Implications of summer breeding frogs from Langebaanweg, South Africa: Regional climate evolution at 5.1 mya

AUTHORS:
Thalassa Matthews[1] iD

G. John Measey[2] iD

†David L. Roberts[3]

†*Deceased*

AFFILIATIONS:
[1]DST–NRF Centre of Excellence for Palaeontology, Iziko South African Museum, Cape Town, South Africa

[2]Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa

[3]Department of Geography, University of the Free State, Bloemfontein, South Africa

CORRESPONDENCE TO:
Thalassa Matthews

EMAIL:
tmatthews@iziko.org.za

No direct palaeoclimatic proxies have been available to indicate the seasonality or amount of rainfall on the west coast of southern Africa during the Early Pliocene. The Benguela Upwelling System (BUS) is today one of the factors responsible for the present-day aridity on the west coast of southern Africa. The initiation of the BUS is frequently linked to the entrenchment of aridity and the establishment of the current winter rainfall pattern on the west coast; however, marine proxies are inconclusive regarding the effects of past fluctuations in the BUS and sea surface temperatures on the rainfall regime. Neither the fossil evidence nor the fact that plants using the C_3 photosynthetic pathway predominate at this time, provide direct evidence of winter rainfall at Langebaanweg. We challenge certain assumptions which are commonly made in the literature regarding the timing of inception of a winter rainfall regime on the west coast and the onset of aridity in the Langebaan region, and provide new evidence as to seasonality of rainfall at Langebaanweg in the Early Pliocene. Herein, the identification of frog species from the genus *Ptychadena* from Langebaanweg provides new and compelling evidence for a summer rainfall regime, or of at least significant summer rainfall, at 5.1 mya in the southwestern Cape of South Africa.

Significance:

- Advances understanding of the evolution of the winter rainfall zone on the west coast of South Africa

- Assesses evidence for the inception of aridity and a winter rainfall regime on the west coast of South Africa

- Fossil Ptychadenidae from the Early Pliocene site of Langebaanweg provide evidence for a summer rainfall regime at 5.1 mya on the west coast of the southwestern Cape.

Introduction

Southern Africa is a predominantly summer rainfall region but the Winter Rainfall Zone (WRZ) situated along the southwestern and southern tip of the African continent, lying at the boundary between southern hemisphere temperate and tropical climate systems, is an exception (Figure 1). Evidence for the inception, geographical extent, intensity and fluctuations of the WRZ prior to the last glacial period is currently fragmented through both time and space, and a coherent understanding of the evolution of this ecosystem, unique in sub-Saharan Africa, has not been attained.[1] Although progress has been made in understanding climate change and rainfall seasonality in the Late Quaternary,[2-5] the fluctuations of these variables over the Neogene are complex and incompletely understood. The Neogene terrestrial fossil record is sporadic and incomplete as a result of the lack of preservation of terrestrial organic materials and thus direct climatic proxies, deposits which are problematic in terms of dating, and a lack of understanding of the geomorphological evolution of the subcontinent.[5,6] Much therefore remains to be elucidated about the inception and evolution of the WRZ. In this paper, we challenge certain assumptions which are commonly made in the literature regarding the inception of a winter rainfall regime on the west coast and the onset of aridity in the Langebaan region, and provide new evidence for rainfall seasonality at Langebaanweg in the Early Pliocene.

The Early Pliocene (~5.1 million years ago (mya)) site of Langebaanweg (LBW) situated on the southwestern coast of South Africa (Figure 1), is a remarkably rich and world-renowned vertebrate fossil site, representing a time period when fossil assemblages are particularly rare in sub-Saharan Africa.[7] LBW is the site of first appearance in the fossil record for numerous taxa, including large and small mammals, birds, reptiles and amphibians.[7-10] LBW sheds light on the critical period during which tectonism led to the latitudinal migration of climate belts, which resulted in widespread reorganisation in atmospheric and ocean circulation.[11] These events were characterised by a more humid episode, with modern aridity becoming established only in the later Pliocene, between ~4 mya and 2.8 mya.[11] Congruently, the fauna at LBW indicates more humid conditions than at present, but the precise nature of the vegetation in the area remains uncertain and until recent research on the frog fauna there were no effective proxies indicating the amount of rainfall, or seasonality, at the fossil site.[10,12-14]

