time and combine all these factors to arrive at explanations for the species distributions we see today. One example is the wide but disjunct distribution of related fynbos-adapted butterflies like *Cassionympha* and some of the *Chrysoritis* and *Thestor* along the southern Cape coastline. During past glacial maxima, when the sea level was much lower than it is today (Campisano, 2012), large areas of the continental shelf were exposed for sufficient time to develop vegetation and present minimal barriers to dispersal of these butterflies. When the sea level rose and inundated these flatlands, those barriers would have returned.

It also explains why we find similar butterfly species in the coastal fynbos of the Western Cape and atop high mountains in the Drakensberg chain. And the number of closely related but different taxa is explained by the local climate conditions favouring speciation over extinction – but at the edges in the south of the region, we know that specialised butterflies are vulnerable to extinction.

There are many other issues that are lost in the mists of time and need explaining. Two of these involve our smallest and weakest-flighted butterflies, namely *Actizera stellata* and the genus *Brephidium*. How did *Actizera stellata* end up in two such widely separated areas as the North-Eastern Cape and the African tropical mountains? Even more so, how did the genus *Brephidium* end up with two species in the arid areas of South Africa, and two species in central America and the southern parts of the United States? Until recently, heavy reliance was placed on plate tectonics to explain such anomalies; however, as in the case of *Brephidium*, this cannot always be the answer. These butterflies are weak fliers, and the separation of Africa from South America is too ancient. They would also not be good candidates for the older theory of oceanic dispersal, because the distances would be too great. It must nevertheless be noted that recently the theory of oceanic dispersal has been resurrected (de Queiroz *et al.*, 2005) Together with this is the reminder that sea levels have not always been as high, and that a rise in sea levels could have inundated forgotten island chains which may have provided links between continents. One such forgotten potential island chain is the Walvis Ridge/Rio Grande Rise (O'Connor & Duncan, 1990), which could have provided a link between Africa and South America at a time when the continents were not far separated, such as would have been the case 45 Mya. This was the suggested route taken by the ancestors of *Manataria* when they crossed from Africa to South America, as mentioned earlier.

## CONCLUSIONS

This article puts forward some explanations as to the enormous diversity and relatively high number of endemic butterfly species present in South Africa. Modern advances in DNA analysis and knowledge of plate tectonics, geomorphology and paleoclimatology have allowed this synthesis. Africa's uplift, isolation, and aridification since the Eocene, and dated phylogenies of butterflies and plants, have lent substance to these hypotheses.

Plate tectonics has transformed Africa from a forested, low-altitude, peneplained landscape which began as part of a disintegrating Gondwana to an (almost) island continent with vastly different relief and climate. Africa has uplifted, warped, and split from its neighbouring land masses. As these moved away and separated further, or collided with other plates, the global climate changed, resulting in aridification, cooling, and huge changes in Africa's vegetation. Forest was replaced with savanna, savanna became grassland. Savanna and grassland became the Karoo biomes, desert, thicket, and fynbos, which in some places were replaced in turn by forest. Uplift and erosion created a landscape with varied relief, so the vegetation remained heterogeneous and corridors and refugia for plants and animals persisted. There is a spectrum from the Congo basin, where conditions must be like what they were on Gondwana, to the deserts in the north and south, alpine vegetation along the mountain chains, and Mediterranean-type macchia vegetation in the Cape regions. Despite the growth of the polar ice caps during the ice ages, Africa never became glaciated in the way that North America or Eurasia were. The climatic fluctuations driven by the Milankovitch cycle induce changes that wash across the landscape like waves on a beach. This means that the plants of Africa (and as a result, the Lepidoptera) exist as a palimpsest of climatic conditions from the Holocene back to the end of the Cretaceous.

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## LITERATURE CITED

ACKERY, P.R., SMITH, C.R. & VANE-WRIGHT, R.I. 1995. *Carcasson's African butterflies.* CSIRO, Australia.

