

**Speciation and evolution of eco-climatic ranges in the
intertropical, African, dung beetle genus, *Diastellopalpus*
van Lansberge**

ADRIAN L.V. DAVIS¹ & CLARKE H. SCHOLTZ

*Scarab Research Group, Dept of Zoology & Entomology, University of Pretoria,
Lynnwood Rd, Pretoria, 0002 South Africa*

¹Corresponding author:

Dr Adrian L.V. Davis

Scarab Research Group

Department of Zoology & Entomology

University of Pretoria

Lynnwood Rd

PRETORIA

0002 South Africa.

Tel: ++27 78 175 8441 (mobile)

Tel: ++27 12 420 2539 (work)

Fax: ++27 12 362 5242 (work)

E-mail: adavis@zoology.up.ac.za

ABSTRACT

We investigate how late Cenozoic orogenics and climatic change might have influenced the history of taxon diversification and current species ranges in an endemic, Afrotropical, insect genus. *Diastellopalpus* van Lansberge is a near basally-derived taxon in the dung beetle tribe Onthophagini (Coleoptera: Scarabaeidae: Scarabaeinae) that has diversified into 32 known species primarily centred on intertropical forests. Basal dichotomies in both published (Josso & Prévost, 2000) and re-analyzed phylogenies divide the species into clades that are geographically centred either to the east or west of the eastern highlands that underwent uplift from the Miocene (16 MY). There is broad climatic overlap between many of the species but clear separation along a minimum spanning tree in ordinal space where they are divided into taxa with either lowland or highland centres of distribution. Observed spatial distributions of six defined species groups (A-F) (Wide:- B: equatorial west to east; D and E: west to central; F: intertropical, west to southeast; Restricted:- A: southeast; C: central) mostly differ from predicted climatic ranges, presumably, due to historical constraints on species dispersal. A trend from dominance of montane or wet lowland forest associations in species of more basally derived lineages (groups A-C) to dominance of drier upland forest and moist woodland associations in species of more terminally derived lineages (groups D-F) is, perhaps, linked to the stepped trend to cooler, dryer climate in the late Cenozoic.

ADDITIONAL KEYWORDS: Africa - *Diastellopalpus* - dung - eco-climatic - evolution - historical biogeography - phylogeny - range - speciation.

INTRODUCTION

In Africa, late Cenozoic taxon diversification has probably been driven by two principal physical processes, orogenics resulting from pressures generated by tectonic movements, and climatic change characterized by a stepwise cooling trend punctuated by serial oscillations between cooler and warmer phases that are associated with trends in global atmospheric CO₂ and polar glaciation (Griffiths, 1993; Potts & Behrensmeyer, 1993; Kampunzu *et al.*, 1998; Lavier *et al.*, 2001; Jahn *et al.*, 2003; Adegbe *et al.*, 2003; Kashiwagi & Shikazono, 2003; Allen & Armstrong, 2008). The present study seeks to support the hypothetical relationship between these historical events and taxon diversification by examining the phylogeny of the dung beetle genus, *Diastellopalpus* van Lansberge, in relation to the present ecological and biogeographical characteristics of its constituent species. This genus has probably evolved over the timescale of these changes since the basal dichotomy between eastern and primarily western centred species groups apparently results from uplift in the east of the continent that dates from the Miocene (Josso & Prévost 2000).

Changes in regional topography result from tectonic pressures generated by the movement of the African/Arabian Plate against the Eurasian Plate. Major regional change has occurred around the Mediterranean Basin from the late Eocene to mid-Pliocene (Meulenkamp & Sissingh, 2001) although

widespread rifting, uplift and volcanism in Africa date from the Miocene onwards (Lavier *et al.*, 2001). These events have occurred, especially, along the east and central west continental margins of the African tectonic plate. In the west, a Miocene age is indicated both for increased offshore sedimentation associated with uplift of the Angolan Bie Plateau (Lavier *et al.*, 2001), and for uplift of the Cameroonians Adamawa highlands along an unconformity (Meyers *et al.*, 1998). In the east, there is an age gradient from older northern to younger southern events (Griffiths, 1993; Kampunzu *et al.*, 1998). Some suggested ages for the Miocene commencement of rifting and uplift are dated at 30-20 MY in Ethiopia (Griffiths, 1993; Meulenkamp & Sissingh, 2001), 16-13 MY in the western Albert/Edward rift (Kampunzu *et al.*, 1998), 16-10 MY in the eastern south Kenyan rift (Gölke & Mechie, 1994), 11 MY at Virunga, 10 MY at Bukavu, 9 MY at Rungwe (Kampunzu *et al.*, 1998), and 8-6 MY in the Malawi Rift (Ring & Betzler, 1995). Field evidence for two phases of uplift from 16-10 Ma and 10 Ma till present (Gölke & Mechie, 1994), is represented by minor uplift in the Miocene and major uplift in the Plio / Pleistocene as in Central Kenya (Baker & Wollenberg, 1971) so that Pleistocene uplift, especially, is responsible for the present fragmented relief of East Africa (Griffiths, 1993). This episodic major uplift and volcanism during the Plio / Pleistocene is apparently asynchronous within the north / south gradient. For instance, the Eastern Arc Mountains of Tanzania comprise much older geological units but have also undergone recent re-uplift (Griffiths, 1993). The generality of uplift or re-uplift commencing in the Miocene suggests an earliest possible date for the origin of montane centred *Diastellopalpus*.

The collision of the Africa/Arabia and Eurasian plates may also have been instrumental in forcing the stepwise cooling and drying climatic trend in the later Cenozoic (Allen & Armstrong, 2008) although this has been driven by various geo-physical processes. There has been continuing drifting apart of the continents, commencement of closure of circum-equatorial currents by the Arabia/Eurasia collision (Allen & Armstrong, 2008), and their replacement by modern north/south cellular ocean currents. This led to isolation of south polar oceanic currents with polar cooling that culminated in glaciation (Smith & Pickering 2003, Barker & Thomas, 2004) probably driven primarily by reduction in global atmospheric CO₂ (Allen & Armstrong, 2008). Increases and decreases in the extent of polar glaciation in the late Cenozoic are correlated with serial oscillations between cooler drier and warmer wetter climatic phases (Potts & Behrensmeyer, 1993) and are associated with axial displacements in the alignment of the planet (Sabadini & Vermeersen, 1997).

The overall stepwise trend to cooler drier climate during the Cenozoic is supported by body size variation of Foraminifera (Schmidt *et al.*, 2004) and by geochemical and geological data (Eyles, 1993; Flowers & Kennet, 1994). The trend is marked by warmer climate in the early Cenozoic (65-42 Ma), fluctuating climate in the middle Cenozoic (42-14 Ma) and cooler climate from the mid Miocene (14 Ma) onwards (Schmidt *et al.*, 2004). During the cooler climate of the late Cenozoic and Quaternary, fluctuating cooler, drier, and warmer, wetter, phases in Africa correlate well with increases and decreases in Northern Hemisphere polar glaciation (Potts & Behrensmeyer, 1993; Jahn *et al.*, 2003; Adegbe *et al.*, 2003). Many cyclic climatic oscillations are indicated for lower latitudes by a continuous 3.5 MY pollen record in the

tropical Andes (5° N) (Hooghiemstra, 1989) where high frequency, low amplitude oscillation occurred from 3.5-2.5 Ma (mid Pliocene) followed by low frequency, high amplitude oscillation thereafter. Steps in intensification of African aridity occur around 2.8 (late Pliocene), 1.7 (Plio-Pleistocene boundary), and 1 Ma (early to mid Pleistocene) (de Menocal, 2004) whereas climatic cycles show differing superimposed periodicities. For instance, after 0.9 Ma in southern Africa, longer cycles of *ca* 100 Ky are overlain by shorter cycles of *ca* 40 Ky (Jahn *et al.*, 2003).

Changes in the geographical distribution of physiognomic vegetation types in Africa have been driven by these steps in increasing aridity and by both longer and shorter-term climatic oscillation. For instance, during the past 400 Ky there have been five arid/moist cycles in West Africa with the late Pleistocene more arid than the mid-Pleistocene (Jahns *et al.*, 1998). In the past 150 Ky there have probably been two periods of linkage between West and Central African rainforests followed by periods of separation (Dupont *et al.*, 2000) with lowland forest refuges centred on the Guinean mountains, coastal Liberia, Ivory Coast, Nigeria, Cameroon, Gabon, Eastern Congo (DRC), and East Africa, during the last glacial maximum (Potts & Behrensmeyer, 1993; Jahns *et al.*, 1998). Over the same time-scale, montane forests have persisted in the Tanzania/Malawi, Cameroon and eastern Congo (DRC) highlands (Potts & Behrensmeyer, 1993). Such changes and persistences are likely to have driven *Diastellopalpus* radiation, isolation and diversification, but the details are not well known.