A recent study of the rich and diverse anuran (frog) community from LBW served as an effective and direct climatic proxy, and showed that this group, sensitive as they are to rainfall and moisture, supported the higher humidity inferred from studies of other faunal groups from the site, and indicated relatively high rainfall.[12,15] The huge contrast between the frog community in the Langebaanweg region today, as compared with 5.1 mya, is clearly indicated by the fact that species richness on the relatively dry west coast of South Africa is low today (1–10 species)[16,17], whereas at LBW, six families and some 19 taxa have been differentiated[12]. The LBW frog fauna is put in context when compared to modern species richness elsewhere in the southwestern Cape, which varies from 11 to 30 species.[16,18]

Currently, southern African Anura are distributed throughout three different rainfall zones: the Summer Rainfall Zone (SRZ), the Winter Rainfall Zone (WRZ) and the Year-round Rainfall Zone (YRZ) which is found on the South African south coast. A number of amphibian taxa from the WRZ and the SRZ overlap in the YRZ.[18]
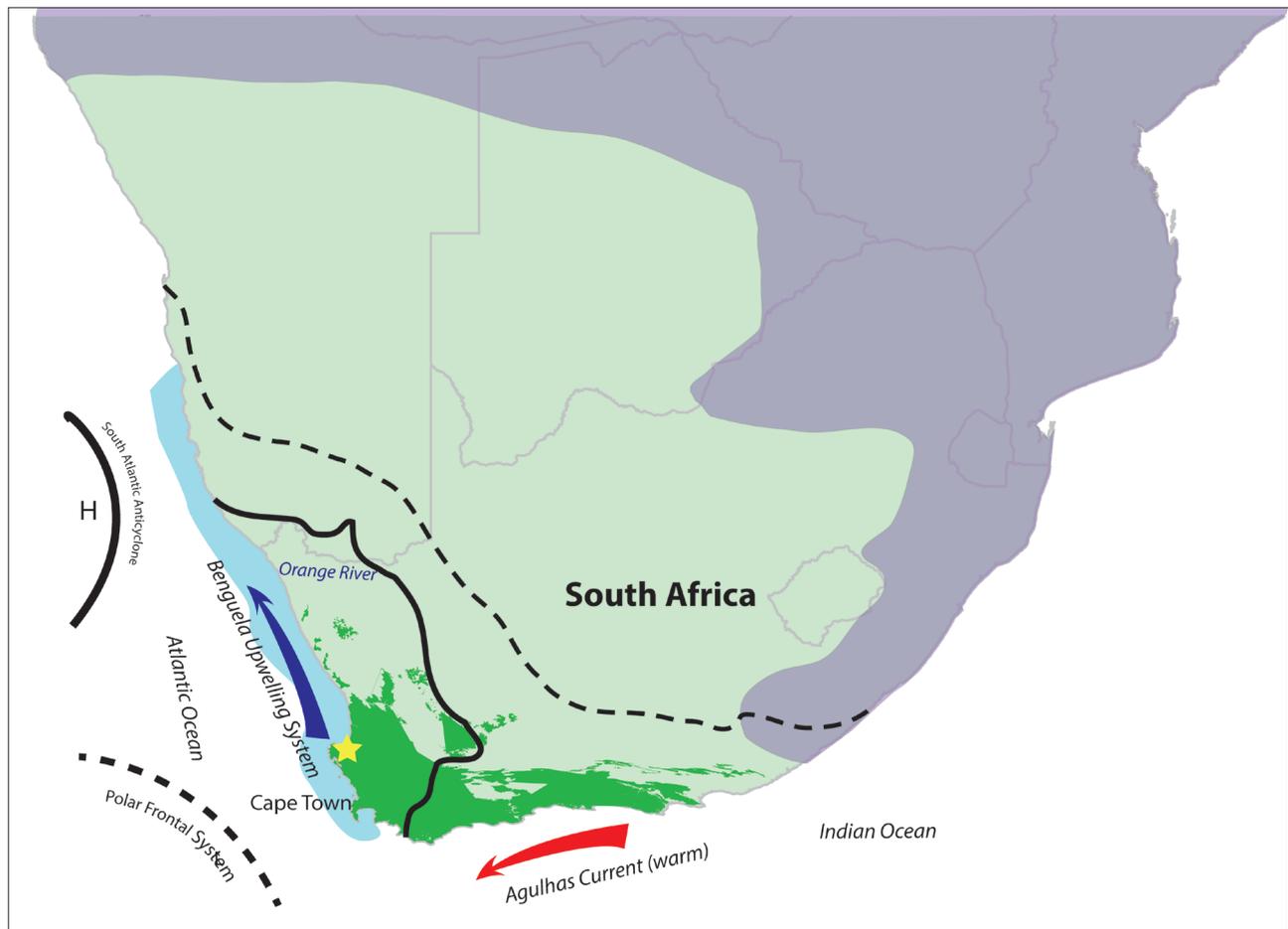
Note: Grey areas indicate the current distribution of Ptychadena *taxa; the star indicates the position of Langebaanweg. The area to the left of the solid line indicates the current Winter Rainfall Zone and the area to the right between the solid and stipled lines indicates the current Year-round Rainfall Zone. To the right of the stipled line is the Summer Rainfall Zone. The Fynbos Biome is indicated in green. Rainfall zones after Chase and Meadows[3].*