ADUSE-POKU, K., VINGERHOEDT, E. & WAHLBERG, N. 2009. Out-of-Africa again: A phylogenetic hypothesis of the genus *Charaxes* (Lepidoptera: Nymphalidae) based on five gene regions. *Mol Phyl & Evol* **53**(2): 463–478. https://doi.org/10.1016/j.ympev.

ADUSE-POKU, K., VAN BERGEN, E., SÁFIÁN, S., COLLINS, S. C., ETIENNE, R. S., HERRERA-ALSINA, L., BRAKEFIELD P. M., BRATTSTRÖM, O., LOHMAN, D.J., & WAHLBERG, N. 2021. Miocene climate and habitat change drove diversification in *Bicyclus*, Africa's largest radiation of Satyrine butterflies. *Syst Biol* **71**(3): 570–588. https://doi.org/10.1093/sysbi o/syab066.

AXELROD, D.I. & RAVEN P.H. 1988. Late Cretaceous and Tertiary vegetation history of Africa. *Biography and Ecology of Southern Africa*. Springer, Netherlands.

BOYLE, J.H., KALISZEWSKI, Z.A., ESPELAND, M., SUDERMAN, J., FLEMING, J., HEATH, A., & PIERCE, N. 2014. Phylogeny of the Aphnaeinae: myrmecophilous African butterflies with carnivorous and herbivorous life histories. *Syst Ent* **40**(1): 169–182. https://doi.org/10.1111/syen.

CAMPISANO, C.J. 2012. Milankovitch cycles, paleoclimatic change, and hominin evolution. *Nature Educ Know* **4**(3): 5.

CERLING, T.U., HARRIS, J.M., MACFADDEN, B.J., LEAKEY, M.G., QUADE, J., EISENMAN, V. & EHRLINGER, J.R., 1997. Global vegetation change through the Miocene/Pliocene boundary *Nature* **389**: 153–158.

COETZEE, J.A. & ROGERS, J. 1982. Palynological and lithological evidence for the Miocene palaeoenvironment in the Saldanha region (South Africa). *Palaeogeography, Palaeoclimatology, Palaeoecology* **39**: 71–85.

COHEN, A.S., DU, A., ROWAN, J., YOST, C.L., BILLINGSLEY, A.L., CAMPISANO, C.J., BROWN, E.T., DEINO, A.L., FEIBEL, C.S., GRANT, K., KINGSTON, J.D., LUPIEN, R., MUIRURI, V., OWEN, R.B., REED, K.E., RUSSELL, J. & STOCKHECKE, M. 2022. Trends, rhythms, and aberrations in global climate 65 Mya to present. *Science* **292:** 686–693. https://doi.org/10.1073/pnas.2107393119.

COLLINS, S.C., DOBSON, J.C.H., & WILLIAMS, M.C. 2021. *Torben Larsen's butterflies of Botswana and their natural history*. JCD Publishers, South Africa. 200 pp.

COTTRELL, C.B. 1985. The absence of coevolutionary associations with Capensis floral element plants in the larval /plant relationships of southwestern Cape butterflies. *Transvaal Museum monographs* **4**: 115–124.

COWLING, R.M., PROCHES, Ş., & PARTRIDGE, T.C. 2009. Explaining the uniqueness of the Cape flora: Incorporating geomorphic evolution as a factor for explaining its diversification. *Mol. Phyl. & Evol.* **51**(1): 64–74. https://doi.org/10.1016/j.ympev.2008.05.034

DE QUEIROZ, A. 2005. The resurrection of oceanic dispersal in historical biogeography. *Trends in Ecol & Evol* **20**(20): 68–73.

DEACON, H.J., HENDEY, Q.B. & LAMBRECHTS, J.J.N. 1983. The Fynbos Region. South African National Scientific Programmes Report No. **75**.