The monophyletic genus, *Diastellopalpus* van Lansberge, is sub-basal in the Onthophagini (Philips, 2004), which is a sub-terminal tribe of the subfamily Scarabaeinae according to the phylogeny of Philips *et al.* (2004). *Diastellopalpus* is restricted to the Afrotropical region where it shows an intertropical distribution pattern and has diversified into 32 known species primarily centred on forest, although collection records also indicate several woodland savanna and one montane grassland species (A.L.V. Davis, Pers. Obs.). Josso & Prévost (2000) suggest that the basal phylogenetic separation between eastern and primarily western centred species groups results from the Miocene uplift in the east of the continent. The subsequent history of uplift and climatic oscillations is complex but is considered important for driving serial speciation, range expansion, and range contraction cycles in both montane and lowland forest-centred populations of *Diastellopalpus*. Therefore, the present study seeks to support orogenic and climatic hypotheses by examining phylogeny relative to predicted versus observed current ranges and ecological characteristics that have probably evolved over the timescale of the changes in the late Cenozoic.

MATERIAL AND METHODS

PHYLOGENY

Josso & Prévost (2000) examined 32 known species of *Diastellopalpus*. They recognized and described 47 morphological characters each comprising from two to four character states. These characters were used to develop a character matrix for 23 species (Josso & Prévost, 2000). It was not possible to analyze the phyletic relationships of the nine remaining species as their characterization was identical to other species included in the matrix. Josso and Prévost's analysis of this character matrix generated 63 equally

parsimonious trees. They were unable to produce an acceptable consensus tree as relationships of seven species remained unresolved. Therefore, they selected one of the 63 trees that best represented their understanding of the phylogeny.

In order to strengthen statistical support for the relationships within the genus, we re-analyzed the data published by Josso & Prévost (2000). We first excluded characters 5 and 39, which were parsimony uninformative. We then used the weighting function in PAUP v. 4.0b10 (Swofford, 2002), which weighted 14 of the remaining 45 characters. This matrix was subjected to maximum parsimony analysis with a heuristic search, which generated two most parsimonious trees. Following this initial analysis, a process of successive weighting was applied based on the rescaled consistency (RC) index. Each successive reanalysis used maximum parsimony, a heuristic search, and right ladderized tree building. The third reweighting of the characters (Table 1), with reanalysis, achieved maximization of the consistency (CI), retention (RI), rescaled consistency (RC), and homoplasy (HI) indices plus the shortest tree length. It also generated a single most parsimonious tree. Bootstrapping with 1000 replications was conducted 10 times on this maximally weighted matrix in order to determine the range in bootstrap values.

CLIMATIC OCCURRENCE

A total of 640 collection localities for *Diastellopalpus* were amassed from published work (Ferreira, 1972; Josso & Prévost, 2000) and museum records (Natural History Museum (London); Humboldt Museum (Berlin); Zoology & Entomology Dept (University of Pretoria); National Collection of Insects (Pretoria)). Grid references were obtained from the gazetteer database of the United States National Geospatial Intelligence Agency at <http://geonames.nga.mil/ggmaviewer/MainFrameSet.asp>. A total of 249 deleted localities included erroneous or alternative spellings that were un-interpretable; old colonial and other names that were not traced; ambiguous records with the same place name occurring in different locations for which the correct location was unverifiable; inexact citations for regions rather than specific localities; clearly erroneous localities that were climatically distant from all other records for that species; and duplications of the same locality record for the same species that were cited by more than one source. Using the grid references for 391 retained localities, climatic distribution data for all 32 species, was extracted using maps of measured and interpolated average altitude, average annual rainfall, and average minimum and maximum daily temperatures for 5x5 km polygons. As spot localities for species varied from 67 observations down to single observations for five species, a balanced matrix of climatic distribution for each species was created using the absolute minimum and maximum values for each climatic variable, and the intervening nine percentile values at 10 percentile intervals. Values for species with only single observations were repeated across the range of 11 values for each of the four climatic variables. This matrix of 32 species by 44 climatic values was converted to a correlation matrix and analyzed to determine the relative similarity between the climatic occurrences of species using non-parametric ordination (multiple dimensional scaling). A minimum-spanning tree was fitted to the data points in the ordination plot using the distance matrix and the Kruskal algorithm contained in the computer programme, Arlequin version 3.1.

(Excoffier *et al.*, 2006). In the ordination plot, species were coded according to their clade or group affiliations in order to examine the degree of consistency between phylogeny and climatic occurrence.

ECOLOGICAL ASSOCIATIONS

Soil, vegetation and dung type associations are important ecological attributes that often influence distribution patterns of dung beetles at both local (Nealis, 1977; Cambefort, 1982; Doube, 1991; Davis, 1994; 1996) and regional scales (Davis, 1993; Davis & Scholtz, 2004). Published data for *Diastellopalpus* species are fragmentary. However, data for vegetation associations were generated by plotting geographical occurrence of species on a map of natural vegetation, which, for Central Africa, was derived from the classification of White (1983). A matrix of 32 species by numbers of observations in each of 27 vegetation types was subjected to hierarchical analysis of oblique factors (Factor Analysis using principal components as the extraction method with varimax-normalized rotation of factors) using Statistica v. 7 (Statsoft Inc., 2004) in order to statistically group *Diastellopalpus* species according to their vegetation associations. These associations were summarized according to occurrence of species groups in five major vegetation types, i.e. wet rainforest (White's types 1A, 3, 8, 9, 16B, 77), drier rainforest (types 2, 4), a mosaic of drier rainforest and secondary grassland (types 11A, 15, 16, 16A), afro-montane vegetation (types 19A, 65), and woodland (types 25, 26, 27, 29A, 29C, 31, 32, 33, 37, 42, 45, 54B, 60).

GENERIC AND SPECIES GROUP RANGES

The GIS-based computer package, Biomapper v. 3.1 0.205 (Hirzel, 2003), was used to predict the potential current distributions of the entire genus as well as the highland and lowland subgroups in the genus and each species clade. Predictions were based on average map data for climatic occurrence drawn from 5x5 km polygons surrounding *Diastellopalpus* spot localities. Before data-extraction, the maps of altitude, average annual rainfall, maximum and minimum daily temperature for the whole of Africa, were subjected to Box-Cox transformation to normalize the data. Ecological Niche Factor Analysis (ENFA) was conducted on the distribution of the genus and groups of *Diastellopalpus* using the transformed data sets. Each analysis yielded four ordination factors that were used to produce factor maps from which a habitat suitability distribution map was calculated using the Distance Harmonic Mean algorithm (Hirzel & Arlettaz, 2003). This algorithm weights observed data, which may be useful when there are low numbers of observations (Hirzel, 2003), as in the present case. Each habitat suitability map was cross validated using 10 replications, except in the case of lowland members of Clade B where there were insufficient observations for cross-validation. All cross-validated maps were constructed using the mean probability values for the replications. They were supported by the mean Spearman's rank correlation value derived from cross-validation. Maps were simplified by reclassifying plotted probabilities of occurrence as ranges, i.e. 0-25%, 25-50%, 50-75% and 75-100% or, in some cases, 50-100%. Although presence and absence data provides a better result, such data are rare for small-bodied animals such as insects compared to the

extensive presence data in museum collections. Biomapper has been demonstrated to provide useful predictions from presence data (Reutter *et al.*, 2003; Chefaoui *et al.*, 2005).

Statistical support for predicted distributions by cross-validation was often relatively low. However, visual comparisons showed that although there were minor differences in detail between habitat suitability and cross-validated maps, there was close similarity between maps in overall pattern. Therefore, the maps are considered as relatively robust predictions of potential distribution for each group of *Diastellopalpus* species.

RESULTS

PHYLOGENY

Reanalysis of the character matrix generated a single tree in which there was >70% bootstrap support for the majority of the branches (Fig. 2). This tree was interpreted as comprising four major clades (A, C, E, F) with relationships unresolved for three taxa with sub-basal derivation (*D. johnstoni*, *D. pluton*, *D. anthonyi*) and for two taxa (*D. tridens*, *D. laevibasis*) with derivation that was basal to the two terminal clades. These taxa with unresolved relationships were treated as two further species groups (“clades” B, D).

ECO-CLIMATIC ASSOCIATIONS

MDS ordination of climatic associations showed that species were distanced fairly evenly along a minimum-spanning tree with little clumping (Fig. 3). Species with negative factor loadings along Dimension 1 were centred at low altitude in high rainfall and high temperature regimes, whereas those with positive factor loadings were centred at higher altitude in lower temperature and mostly lower rainfall regimes (Fig. 4). Whereas three clades or groups comprised species with entirely higher (A) or lower distributional centres (D, E), the other three included both lowland and highland centred species.

Analysis of species vegetation associations defined seven clusters of species (Fig. 5), which follow a phylogenetic trend (Fig. 2). Species centred in montane vegetation or wet lowland forest dominate in the most basally derived lineages (Clades A-C: 14 out of 18 species), whereas species centred in upland dryer forest, forest / grassland mosaic, or moist woodland dominate in the most derived lineage (Clades D-F: 10 out of 14 species).