Figure 1: Locality of the fossil site of Langebaanweg and current climatic and oceanographic conditions at the southern tip of Africa.

All frog families and genera previously identified at LBW were ambiguous in terms of the seasonality of rainfall as all but one of the species (a SRZ taxon) identified currently occur within all three rainfall regimes (Table 1). In the present study, we take a step further, utilising the recent identification at LBW of two species of the genus *Ptychadena* (family Ptychadenidae) to shed further light on the seasonality of rainfall at this site. Additionally, this discovery further elucidates the biogeography of the family Ptychadenidae.

Climatic history of the Winter Rainfall Zone

The WRZ receives predominantly winter rainfall from eastward migrating cold fronts embedded in polar cyclonic systems originating over the South Atlantic.[19,20] During summer, the South Atlantic Anticyclone is well developed and migrates to the south, blocking both the westward propagation of easterly waves that bring summer rainfall to much of southern Africa, and the polar frontal systems. The influence of the polar frontal systems diminishes northwards and is linked to decreasing rainfall and increasing aridity.[14] The cold, nutrient-rich Benguela Upwelling System (BUS) supports a diverse and rich range of marine life along the southwestern African coast.[21] The South Atlantic Anticyclone promotes the BUS and is thus the main cause of the present aridity along the southwestern African coast, the Namib, and the dryness of the adjacent interior of the sub-continent.[5,20,22-25] In general, the climate on the west coast is determined by the complex seasonal shifts and interplay of the prevailing winds over the Benguela region.[5] Fluctuations in summer rainfall are linked to upwelling intensity in the BUS[26] and along the south coast[5]. The situation is complex, as indicated by the fact that Chase et al.[5] found that at a hyrax-midden site falling within the present

WRZ, but close to the border with the SRZ, summer rainfall variability over the Holocene during the last 7000 years had the greatest impact on water availability, and was the primary determinant of humidity. Analysis of herbivore tooth enamel indicates that there were incursions of C_4 vegetation in the mid-Pleistocene,[27] which could be related to decreased atmospheric pCO_2 conditions during interglacial periods, or possibly to changes in rainfall seasonality.

Recent research on marine proxies for sea surface temperature (SST) in the southern Cape Basin – such as calcareous dinoflagellate cysts and alkenones – suggests the inception of the BUS at about 10.5–10 mya.[28,29] How the BUS became established is comprehensively summarised in Neumann and Bamford[6]. Some authors[29,30] have suggested that tectonic uplift in southwestern Africa would have led to a cooling in the BUS at 12 mya, and after 5 mya, but the timing and cause of such tectonic events, and even their occurrence, is controversial[6,31]. The initiation of the BUS has frequently been linked in the literature to summer aridity and the entrenchment of the current winter rainfall pattern on the west coast[6,24,32,33], and this in turn has been taken to have influenced other processes, such as the diversification of plants (see Altwegg et al.[33] – although a recent analysis[1] failed to find proof that seasonal aridity at ~8 mya triggered floristic radiation and diversification in the Cape Floral Region).