DINGLE, R.Y. & ENDEY, B. 1984. Late Mesozoic and Tertiary sediment supply to the eastern Cape Basin (S.E. Atlantic) and palaeo-drainage systems in southwestern Africa. *Mar Geol* **56**: 13–26.

EDGE, D.A. & VAN HAMBURG, H. 2008. Larval feeding behaviour and myrmecophily of the Brenton Blue, *Orachrysops niobe* (Trimen) (Lepidoptera: Lycaenidae). *J Res Lep* **42**: 21–33.

EDWARDS, C.B., ZIPKIN, E.F., HENRY, E.H., HADDAD, N.M., FORISTER, M.L., BURLS, K.J., CAMPBELL, S.P., CRONE, E.E., DIFFENDORFER, J., SCHULTZ, C.B., *et al.* 2025. Rapid butterfly declines across the United States during the 21st century. *Science* **387**: 1090–1904. https://doi.org/10.1126/science.adp4671 .

EHRLINGER, J.R., CERLING, T.E., & HELIKER, B.R., 1997. $C_4$ photosynthesis, atmospheric $CO_2$, and climate. *Oecologia* **112**: 285–299.

ESPELAND, M., CHAZOT, N., CONDAMINE, F.L., LEMMON, A. R., LEMMON, E. M., PRINGLE, E.L., Heath, A., COLLINS, S.C, TIREN, W., MUTISO, M., LEES, D.C., FISHER, S., MURPHY, R., WOODHALL, S.E., TROPEK, R., AHLBORN, S.S., COCKBURN, K., DOBSON, J.C.H., BOUYER, T., KALISZEWSKA, Z.A., BAKER, C.C.M., TALAVERA, G., VILA, R., GARDINER, A.J., WILLIAMS, M.C., MARTINS, D.J., SÁFIÁN, S., EDGE, D.A. & PIERCE, N.E. 2023. Rapid radiation of ant parasitic butterflies during the Miocene aridification of Africa. *Ecol & Evol*, 13:e10046. https://doi.org/10.1002/ece3.10046

GALLAHER, T.J., PETERSON, P.M., SORENG, R.J., ZULOAGA, F.O., LI, D.-Z., CLARK, L.G., TYRRELL, C.D., WELKER, C.A.D., KELLOGG, E.A. and TEISHER, J.K. 2022. Grasses through space and time: An overview of the biogeographical and macroevolutionary history of Poaceae. *J Syst Evol* **60**: 522–569. https://doi.org/10.1111/jse.12857

GASSE, F. Climate and hydrological changes in tropical Africa during the past million years. 2006. *Comptes Rendus Palevol* **5**: (1–2): 35–43. ISSN 1631-0683.

GRISHIN, N.V. 2023. p. 45 *In*: Zhang, J., Cong, Q., Shen, J., Song, L. & Grishin, N.V, 2023. Butterfly Classification and Species Discovery Using Genomics. *The Taxonomic Report of the International Lepidoptera Survey* **11**(3).

HANDLEY, L., O'HALLORAN, A., PEARSON, P.N., HAWKINS, E., NICHOLAS, C.J., SCHOUTEN, S., MCMILLAN, I.K. & PANCOST, R.D. 2012. Changes in the hydrological cycle in tropical East Africa during the Paleocene-Eocene Thermal Maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology* **329–330**: 10–21. Elsevier. https://doi.org/10.1016/j.palaeo.2012.02.002.

HEATH, A., NEWPORT, M.A. & HANCOCK, D. 2002. *The butterflies of Zambia.* African Research Institute & Lepidopterists' Society of Africa.

HEATH, A. & PRINGLE, E.L. 2004. A review of the southern African genus *Thestor* Hübner (Lepidoptera: Lycaenidae: Miletinae) *Metamorphosis* **15**(3): 91–151.