PREDICTED POTENTIAL VERSUS OBSERVED DISTRIBUTION PATTERNS

Both predicted and observed distributions for *Diastellopalpus* indicate an intertropical pattern of occurrence (Figs 6A) with lowland species centred on the Congo Basin and/or wetter parts of West Africa (Figs 1, 6B), and highland species centred on the extensive and diffuse highland blocks in the east and the west (Figs 1, 6C). Despite the high probabilities of predicted occurrence, there are no observed records for *Diastellopalpus* from the isolated Ethiopian highlands or any precise records from the lowlands of the southeast Congo Basin.

Predictions of potential ranges for the highland or lowland components of each clade are broadly similar (Figs 7-12). Pan-intertropical highland distributions are predicted for each highland component and pan-wet intertropical lowland distributions are predicted for most lowland components. However, the recorded distributions of the species comprising each component differ markedly between clades.

Clade A derives from the basal node of the phylogeny (Fig. 2). Based on climatic data, its seven species could potentially occur throughout the eastern highlands and the western escarpment of the Bie Plateau in Angola (Figs 7A). However, most of the 60 locality records are centred on a narrow band of moist montane localities (Figs 1, 5, 7A-C) along the southeast escarpment extending from Mount Mlanje in southern Malawi to the North Pare Mountains in northern Tanzania. This overall pattern is duplicated by both of the major subclades (Figs 7B, 7C).

The interrelationships of the three species of “clade” B are unresolved but derive from the basal node of the remaining clades (Fig. 2). The species show disjunct, primarily equatorial distributions. *D. johnstoni* is centred in high altitude Afromontane vegetation (Figs 2, 5, 8A, 8C) with records from highland blocks in east and west central Africa that are widely separated by an intervening region across central Africa that shows extreme climatic unsuitability for the species (Fig. 8A). Both *D. pluton* and *D. anthonyi* show distributions centred on wet lowland forest (Figs 2, 5, 8B, 8C). *D. pluton* is the only *Diastellopalpus* species endemic to West Africa. *D. anthonyi* has been recorded in west central Africa but only in a small part of the potentially suitable lowland climate (Figs 8B, 8C).

The eight species of clade C also comprise both highland and lowland components (Figs 2, 9A, 9B). They are recorded only around the highland rim (Fig. 9C) or within the Congo Basin (Figs 9D, 9E) despite suitable wet climate for the lowland species in West Africa (Fig. 9B). The highland species occupy a similar range to that of *D. johnstoni* but are represented by different species in the different highland blocks. Their vegetation associations vary from afromontane centred in the Adamawa (*D. nigerrimus*) or East Central highlands (*D. basilobatus*), to dryer forest centred in the East Central and eastern highlands (*D. semirubidus*). There is also a moist woodland centred species on the northwest escarpment of the Bie Plateau (*D. hassoni*) (Figs 5, 9C). The remaining species of the lowland to upland subclade are centred on wet forest over much of the Congo Basin (*D. sulciger*), on wet forest primarily in the northwest (*D. murrayi*) or central (*D. drumonti*) parts of the basin, or in dryer forest of the Bateke Plateau north of the River Congo (*D. camiadei*) (Figs 5, 9D, 9E).

Members of the three terminal clades share a basal polytomy and show a progression in distributional centres from wet lowland forest to dryer upland forest to dryer upland woodland. The two species of “clade” D occur throughout the lowlands of West Africa and the northern part of the Congo Basin (*D. tridens*, *D. laevibasis*) to Uganda (only *D. laevibasis*) where they show a bias to wetter rainforest (Figs 2, 5, 10A, B). There are no records for the species from the southern part of the Congo Basin despite predicted highly suitable climate.

The eight species of clade E show a distinctive predicted pattern from lowlands to uplands. This forms a band that circumscribes the centre of the Congo Basin with patches also occurring in West Africa

(Fig. 11A). Some members of one subclade (*D. noctis*, *D. conradti*) are centred in wet lowland forest (Figs 2, 5) from West Africa to the Congo Basin but differ in distribution to clades B and D in also occurring to the south of the River Congo (*D. conradti*) where a further member (*D. balubanus*) is found in upland dry forest (Figs 5, 11B, 11C). Members of the other subclade are restricted to dryer forest of the Congo Basin (Figs 2, 5, 11C). Distributions of two species are centred to the north of the River Congo across the entire basin to Uganda (*D. gilleti*) or on the Bateke Plateau (*D. pseudoschulzae*). The remaining three species occur to the southwest and south of the River Congo (*D. schulzae*, *D. walteri*, *D. legrandi*).

The four species of Clade F show upland distributional centres in dry forest or moist woodland (Figs 2, 5). Observed combined distributions of the species reflect predicted distribution more closely than in any other clade (see Spearman rank correlations for Figs 7-12). Occurrence is recorded across all of the intertropical highland blocks including the southerly lying highlands of the Bie Plateau and eastern highlands of Zimbabwe (Figs 1, 12A-C). However, the members of the two subclades differ strongly in appearance and in individual distribution patterns (Figs 12B, 12C). One subclade occupies the entire range of intertropical uplands with distributions centred to the northwest (*D. lamellicollis*) or southeast (*D. quinquedens*). The other subclade shows species centred at the northeast edge of the Congo Basin (*D. jirouxi*) and on the southerly-lying highlands from the western to the eastern seaboard (*D. infernalis*). It is noteworthy that woodland-centred members of both subclades occur in the southeastern seaboard region that is otherwise occupied almost exclusively by primarily montane-centred members of Clade A.

DISCUSSION

PHYLOGENY

As both functional and historical studies were constructed around the phylogeny, it was necessary to provide strong support for evolutionary relationships in *Diastellopalpus*. The re-analysis of the character matrix of Josso & Prévost (2000) generated a single tree that is strongly supported by bootstrap values. It is also more strongly supported by indices (Tree length = 37.8, R.C. = 0.439, C.I. = 0.540, R.I. = 0.813, H.I. = 0.460) than that selected by Josso & Prévost (2000) from 63 equally parsimonious trees (Tree length = 162, C.I. = 0.407, R.I. = 0.668). Even so, most relationships shown by the two trees are identical with three exceptions. Firstly, in the tree of Josso & Prévost, *D. anthonyi* is basal to the sister species of *D. johnstoni* and *D. pluton* in a sub-basal clade whereas, in Figure 2, the relationships of these sub-basal species are unresolved. Secondly, in the tree of Josso & Prévost, *D. basilobatus* is basal to *D. semirubidus*, which is basal to the *D. murrayi* / *sulciger* subclade. By contrast, in Figure 1, *D. basilobatus* / *semirubidus* is a sister subclade to that of *D. murrayi* / *sulciger*. Thirdly, in Figure 2, the relationships of *D. tridens* and *D. laevibasis* are unresolved on the basal node of the two terminal clades, these two species having been placed as the basal and second most basal taxa of the *D. noctis* / *conradti* / *gilleti* / *schulzae* clade in the phylogeny of Josso & Prévost.

CURRENT GEOGRAPHICAL AND FUNCTIONAL PATTERNS

Josso & Prévost (2000) divide the current geographical distribution of *Diastellopalpus* into three regions based on geographical isolation of species within an area mainly to the east of the rift valley (1) or on vegetation associations of species with either the savanna (2) or the rainforest (3) extending westwards from East to West Africa. This distribution represents major southeastern, central and western geographical centres, each comprising subregional centres separated by current barriers to dispersal within and between regions.

The western, Guinean regional centre confines populations of six species, one endemic and five shared with the central region. Subregionally, five species are centred in forest along the coast or in the Fouta Djallon / Guinean highlands and one is centred in moist upland woodland regions defined by White (1983). The forest and uplands of this region are currently isolated from the central region at the low altitude, lower rainfall, Dahomey Gap.

The southeastern region confines populations of 10 species, eight endemic and two shared with the peripheral woodland or montane grassland areas of the central region. Subregionally, eight species show principal centres in montane regions and two are centred mainly in moist upland woodland. Species in the forest and moist upland savannas of the southeast centre are currently isolated by low inland rainfall in the north and by hot lowlands of the Luangwa and Zambezi Valleys in the south. In the centre, a lower rainfall corridor to the west of Mt Rungwe (1060 mm p/a maximum) may be a barrier to range expansion from the regional island of montane vegetation (White, 1983).

The much larger Congolian centre comprises the rainforest of the Congo Basin, the fringing moist upland savannas and the peripheral highland blocks. It confines populations of 23 species, 17 endemic and six shared with the southeastern and western centres. Subregionally, 17 species show a bias to various subregional forest centres ranging from swamp, riparian, wet or dryer forest, three species are primarily centred in fringing moist upland woodland regions, and three species are primarily centred in peripheral montane patches.