The connection between the BUS and seasonality of rainfall is unclear as estimates of the evolution of SSTs are not available[34] and the marine record indicates that the BUS and SSTs have fluctuated considerably over time in the late Neogene. High glacio-eustatic sea levels and the presence of warm-water molluscan taxa in the middle to late Pliocene[35,36] add further complexity to deciphering the evolution of oceanic and climatic conditions in the current WRZ.

Table 1: Distribution of extant frog families and genera according to the current rainfall regime. Fossil taxa found at Langebaanweg are bolded.

Family	Genera		
	Summer rainfall	Winter rainfall	Year-round rainfall
Arthroleptidae			
	Arthroleptis	–	–
	Leptopelis	–	–
Hyperoliidae			
	Hyperolius	***Hyperolius***	***Hyperolius***
	Afrixalus	–	*Afrixalus*
	Semnodactylus	*Semnodactylus*	*Semnodactylus*
	Kassina	–	–
Heleophrynidae			
	Heleophryne	***Heleophryne***	***Heleophryne***
	Hadromophryne	–	–
Brevicipitidae			
	Breviceps	***Breviceps***	***Breviceps***
Pyxicephalidae			
	Amietia	*Amietia*	*Amietia*
	Anhydrophryne	–	
	Cacosternum	*Cacosternum*	*Cacosternum*
	Strongylopus	*Strongylopus*	*Strongylopus*
	Tomopterna	***Tomopterna***	***Tomopterna***
	Pyxicephalus	–	–
	Natalobatrachus	–	–
	–	*Microbatrachella Arthroleptella*	–
	–	*Poyntonia*	–
Phrynobatrachidae			
	Phrynobatrachus	–	–
Ptychadenidae			
	Ptychadena		
	Hildebrandtia	–	–
	Lanzarana	–	–
Bufonidae			
	Amietophrynus	***Amietophrynus***	***Amietophrynus***
	Vandijkophrynus	*Vandijkophrynus*	*Vandijkophrynus*
	Poyntonophrynus	*Poyntonophrynus*	*Poyntonophrynus*
	Schismaderma	–	–
	–	*Capensibufo*	*Capensibufo*
Pipidae			
	Xenopus	***Xenopus***	***Xenopus***
Microhylidae			
	Phrynomantis	–	–
Hemisotidae		–	–
	Hemisus	–	–
Rhacophoridae		–	–
	Chiromantis	–	–
Families	12	6	6
Genera	29	17	14

There is also evidence of an oceanic subsurface warming between 6.5 mya and 5.0 mya which may be related to variability in the strength of North Atlantic deepwater formation on the temperatures of the intermediate waters of the South Atlantic.[34] The climatic data during LBW times are ambiguous in terms of oceanographic conditions, with SSTs apparently in sharp decline, but with low productivity (suggesting reduced upwelling) indicated by a drop in total organic carbon.[34] The fossil-bearing members of the Varswater Formation present at LBW conversely contain an abundance of authigenic phosphate, which is widely interpreted as being indicative of strong upwelling (Roberts et al.[14] and references therein). The presence of some mollusc taxa from LBW which are currently found northwards from East London and eastwards from False Bay suggest warmer ocean temperatures than present.[37]

Identification and provenance of *Ptychadena* at Langebaanweg

The majority of fossils from LBW were recovered from two highly fossiliferous members which form part of the Varswater Formation, namely the Muishondfontein Pelletal Phosphate Member (MPPM) and the Langeberg Quartzose Sand Member (LQSM). See Roberts et al.[14] for further details on the geology of the site.

An examination of LQSM sediments (~5.1 mya) collected from a mine dump during phosphate-mining operations several decades ago was recently undertaken. The interpretation of the LQSM in the area from which the dump derived (the so-called 'east stream') was that it represented a river floodplain.[38] In the course of this study, an additional anuran genus (accession number SAM-PQL-70839) was identified – *Ptychadena* (Family: Ptychadenidae) – on the basis of a single sacrum (Figure 2). Subsequently a further ptychadenid, which appears to belong to a relatively larger species, was recovered from MPPM deposits which were excavated from the main dig site at the West Coast Fossil Park from square G5 (accession number SAM-PQL-71524) (Figure 2). The larger Ptychadenid showed several morphological differences to the smaller taxon, including a greater distance between the anterior and posterior articular ends of the sacrum (best seen in ventral view, Figure 2b and 2f), a larger neural spine, and a wider spacing of the sacral articular condyles.