HEATH, A., PRINGLE, E.L. & QUEK, S-P. 2023a. *Chrysoritis* Butler (Papilionoidea: Lycaenidae:

Aphnaeinae) – Part II: Natural history: morphology, ecology, and behaviour, with accounts of larval ecology and insights into the aphytophagous *C. dicksoni* (Gabriel). *Metamorphosis* **34**: 1–10. https://dx.doi/10.4314/met.v34i1.01.

HEATH, A., PRINGLE, E.L. & QUEK, S-P. 2023b. *Chrysoritis* Butler (Papilionoidea: Lycaenidae: Aphnaeinae) – Part III: An integrative taxonomic revision. *Metamorphosis* **34**: 11–28. https://dx.doi/10.4314/met.v34i1.02.

HUNTLEY, B.J. 2023. *The Namib Desert Biome*. *In*: *Ecology of Angola*. Springer, Cham. https://doi.org/10.1007/978-3-031-18923-4_16.

JANSSON, R. & DYNESIUS, M. 2002. The fate of clades in a world of recurrent climatic change: Milanchovitch oscillations and evolution. *Annu Rev Ecol Syst* **33**: 741–777.

KALISZEWSKA, Z.A., LOHMAN, D.J., SOMMER, K., ADELSON, G., RAND, D.B., MATHEW, J., TALAVERA, G. & PIERCE, N. 2015. When caterpillars attack: Biogeography and life history evolution of the Miletinae (Lepidoptera: Lycaenidae). *Evolution* **69**: 571–588. https://doi.org/10.1111/evo.12599.

KAWAHARA, A.Y., STORER, C., CARVALHO, A.P.S., PLOTKIN, D.M., CONDAMINE, F.L., BRAGA, M.P., ELLIS, E.A., ST LAURENT, R.A., LI, X., BARVE, V., CAI, L., EARL, C., FRANDSEN, P.B., OWENS, H.L., VALENCIA-MONTOYA, W.A., ADUSE-POKU, K., TOUSSAINT, E.F.A., DEXTER, K.M., DOLECK T., MARKEE, A., *et al.* 2023. A global phylogeny of butterflies reveals their evolutionary history, ancestral hosts and biogeographic origins. *Nat Ecol Evol* **7**(6): 903–913. https://doi.org/10.1038/s41559-023-02041-9.

KLEIN, R.G. 1977. The ecology of early man in southern Africa. *Science* **197**: 115–126.

KRUGER, F.J. & TAYLOR, H.C. 1979. Plant species diversity in Cape fynbos: gamma and delta diversity. *Vegetation* **41**: 85–93.

LARSEN, T.B. 1991. *The butterflies of Kenya and their natural history.* Oxford University Press.

LAWRENCE, J.M. & WILLIAMS, M.C. 2021. *An illustrated history of butterflies of the Afrotropical Indian Ocean islands.* 248 pp. Siri Scientific Press, Manchester, United Kingdom.

LIVERMORE, R., NANKIVELL, A., EAGLES, G. & MORRIS, P. 2005. Paleogene opening of Drake passage. *Earth Planet Sci. Lett.* **236**(1–2): 459–470. https://doi.org/10.1016/j.epsl.2005.03.027.

MACGREGOR, C.J., THOMAS, C.D., ROY, D.B., BEAUMONT, M.A., BELL, J.R., BRERETON, T., BRIDLE, J.R., DYTHAM, C., FOX, R., GOTTHARD, K., HOFFMANN, A.A., MARTIN, G., MIDDLEBROOK, I., NYLIN, S., PLATTS, P.J., RASTEIRO, R., SACCHERI, I.J., VILLOUTREIX, R., WHEAT, C.W., & HILL, J.K. 2019. Climate-induced phenology shifts linked to range expansions in species with multiple reproductive cycles per year. *Nat Commun* **10**(1): 4455. https://doi.org/10.1038/s41467-019-12479-w.