HISTORICAL CONTEXT OF CURRENT PATTERNS

Despite relatively even distancing of most species in ordinal space, there was wide spatial, altitudinal, rainfall and temperature overlap between taxa. This was reflected in the wide predicted potential climatic distributions for species groups that essentially comprised a pattern centred either in the highlands or in the lowlands. Predicted distribution for species groups was usually wider than observed distribution and reflected a complex arrangement of climatic barriers to range expansion by species populations both within and between major regions. These differences in emphasis within a highland or lowland pattern would result from the different geographical origins and different histories of the lineages, species, and species populations. This history is complex owing to some asynchronicity in orogenesis events and the serial nature of historical cycles of physical change that have probably driven the processes of range contraction, spatial isolation, speciation, range expansion, and range overlap. There is the possibility of repeated patterns of

lateral and upward retreat by cool highland centred species during warm, wet interglacials and expansion downwards and laterally during cooler, dryer glacials. The possibility of opposite trends (downward and lateral or lateral and upward) in lowland species would be centred on wetter coastal foci, the central Congo Basin, and upland or mountain foothill refuges.

Currently, most species show spatial overlap with other *Diastellopalpus* species over at least part of their ranges although only single species occur at some localities, particularly at the edge of the generic range. Overlapping species may show differing ecological attributes that permit local coexistence. Alternatively they may show unbalanced relative abundances that reflect differences in either local environmental suitability or competitive capacity. However, the overall status of ecological associations in *Diastellopalpus* is difficult to assess owing to the fragmentary knowledge of relative local abundances, diel flight periodicity, or soil, vegetation and dung type associations. In the few published studies at single localities, a range from one to six *Diastellopalpus* species has been recorded. In the low-altitude Guinean forests of Taï (Ivory Coast) and Ankasa Conservation Area (Ghana), three coexisting species show clear differences in ecological attributes. *D. laevibasis* is associated with elephant dung whereas the day-flying *D. tridens* and crepuscular-active *D. noctis* are associated with omnivore dung (Cambefort & Walter, 1991; Philips, Davis & Foster, Pers. Obs.). At ca 500 m in Makokou Forest (Gabon), six species co-occur. *D. laevibasis* occurs on elephant dung, the rare *D. anthonyi* on several dung types, and the others primarily on omnivore dung, with *D. gilleti* three times more abundant than *D. conradti*, *D. sulciger*, and the sister *D. murrayi* (Cambefort & Walter, 1991). At ca 900 m in the cool, wet, East Usambara Mts (Tanzania), two species co-occurred, the relatively abundant, day-flying *D. monapoides* and the less abundant night-flying *D. thomsoni* (Newmark, Davis, & Rickhart, Unpubl. Obs.).

DIVERSIFICATION HISTORY AND RANGE EVOLUTION

The ancestor of *Diastellopalpus* has diversified into 32 known species with a combined intertropical distribution range that is absent from Ethiopia. The first event in the diversification probably dates from uplift along the eastern edge of Africa (Josso & Prévost, 2000) that dates from Miocene (Griffiths, 1993) or post-Miocene age. This separated eastern and western forest blocks (Burgess *et al.*, 1998) and created intervening upland woodland according to the fossil record (Potts & Behrensmyer, 1993). These events would account for the isolation of the basal clade along the southeastern edge of the southeastern highlands and the centring of most species of the remaining clades in East Central, Central and/or West Africa. The subsequent history is complex with diversification into several major lineages. Although more basal derivation may represent earlier divergence of ancestors some of the diversification within lineages may be in parallel and may represent response to the same physical events. However, it is not possible to fit a timescale to this phylogeny based on morphological data in order to determine a divergence chronology and to temporally offset or align species.

In *Diastellopalpus*, uplift, and the overall cooling and drying trend in the later Cenozoic (Flowers & Kennett, 1994; Kashiwagi & Shikazono, 2003; Schmidt *et al.*, 2004), is paralleled by the trend from

association with wetter vegetation types and uplifted montane regions in basal lineages to association with dryer adapted vegetation types in derived lineages. This suggests extensive late Cenozoic diversification in *Diastellopalpus*. However, diversification coeval with Quaternary climatic events is apparently not supported by the fossil record for other insect taxa (Coope, 2004) although this finding is based primarily on northern temperate faunas.

BASAL EASTERN CLADE A

As Clade A could potentially show a highland-centred distribution throughout east, east central and west central Africa, geographical barriers to dispersal from the southeast escarpment must have persisted over a long historical period. The clade represents nearly a quarter of the described species of *Diastellopalpus* and, although the range is small, it is topographically diverse. It is apparently restricted to montane and a few coastal forest patches extending from the northeast Tanzanian coast, along the geologically old but recently re-uplifted Eastern Arc (Griffiths, 1993), down the west of the Malawi rift, and probably as far as the central Mozambique coastal sand forests, which support an undescribed species that probably belongs in this group. The two principal subclades show parallel but differing patterns of north - south speciation. In the *D. neavei* group, steps in speciation trend from south to north in opposition to the chronological north to south trend in the commencement of rifting (Griffiths, 1993; Kampunzu *et al.*, 1998). In the *D. fuelleborni* group, species separation appears centred in the Kipengere - Mt Rungwe - Livingstone Mts area of southern Tanzania and northern Malawi. This region is clearly important for both subclades as ranges or range edges of five species occur in this region, i.e. those of *D. monapoides*, *D. metriogonus* and *D. dudleyi*, in the one subclade, and those of *D. fuelleborni* and *D. cambeforti* in the other subclade. The more localized patterns are also of interest as sister species occur on the south of the Kipengere Range and Mt Rungwe (*D. metriogonus*) or on Mt Uzumara / Vipya Plateau (*D. dudleyi*) but with the intervening Nyika Plateau hosting a more distantly related species belonging to the other subclade (*D. cambeforti*) (Josso & Prévost, 2000). Subspeciation between Malawi and Tanzanian populations of the widespread *D. thomsoni* (Josso & Prévost, 2000) may result from the most recent range expansion and contraction in Clade A species.

BASAL WESTERN “CLADE” B

.Historical constraints on a potentially much wider occurrence of the three species of “Clade” B have led to a fragmented western, west central and eastern equatorial distribution with extreme characteristics. *D. johnstoni* has been observed to be the only montane grassland species in the genus. It is distinctive in appearance with wide disjunctions between populations in the extreme east, east central and west central highlands, suggesting a fairly recent range expansion across 2000 km of north central Africa followed by a contraction of range from this region that is now climatically unsuitable. This range expansion and contraction has perhaps occurred in response to climatic change during the more intense glacial/interglacial cycles of the late Pleistocene (de Menocal, 2004). *D. pluton* is the only endemic West African *Diastellopalpus*. As it is poorly represented in collections, and two of four localities are on Mont de Dans

and Haut Cavally in Côte d'Ivoire, the species may be centred on the fragmented and isolated Guinean Highlands, perhaps in wet upland or montane forest that dominate the natural mountain vegetation (Morton, 1986). *D. anthonyi* is poorly known and uncommon despite a wide potential predicted range. At 500m in Makokou Forest (Gabon, west central Africa) it was the rarest of six co-existing *Diastellopalpus* species (Cambefort & Walter, 1991).

SUB-BASAL WESTERN CLADE C

Locality records for this group show that there has been no expansion of range to West Africa across the Dahomey Gap despite probable forest links in the late Pleistocene (Dupont *et al.*, 2003). Therefore, geographical constraints have presumably restricted its constituent species to the wet Congo lowlands (Congo Basin wet forest: *D. sulciger*; Central Congo Basin swamp and riparian forest: *D. drumonti*, mostly to the north of the River Congo with a few records to the southwest), peripheral upland wet forests (Adamawa and East Central uplands: *D. murrayi*), upland dry forests (Bateke Plateau: *D. camiadei*), upland moist woodland (northeast Bie Plateau: *D. hassoni*), montane highlands (Adamawa highlands: *D. nigerrimus*; East Central highlands: *D. basilobatus*), or highland dry forest (East Central highlands and Kakamega Forest: *D. semirubidus*). These patterns may have resulted from coeval fragmentation followed by tracking the upward or lateral retreat of cool or wet forest. Alternatively, they may represent origin in serial events starting with basal montane ancestors giving rise to lowland taxa that have tracked wetter or, in the case of *D. hassoni*, cooler refugia. Such a reinvasion of tropical lowlands by highland taxa has been demonstrated in Neotropical hummingbirds (Bleiweiss, 1998) and may have occurred during cooler climatic phases that are marked by increase in fossil pollen counts for montane trees in lowland centres (Collinvaux *et al.*, 2000). Ecological characteristics for *D. hassoni* remain speculative owing to imprecise locality data for the single record of the species in Cuanza do Sul Province, Angola. However, humid, semi-deciduous, forest patches occur on the higher slopes of the escarpment and may have acted as refugia as in birds (Hall, 1960; Hawkins, 1993).

TERMINAL WESTERN "CLADE" D AND CLADES E AND F

Range expansions by forest species of "Clades" D and E have been historically constrained to West and Central Africa despite potentially suitable climate in the southeast, which has been reached only by woodland species of Clade F. Speciation and subspeciation patterns in these clades suggest a complex history of evolution from wet forest to dry forest to woodland centred taxa that may be related to serial range expansions, contractions, and isolations associated with the alternating warm wet and cool dry phases of the Pleistocene with recurring breakages in forest links between West Africa and the Congolian region.