The sacrum of a modern Ptychadenid, *Ptychadena mascareniensis*, from the Iziko South African Museum (ZR-045512), was scanned using microcomputed tomography and then measured for comparative purposes (see Figure 2 for positioning of measurements). This species currently enjoys a wide distribution in western, eastern and central Africa, extending down into South Africa. The breadth of the sacrum was 3.27 mm and the height 1.46 mm. The modern *Ptychadena* thus falls in between the two fossil taxa in terms of size as the smaller of the fossil taxa (SAM-PQL-70839) measured 2.79 mm by 1.39 mm, and the larger (SAM-PQL-71524) 4.60 mm by 1.88 mm for breadth and height, respectively.

Extant Ptychadenidae comprise the genera *Ptychadena, Hildebrandtia* and *Lanzarana*, and are monophyletic.[39] Four unique morphological synapomorphies are noted, including the symmetrical fusion of the eighth presacral vertebra with the sacral vertebra (sacrum), forming a composite sacrum.[40] The LBW ptychadenid sacrum displays the fusion of the presacral vertebra and sacrum, together with the distinctive anterolateral orientation and morphology of the transverse processes of members of the genus *Ptychadena*, including a characteristic foramen above the centrum that serves as the outlet for the spinal nerve (as noted by Blackburn et al.[41]). In addition, *Ptychadena* species differ from many ranids in that the neural arches of the composite sacrum lack deep grooves and fossae on the dorsal surface and exhibit a single minute low-lying neural spine.[40] Blackburn et al.[41] provide conclusive evidence, through a thorough investigation of extant and fossil taxa, that the Ptychadenidae are the only major clade of frogs with the above sacral morphologies, making the identification of the LBW taxa indisputable.

LBW extends our knowledge of the fossil distribution of ptychadenids to include the southwestern Cape at 5.1 mya, and represents the most southerly occurrence of this genus to date in the African fossil record. The fossil frog bones reported on in this paper are curated by the Iziko South African Museum, Cape Town, and each bone reported on has been allocated an identifying accession number.

Other fossil sites containing Ptychadena *species*

The antiquity of the *Ptychadena* lineage is indicated by the earliest appearance of *Ptychadena* in the fossil record in the late Oligocene sediments (~25 mya) from the Nsungwe Formation in southwestern Tanzania.[40] This record represents the earliest of fossil anurans from Africa below the equator, and is the earliest definitive record of any family within the diverse ranoid clade Natatanura (sensu Blackburn et al.[41] and Frost et al.[42]). Other appearances of Ptychadenidae in the fossil record include those of the Middle Miocene at Beni Mellal in Morocco[43] and Pleistocene deposits from Madagascar[44].
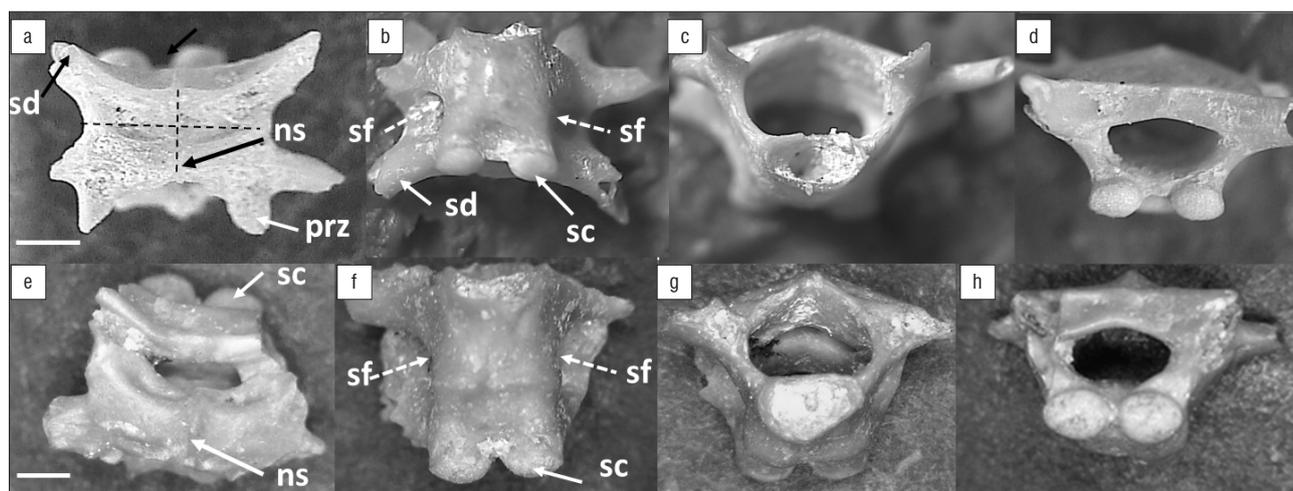
prz, prezygapophysis; ns, neural spine; sc, sacral articular condyles; sd; sacral diapophysis; sf, spinal foramina