MATHEW, J. 2003. Aphytophagy in the Miletinae (Lycaenidae): phylogeny, ecology, and conservation. Dissertation, Biological Sciences, Old Dominion University. https://doi.org/10.25777/v7rh-mb21.

MCCARTHY, T. & RUBIDGE, B. 2005. *The story of earth and life: a Southern African perspective on a 4.6-billion-year journey*. Cape Town: Struik.

MECENERO, S., BALL, J.C., EDGE, D.A., HAMER, M.L., HENNING, G.A., KRÜGER, M., PRINGLE, E.L., TERBLANCHE, R.F. & WILLIAMS, M.C. (eds) 2013. *Conservation assessment of butterflies of South Africa, Lesotho and Swaziland: Red list and atlas.* Saftronics (Pty) Ltd., Johannesburg & the Animal Demography Unit, Cape Town.

MUCINA, L. & RUTHERFORD, M.C. (eds). 2006. The Vegetation of South Africa, Lesotho and Swaziland. *Strelitizia* **19**. South African National Biodiversity Institute, Pretoria, South Africa.

MUCINA, L., RUTHERFORD, M.C., POWRIE, L.W., VAN NIEKERK, A. & VAN DER MERWE, J.H. (eds). 2014. Vegetation Field Atlas of Continental South Africa, Lesotho and Swaziland *Strelitzia* **33**. South African National Biodiversity Institute, Pretoria.

NATHAN, R. 2001. *Dispersal Biogeography*. *In*: *Encyclopedia of Biodiversity*. pp.127–152. Elsevier https://doi.org/10.1016/B0-12-226865-2/00073-0.

O'CONNOR, J.M. & DUNCAN, R.A 1990. Evolution of the Walvis Ridge-Rio Grande Rise hot spot system: Implications for African and South American Plate motions over plumes. *J Geophys Res* **95**(B11): 17475–17502. https://doi.org/10.1029/JB095iB11p17475.

OLLIER, C.D. & MARKER, M.E. 1985. The great escarpment of southern Africa. *Zeitschr Geomorphol N.F.,* Suppl **54**: 37–46.

PARTRIDGE, T.C. 1997. Evolution of landscapes. Chapter 1 *In*: Cowling, R.M., Richardson, D.M. & Pierce, S.M. (Eds), *Vegetation of southern Africa*, pp. 1–20. Cambridge Univ. Press, Cambridge.

PARTRIDGE, T.C, 1998. Of diamonds, dinosaurs and diastrophism: 150 million years of landscape evolution in southern Africa. *S Afr J Geol* **101**(3): 167–184.

PARTRIDGE, T.C., MAUD, R.R. 1987. Geomorphic evolution of southern Africa since the Mesozoic. *S Afr J Geol* **90**: 179–208.

PRICE, B.W., VILLET, M.H., WALTON, S.M. & BARKER N.P. 2011. Using molecules and morphology to infer the phylogenetic relationships and evolutionary history of the Dirini (Nymphalidae: Satyrinae), a tribe of butterflies endemic to Southern Africa. *Syst Entomol* **36**:300–316. https://doi.org/10.1111/j.1365-3113.

PRINGLE, E.L., HENNNG, G.A. & BALL, J.B. (eds). 1994. *Pennington's butterflies of southern Africa.* (2nd edition). Struik Winchester, Cape Town.

QUEK, S-P., PRINGLE, E.L. & HEATH, A. 2022. *Chrysoritis* Butler (Papilionoidea: Lycaenidae: Aphnaeinae) – Part I: Molecular phylogenetic analyses of a South African genus of myrmecophilous butterflies. *Metamorphosis* **33**: 107–126. https://doi.org/10.4314/met.v33i1.13.

SAGE, R.F. 2004. The evolution of $C_4$ photosynthesis. *New Phytol* **161**(2): 341–370. https://doi.org/10.1111/j.1469-8137.2004.00974.x.