The basal "Clade" D wet forest species (*D. laevibasis*, *D. tridens*) are very widely distributed with *D. tridens* occurring outside the present limits of the western forest belt in a riparian forest refuge along the Casamance River of Senegal (White, 1983) and in the Dahomey Gap where forested hills still occur on the Accra grassy plain (White, 1983). Whereas *D. tridens* shows subspeciation between West African and north

Congolian centres (Josso & Prévost, 2000), *D. laevibasis* penetrates to the Ugandan dry upland forest and is the same species in West African, north Congolian and East African centres. These patterns suggest fairly recent range expansions and contractions. Owing to its apparent occurrence in riparian vegetation, *D. tridens* is the only species co-occurring with *D. drumonti* in areas dominated by swamp forest in the northern part of its range in the central Congo Basin. However, it has apparently been unable to penetrate southwards to the wide areas of predicted suitable climate in the south Congo Basin.

Collectively, the wet and dry forest members of Clade E also show a distribution between West Africa, the north Congo and Uganda with further extended distribution into the southern Congo between the west coast and the central basin. This apparent diverging pattern of distribution to the north and south of the central basin circumscribes the seasonally inundated muddy swamp and riparian forests (types 8 and 9 – White, 1983) of the Central Congo that may have been an enduring barrier in the late Cenozoic. The apparent absence of records from the predicted suitable climate in the southeast Congo Basin may be a collecting artifact as there are imprecise citations for *D. schultzei* from the south Congo recorded in both Kasai and Shaba (=Katanga) Provinces (Josso & Prévost, 2000). The *D. noctis* / *D. conradti* subclade is distributed in wet forest between West Africa and the Congo with occurrence of *D. conradti* in wet forest and speciation of *D. balubanus* in dry forest of the south Congo. However, the *D. gilleti* and *D. schulzae* subclades are historically constrained to dry forest association in the Congolian region. *D. gilleti* occurs in the north, eastwards to Uganda, and *D. walteri* and *D. legrandi* to the south. *D. pseudoschultzae* occurs to the north of the Congo River on the Bateke Plateau and *D. schultzae* to the south on outliers of the plateau and, possibly, further afield. The south Congo Basin is distant from the highest rainfall centres, or refugia of wet forest to the north, and is dominated by species of dryer forest and forest / grassland mosaic.

Overall, Clade F is the driest adapted of the groups in dry forest and moist woodland. Members of the two subclades are dissimilar in appearance and show dissimilar distribution patterns. It is probable that ancestors of each subclade underwent southwards range expansion and penetration across the barrier into the southeastern region at different times. In the one subclade penetration was followed by speciation of *D. quinquedens* whereas *D. lamellicollis* has probably undergone recent range expansion across the area between southeast and West Africa followed by retreat to moister cooler centres in the Fouta Djallon / Guinean highlands, Jos, Mandara and Bie Plateaux and the Adamawa, southern east central and eastern highlands. Range expansion and isolation patterns in the other subclade resulted in speciation of *D. jirouxi* in dry forest of the northeast Congo with *D. infernalis* centred on moister upland woodland of the Bie Plateau, southern east central uplands, and southeastern uplands.

CONCLUSIONS

The present work outlines speciation patterns of *Diastellopalpus* and indicates how historical events may have widened or constrained observed geographic ranges and driven ecological associations. It suggests a trend in speciation from basally-derived taxa associated with cooler or moister ecological settings to terminally-derived taxa associated with warmer or dryer vegetation types. However, the data are unsuitable

for predicting absolute time-scales of speciation events or for detecting possible range contractions or expansions. They are also insufficiently detailed for determining the tracks followed at both species and population scales to yield the current observed ranges. Thus, it is necessary to conduct more rigorous analyses using molecular data. Further material should be collected from forest and woodland in all three main geographical centres in west, central and southeast Africa concentrating on known or suspected late Cenozoic refugia that are found primarily in wet coastal or wet inland regions, isolated mountain blocks or their outliers.

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Table 1. Final weighting of Josso & Prévost's character matrix used to analyze the phylogeny of *Diastellopalpus* species. Descriptions of the 47 characters, character states and the character matrix, are given in Josso & Prévost (2000).

Char.	Weight	Char.	Weight	Char.	Weight	Char.	Weight	Char.	Weight	Char.	Weight
1.	1.000	9.	0.111	17.	0.444	25.	1.000	33.	0.000	41.	0.111
2.	1.000	10.	1.000	18.	0.219	26.	0.000	34.	0.167	42.	0.000
3.	0.675	11.	0.063	19.	0.127	27.	0.040	35.	0.222	43.	0.143
4.	1.000	12.	0.250	20.	0.280	28.	0.250	36.	1.000	44.	0.444
5.	Excluded	13.	0.300	21.	0.000	29.	0.074	37.	0.375	45.	0.175
6.	0.417	14.	0.063	22.	0.222	30.	0.333	38.	0.000	46.	1.000
7.	0.250	15.	0.036	23.	0.175	31.	0.333	39.	Excluded	47.	0.063
8.	0.231	16.	0.222	24.	0.175	32.	0.200	40.	0.375		

Figure legends

Figure 1. Maps of Africa showing highland blocks and high rainfall centres.

Figure 2. Cladogram showing the phylogenetic relationships between 23 species or species complexes of *Diastellopalpus* (C.I. = 0.540, R.I. = 0.813). Numbers on the branches are the range of bootstrap values obtained in 10 analyses each with 1000 repetitions. Species with asterisks are members of complexes of very closely related species that are listed in offset. Vegetation associations are derived from the classification in Figure 5 (M = Montane-centred, WF = Wet forest centred, DF = Dry forest centred, DF/G = Dry forest / grassland mosaic centred, W = moist woodland centred).

Figure 3. MDS ordination plot and minimum spanning tree comparing similarities between the climatic distributions of 32 species of *Diastellopalpus*. Species are coded according to phylogenetic relationships (see Figure 2).

Figure 4. Scatter plots of maximum, minimum and intervening values at 10 percentile intervals for climatic associations of 32 *Diastellopalpus* species plotted against Dimension 1 from Figure 3 with results for linear regression. A. Altitude, B. Average annual rainfall, C. Minimum average daily temperature, D. Maximum average daily temperature.

Figure 5. Ordination plot showing groups of *Diastellopalpus* species that were statistically-defined according to the principal bias in their vegetation associations.

Figure 6. Mean potential climatic distribution of the endemic Afrotropical genus, *Diastellopalpus* (6A1), predicted from 391 sets of observations (mean Spearman rank correlation from cross validation = 0.74), mean potential climatic distribution of the lowland species with negative loading values along Dimension 1 in Figure 3 (6B1) predicted from 153 sets of observations (mean Spearman rank correlation from cross validation = 0.90), and mean potential climatic distribution of the highland species with positive loading values along Dimension 1 in Figure 3 (6C1) predicted from 238 sets of observations (mean Spearman rank correlation from cross validation = 0.78), with their spot occurrences in intertropical Africa (6A2, 6B2, 6C2).

Figure 7. Mean potential climatic distribution of Clade A (Figure 2) (7A) predicted from 60 sets of observations (mean Spearman rank correlation from cross validation = 0.55) and spot occurrences (7B, 7C) of the seven species in two subclades that are restricted to southeast Africa.

Figure 8. Mean potential climatic distribution of one highland (8A) (mean Spearman rank correlation from cross validation = 0.36) and two lowland species (8B) in Group B (Figure 2) predicted from 32 and six sets of observations, respectively, with their spot occurrences in equatorial Africa (8C).

Figure 9. Mean potential climatic distribution of the four highland (9A) (mean Spearman rank correlation from cross validation = 0.15) and four lowland species (9B) (mean Spearman rank correlation from cross validation = 0.34) of Clade C (Figure 2) predicted from 14 and 45 sets of observations, respectively, with their spot occurrences in central Africa (9C-9E).

Figures 10 and 11. Mean potential climatic distribution of the two species in Group D (Figure 2) (10A) predicted from 59 sets of observations (mean Spearman rank correlation from cross validation = 0.33) and their spot occurrences from West to central Africa (10B). Mean potential climatic distribution of the eight species in Clade E (Figure 2) (11A) predicted from 46 sets of observations (mean Spearman rank correlation from cross validation = 0.43) and their spot occurrences from West to central Africa (11B, 11C).

Figure 12. Mean potential climatic distribution of the four species in Clade F (Figure 2) (12A) predicted from 132 sets of observations (mean Spearman rank correlation from cross validation = 0.84) and their spot occurrences in intertropical Africa (12B, 12C).