Scale bar equals 1 mm

Figure 2: (Top) *Ptychadena* indet. sp. 1 (Family: Ptychadenidae) from Langebaanweg, requisition number SAM-PQL-70839, in (a) dorsal, (b) ventral, (c) anterior and (d) posterior views. (Bottom) *Ptychadena* indet. sp. 2 (Family: Ptychadenidae) from Langebaanweg, requisition number SAM-PQL-71524, in (e) dorsal, (f) ventral, (g) anterior and (h) posterior views.

Phylogeography of Ptychadena

Extant ptychadenids comprise 55 species within the genera *Hildebrandtia*, *Lanzarana* and *Ptychadena*, and are widespread tropical and subtropical species distributed throughout Madagascar, sub-Saharan Africa, the Seychelles and the Mascarene islands[39], with the exception of two species found in the Nile Delta[40]. The distribution of the genus *Ptychadena* in southern Africa is delimited in areas where rainfall is above 60 mm in January and the minimum temperature is above 8 °C in September. These two variables represent 36.4% and 29.0% of the distribution of the genus in southern Africa, respectively (G.J.M. unpublished data). These two parameters describe the distribution of extant species from East London to the northeast, under the influence of the SRZ and increasing temperatures (Figure 1).

In the current WRZ, all modern species breed in winter, with the exception of two invasive species from the SRZ.[45] Some genera and families are found in both the WRZ and SRZ, and the remaining southern African families and genera are found in the SRZ and breed in summer (Table 1). Six amphibian families have been identified from LBW (Hyperoliidae, Brevicipitidae, Pxyicephalidae, Pipidae, Heleophrynidae and Bufonidae), and 19 different taxa, 10 of which remain unidentified, have been differentiated.[12] Genera identified include *Hyperolius*, *Breviceps*, *Tomopterna*, *Xenopus*, *Heleophryne* and *Amietophrynus*.[12] All the frog families and genera identified from LBW[12] currently occur in all three rainfall regimes (SRZ, WRZ and YRZ), with endemism to the WRZ only existing at species level in these genera[16]. Matthews et al.[12] tentatively identified *Kassina* (a genus restricted to the SRZ) – an identification which has subsequently been confirmed by computed tomography scans of comparative material, but the family to which it belongs (Hyperoliidae) contains other genera which are found in the current WRZ. Interestingly, histological studies done on the aquatic *Xenopus* (Family: Pipidae; common name: the African clawed frog) femora from LBW (paper in preparation) suggest marked seasonality as clear LAGS (lines of arrested growth) are evident.

Phylogeographic structuring in the distribution of anuran taxa with respect to the winter and summer rainfall regions has been recorded,[46] but little is known about the evolution of this pattern which clearly has deep roots. In the literature, the southern African amphibian fauna is commonly divided into two main groups – the so-called 'tropical' (a term used to describe the specioze tropical frog fauna distributed widely in the northeastern parts of southern Africa) and the unique 'Cape' frog faunas of the southwestern Cape which are characterised by extremely high rates of endemism and contain a large number of species with narrow niche envelopes.[16,17,47,48] These two groups correspond to the SRZ (the tropical frog fauna) and WRZ (the Cape frog fauna), and their breeding periods are delineated by mean annual precipitation in the summer or winter rainfall months, respectively.[17,48] The two rainfall regimes have such a high turnover in species that it is evident at a global scale.[49] Nonetheless, there are some genera that straddle both rainfall zones, but the population genetics of these taxa suggest deep genetic divisions, such that populations are confined to one zone or the other.[46]