SCHER, H.D. & MARTIN, E.E. 2006. Timing and climatic consequences of the opening of Drake Passage. *Science* **312**: 428–430. https://doi.org/10.1126/science.1120044.

SCOTT, L., ANDERSON, H.M. & ANDERSON, J.M. 1997. *Vegetation history*. Chapter 4 *In*: Cowling, R.M., Richardson, D.M. & Pierce, S.M. (Eds). *Vegetation history of Southern Africa.* Cambridge Univ Press, Cambridge.

SMITH, A.G., SMITH, D.G. & FUNNELL B.M. 1994. *Atlas of Mesozoic and Cenozoic Coastlines.* Cambridge Univ Press, Cambridge. p 109.

STANLEY, J.R., BRAUN, J., BABY, G. *et al.* 2021. Constraining plateau uplift in southern Africa by combining thermochronology, sediment flux, topography, and landscape evolution modelling. *J Geophys Res: Solid Earth*, **126**: e2020JB021243. https://doi.org/10.1029/2020JB021243

TALAVERA, G., KALISZEWSKA, Z.A., HEATH, A., & PIERCE, N.E. 2020. Recent diversification of *Chrysoritis* butterflies in the South African *Mol Phyl & Evol* **148**: 106817. https://doi.org/10.1016/j.ympev.2020.106817.

THIERGART, F., FRANTZ, U. & RAUKOPF, K. 1962. Palynologische Untersuchungen von Tertiärkohlen und einer Oberflächenprobenahe Knysna, Südafrika. *Adv Front Plant Sci* **4**: 151–178.

VAN STEENDEREN, C.J.M., PRINGLE, E.L. & VILLET, M.H. 2023. Historical diversification of *Pseudonympha* Wallengren, 1857 (Lepidoptera: Nymphalidae: Satyrinae). *J. Nat. Hist.* **57**: 29–32. https://doi.org/10.1080/00222933.

VAN ZINDEREN BAKKER, E.M. 1957. *A pollen analytical investigation of the Florisbad deposits (South Africa)*. pp. 56–67 *In*: Clark, J.D. & Cole, S. (Eds), *Proceedings of the Third Pan African Congress on Prehistory*. Livingstone, Chatto & Windus, London.

VAN ZINDEREN BAKKER, E.M. 1989. Middle Stone Age palaeoenvironments at Florisbad (South Africa). *Palaeoecology of Africa* **20:** 133–154.

VAN ZINDEREN BAKKER, E.M. & MERCER J.H. 1986. Major late cainozoic climatic events and palaeoenvironmental changes in Africa viewed in a worldwide context. *Palaeogeography, Palaeoclimatology, Palaeoecology.* **56**(3–4): 217–235. https://doi.org/10.1016/0031-0182(86)90095-7.

VRBA, P, SUCHÁČKOVÁ, B.A, ANDRES, M, NEDVĚD, O., ŠIMEK, P. & KONVIČKA, M. 2022. Exploring cold hardiness within a butterfly clade: Supercooling ability and polyol profiles in European Satyrinae. *Insects* **13**(4): 369. https://doi.org/10.3390/insects13040369

WANG, R.J., AL-SAFFAR, S.I., ROGERS, J. & HAHN, M.W. 2023. Human generation times across the past 250,000 years. Sci Adv *Evol Biol* **9**(1): 7047. https://doi.org/10.1126/sciadv.abm7047.

ZACHOS, J.C., PAGANI, M., SLOAN, L., THOMAS, E. & BILLUPS, K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**: 686–693. https://doi.org/10.1126/science.1059412.

ZHAO, Z., HEIDEMAN, N., BESTER, P., JORDAAN, A., & HOFMEYR, M.D. 2020. Climatic and topographic changes since the Miocene influenced the diversification and biogeography of the tent tortoise (*Psammobates tentorius*) species complex in Southern Africa. BMC Evolutionary Biology **20**: 153 (2020). https://doi.org/10.21203/rs.3.rs-35038/v4.