FIGURE 1

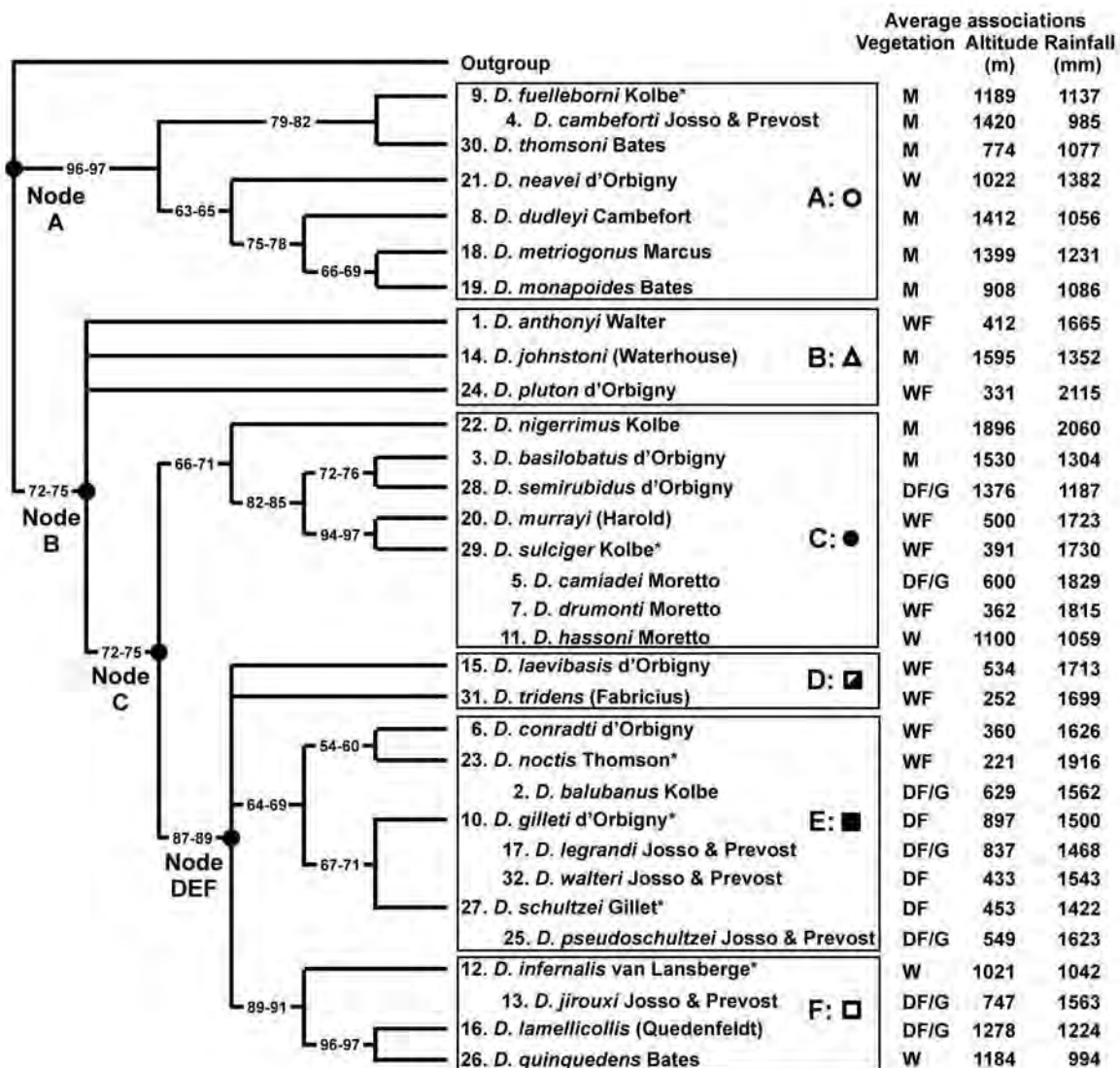


FIGURE 2

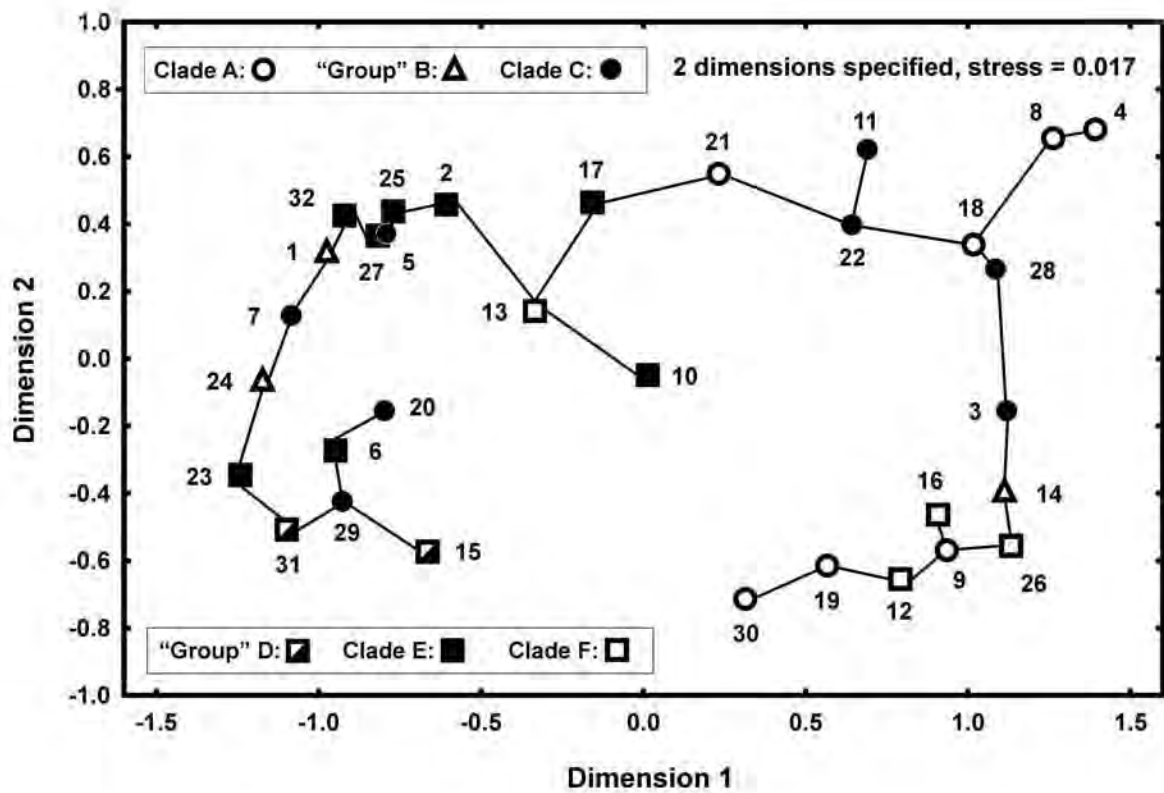


FIGURE 3

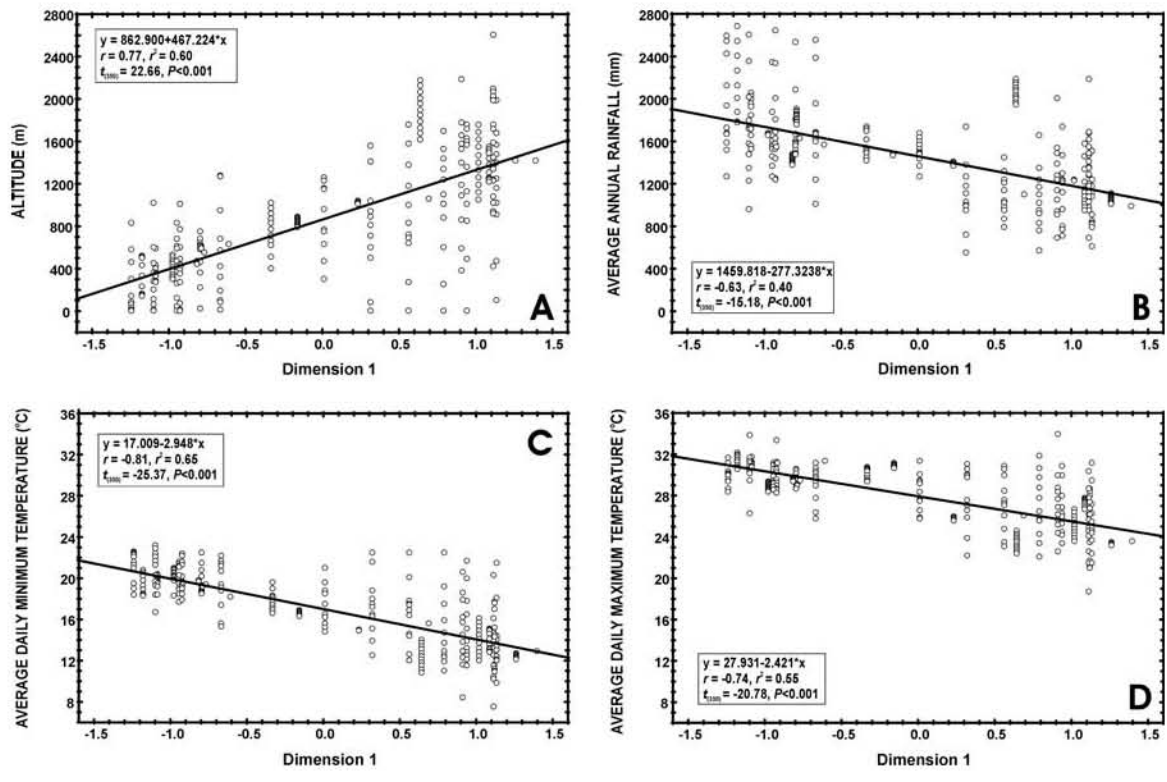


FIGURE 4

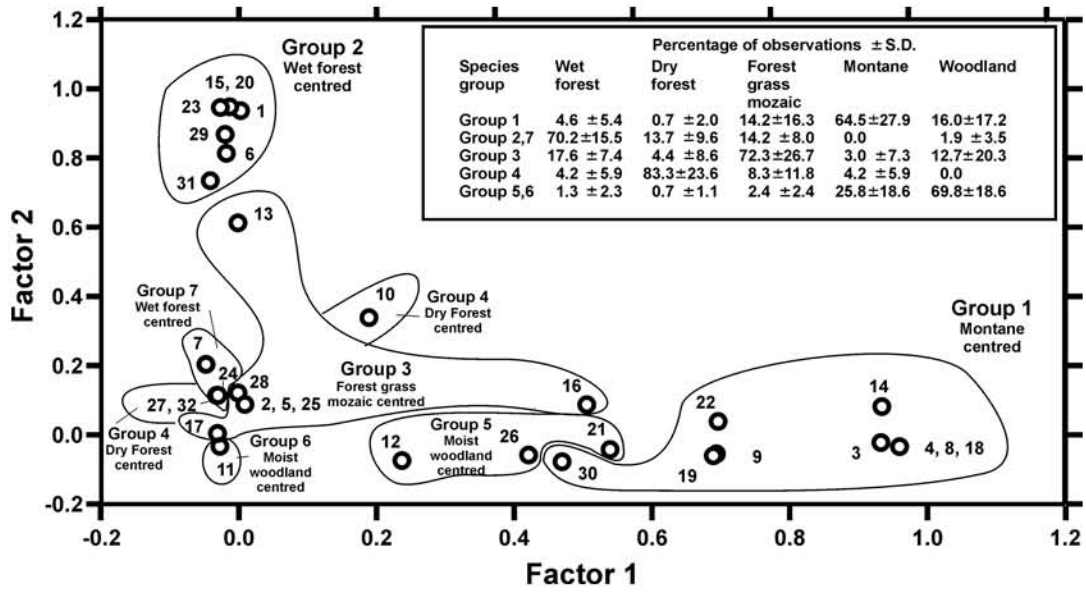


FIGURE 5