Discussion

The palaeoenvironment at Langebaanweg

Fossil pollen is frequently used in palaeoenvironmental reconstruction to ascertain whether C_3 plants (those which fix and reduce inorganic CO_2 into organic compounds using the C_3 photosynthetic pathway) or C_4 plants (those which employ the C_4 photosynthetic pathway) dominated a palaeo-landscape. Grasses categorised as C_4 vegetation are typically associated with a summer rainfall regime, and C_3 grasses with the WRZ. Franz-Odendaal et al.'s[32] research on the large mammals from LBW indicated that the expected grazers (e.g. alcelaphine, hippopotamus and rhinoceros), as well as browsing species, showed δ13C values which indicated that LBW was a C_3 dominated environment. This finding was corroborated by a study of phytoliths from the site.[50] The small mammals from LBW, such as the rats and mice, suggest a fynbos component to the vegetation[9], as does fossil pollen[51,52]. The presence of cool-growing C_3 grasses at LBW during the deposition of MPPM sediments was taken to indicate that the present-day climatic regime of winter wet/summer dry was established early in the Pliocene epoch.[32] Using the vegetation to establish the rainfall regime is, however, questionable, given that fynbos and C_3 grasses both have a C_3 signature, and the contribution of C_3 grasses versus that of C_3 fynbos at LBW is undetermined. In addition, there are indications that the contribution from C_3 grasses to the general C_3 signature at LBW was small, as Stynder[10] suggests that fossil bovid species indicate that grass was scarce, and the environment may have been heavily wooded. The presence of woodland is supported by the presence of certain bird taxa, but arid and semi-arid landscapes are also represented.[7,9] The precise nature of the Early Pliocene vegetation at LBW remains elusive, has no modern analogue, and cannot contribute in any verifiable way to ascertaining the rainfall regime, or provide information on seasonality, at LBW. The fact that fynbos was present on the west coast during the Early Pliocene has been used as evidence of a WRZ; however, the premises on which this association is based are arguable and are discussed further in the next section.

Inception of the WRZ and aridification of the west coast

Of the eight frog genera found at LBW, six (*Hyperolius*, *Breviceps*, *Tomopterna*, *Heleophryne*, *Amietophrynus* and *Xenopus*) are found in summer, winter and year-round rainfall areas. The evidence of seasonality provided by *Kassina* is not clear-cut as, although this taxon is currently found in the SRZ, other members of the Hyperoliidae, such as *Semnodactylus*, are found in the current WRZ and YRZ. *Ptychadena* is, however, currently not found in the more southerly and western areas of South Africa, or in any parts of the WRZ[16], suggesting that this family has evolved and adapted to live in the SRZ.

The ptychadenids are a marker SRZ species, as they are found only in this rainfall zone, and the presence of *Ptychadena* at LBW thus provides strong evidence of a summer rainfall regime, or at least of a rainfall regime which included summer rainfall. The faunal evidence from LBW clearly indicates that at 5.1 mya the region was still receiving a relatively high rainfall, which fell partly, if not entirely, in summer.

This finding has important implications for studies involving the evolution of west coast flora and fauna, and the interpretation of phylogenetic studies which use molecular clock estimates to interpret the timing of lineage divergence. As mentioned previously, such studies have typically used the formation of the BUS as a proxy for the inception of the winter rainfall regime along the West Coast and the beginning of aridification.[6,24,32,33] Certain fynbos taxa such as Restionaceae, Ericaceae and Proteaceae formed part of the vegetation in southwestern Africa during the Palaeogene[53] and fossil pollen research indicates that fynbos taxa have formed part of west coast ecosystems since well before the inception of BUS and a winter rainfall regime[14,15,23,51,52,54]. Hoffman et al.'s[1] habitat reconstruction for the dated phylogenies of 12 plant clades from the Cape Floral Region in southern Africa indicated that they evolved in aseasonal rainfall environments. In addition, this research indicated that the initial development of aridity in the Cape Floral Region was not linked to the onset of strong rainfall seasonality – contradicting the common assumption that aridity and the development of a strongly seasonal winter rainfall regime on the west coast occurred at the same time and are effectively linked. This de-linking of these two variables indicates that commonly made assumptions in the literature are incorrect, and illustrates how much still remains to be elucidated about the evolution of the WRZ.

On a global scale, the middle Miocene is considered to have been a time of reduced seasonality and relatively stable climate with elevated temperatures and high humidity and rainfall.[1,6,52] Scisio et al.[52] studied the pollen from cores from the Miocene age Elandsfontyn Formation at LBW, which underlies the younger, main fossil-bearing deposits at the site. A strong contribution from plants that currently occur in tropical and subtropical conditions in the summer rainfall region in eastern South Africa is noted. The climate was wetter, and probably warmer, as indicated by the presence of palms and subtropical trees, the absence of Ericaceae, and the occurrence of only two Stoebe-type pollens. The fossil pollen evidence available which pre-dates LBW thus suggests that rainfall may have been either inter-annual, or characterised by a greater contribution of summer rain.[52]

Roberts et al.[15] suggested that the current pronounced aridity gradient from south to north on the west coast may have had its inception in the earlier Miocene. Hoffmann et al.[1] suggested that the Middle Miocene (13–17 mya) saw the development of perennial to weakly seasonal arid conditions, with the strongly seasonal rainfall regime of the west coast arising ~6.5–8 mya. Neumann and Bamford[6] suggest that aridification of the west coast began post Middle Miocene. Based on a palynology study of sediments retrieved from the Atlantic off the mouth of the Orange River, Du pont et al.[54] note that between 10 mya and 6 mya, pollen types from plants of tropical affinity disappeared, and those from the Cape flora gradually increased. The onset of aridity on the west coast has thus been postulated to pre-date the LBW fossils by 3–5 mya. This postulate has, however, been based on palaeoclimatic proxies situated much further to the north of LBW in Namibia[31,55] and the Orange River[54]. The LBW frog community indicates a relatively high rainfall[12], as do some other fossil taxa[13], and the fact that woodland appears to have been widespread[10]. The evidence from LBW strongly contradicts assertions that aridification of the west coast in the region was well established by 5.1 mya, although such a scenario was certainly applicable further northwards, with aridity in the Namib dating back to 16 Ma.[55] However, relatively moister conditions appear to have prevailed in the southern, as opposed to the central, Namib desert during the Miocene and the flora appears to have remained C_3 in both regions until the Pliocene.[56]

The marine evidence mentioned previously is inconclusive regarding the effects of fluctuations in the BUS and SSTs on the rainfall regime during the Early Pliocene. Much uncertainty therefore exists as to the exact status of the strength, and effect, of the BUS and SSTs, and the inferences drawn from other palaeoclimatic proxies are contestable. Neither the fossil evidence, the fossil pollen data, nor the fact that C_3 plants predominate, provide direct evidence of winter rainfall at LBW, or indeed of the period of inception of the WRZ.

Conclusions

The majority of anuran taxa at LBW are currently found in the SRZ and WRZ, and consequently are not diagnostic in terms of the rainfall regime. However, the identification of two *Ptychadena* species from LBW, as well as the presence of *Kassina*, provides new evidence of a summer rainfall regime, or of at least some significant summer rainfall, at ~5.1 mya on the southwestern coast of southern Africa. This evidence is a significant contribution to our understanding of the evolution of seasonality on the west coast in the LBW region and challenges the commonly held assumption that the WRZ has been established on the west coast since the later Miocene/Early Pliocene. The presence of a *Ptychadena* species also contributes to our knowledge of the palaeo-distribution of the family, which is currently widespread in sub-Saharan Africa, and has endured since the Oligocene in Tanzania.

Acknowledgements

Authors' contributions

T.M. was the project leader; undertook the fossil research and provided the first draft of the manuscript. D.L.R. provided information on climatic change and conditions over the Miocene and Pliocene and made conceptual contributions. G.J.M. made conceptual contributions and provided information on the frog taxa mentioned in the paper. All three authors contributed to writing the manuscript.

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