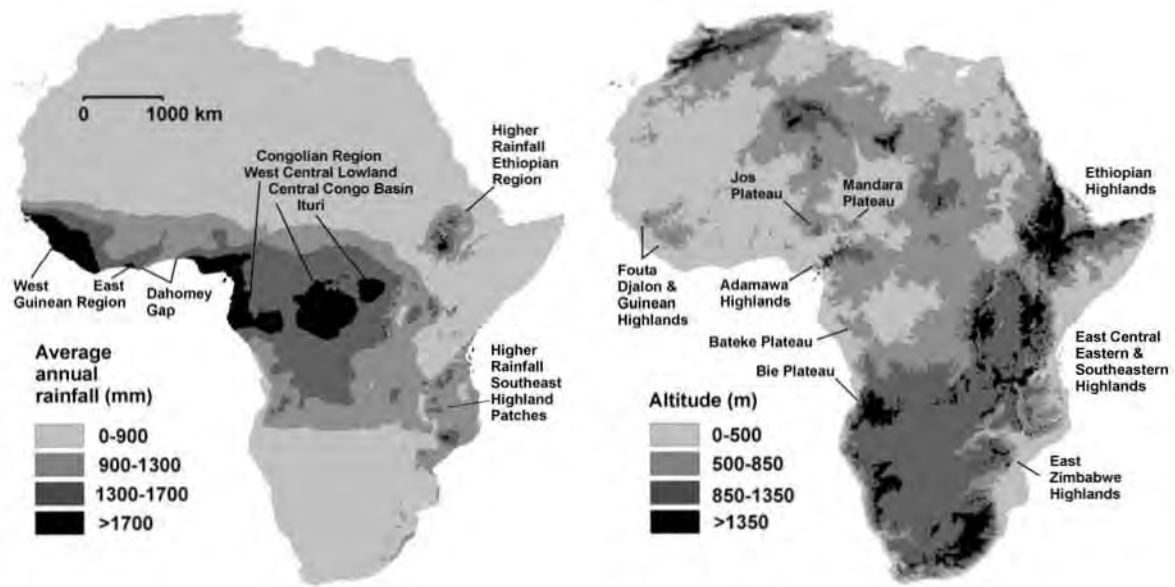


FIGURE 6

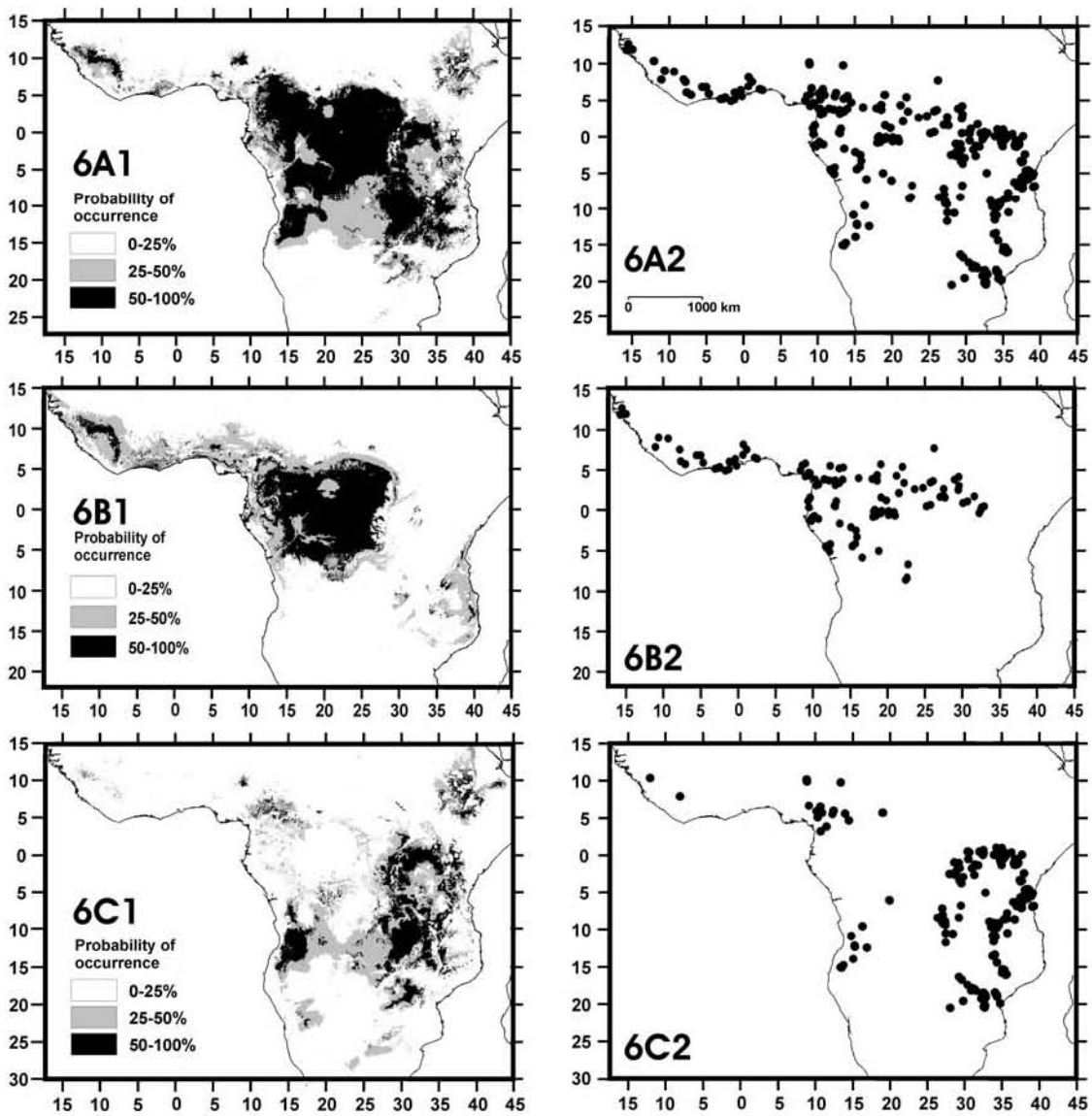


FIGURE 7

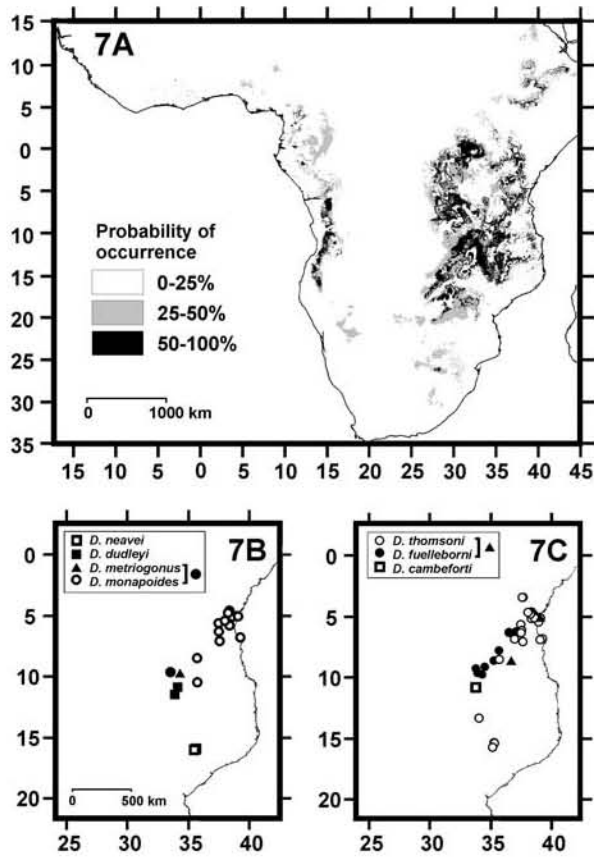


FIGURE 8

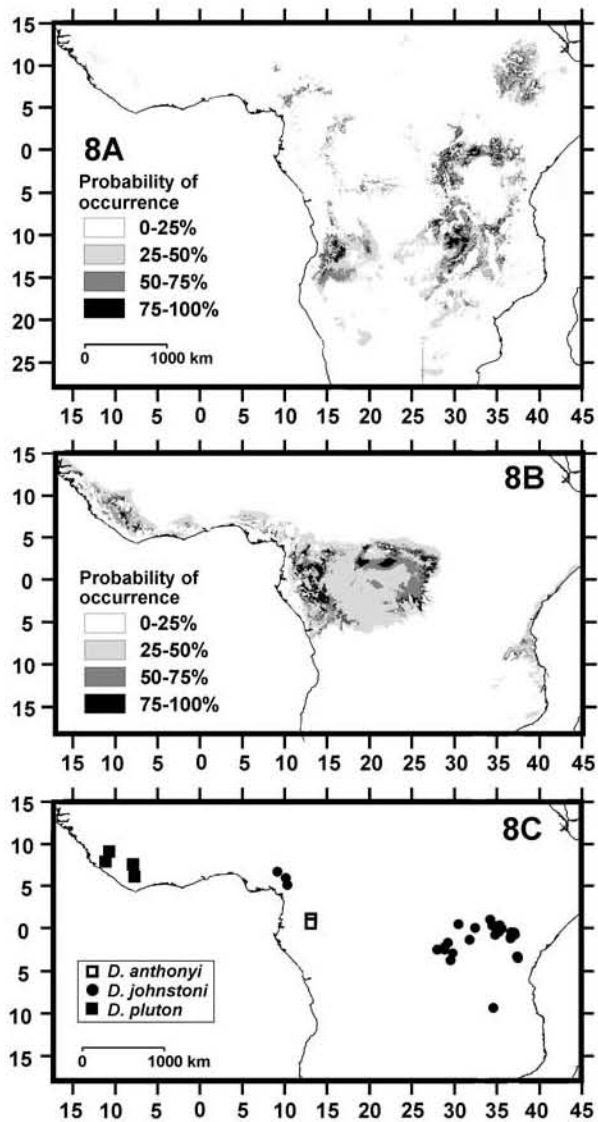


FIGURE 9

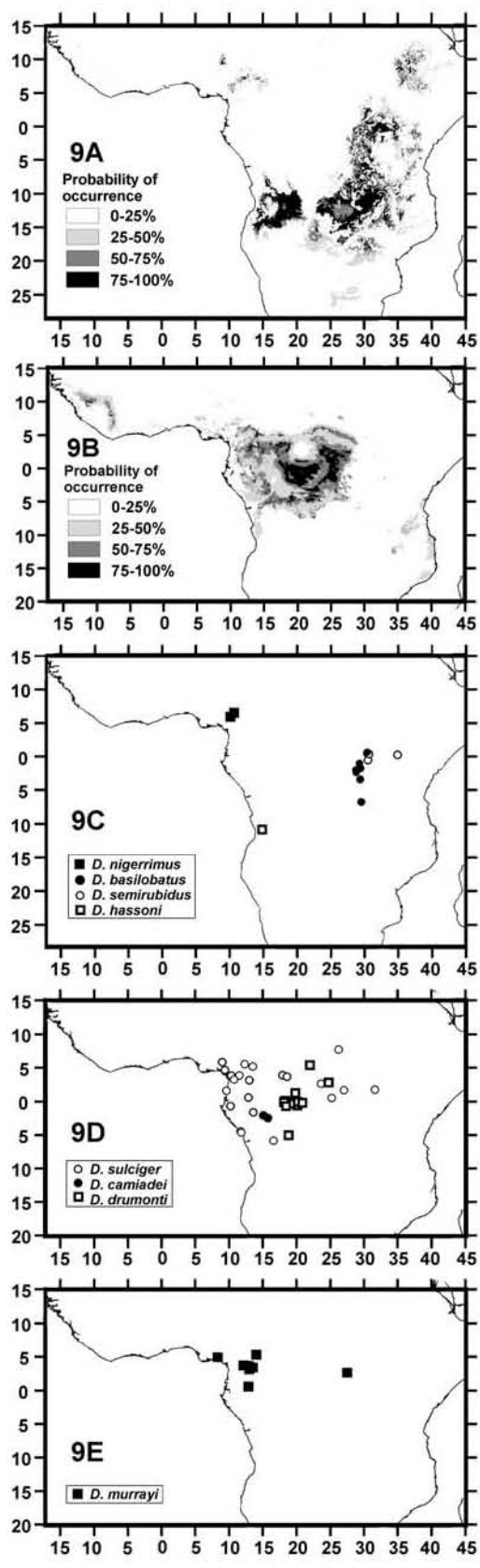


FIGURE 10 & 11

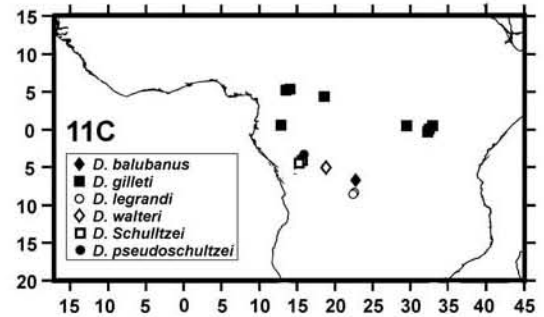
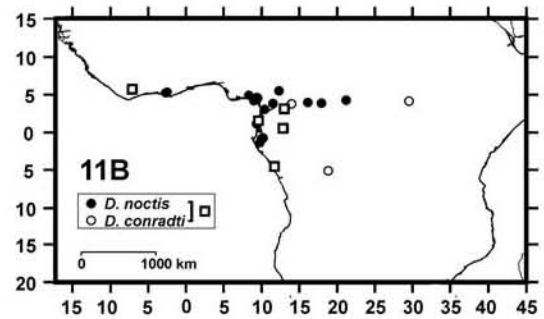
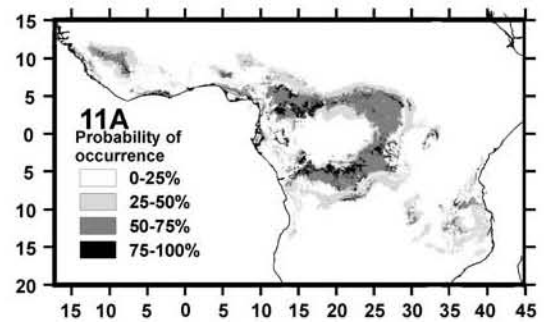
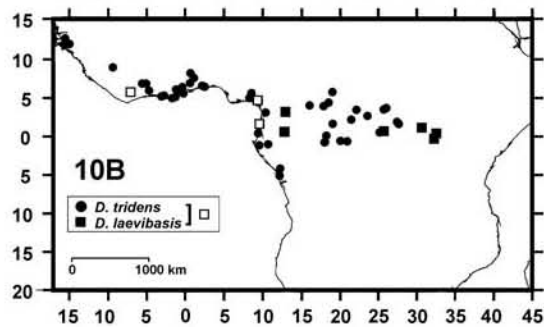
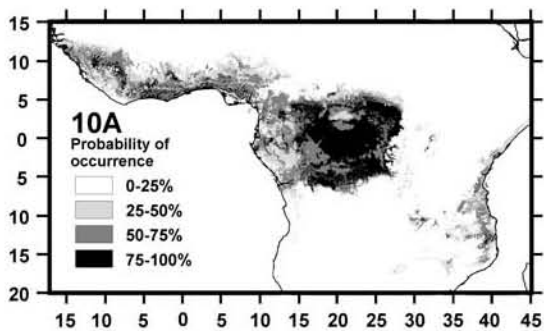


FIGURE 12

