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Mechanisms and tempo of evolution in the African Guineo–Congolian rainforest

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This paper reviews how and when African rainforest diversity arose, presenting evidence from both plant and animal studies. Preliminary investigations show that these African forests are an assemblage of species of varying age. Phylogenetic evidence, from both African rainforest angiosperms and vertebrates, suggest a Tertiary origin for the major lineages in some of these groups. In groups where savannah species are well represented and rainforest species are a minority, the latter appear to be relicts of a Mid-Tertiary rainforest. By contrast, species that are primarily adapted to rainforest have arisen in the past 10 Myr with the main morphological innovations dating from the Late Miocene, and Quaternary speciation dominating in large, morphologically homogeneous groups. The small number of species-level phylogenies for African rainforest plants hinders a more incisive and detailed study into the historical assembly of these continental forests.

Keywords: Africa; rainforest; speciation; molecular dating; phylogeny

1. INTRODUCTION

The present-day composition of continental tropical floras has been shaped by a combination of continental drift, past climatic changes, geological activity and stochastic dispersal events. Africa has felt the effects of a unique combination of these factors, which have driven speciation and extinction, leaving the diversity observed today. Molecular phylogenies in general, and species-level phylogenies in particular, can be used to uncover patterns in rainforest diversification. For Africa, important advances are being made in this field for vertebrates (Moritz *et al.* 2000), but our knowledge for plants remains comparatively poor. Nevertheless, work is beginning to emerge that can give a preliminary idea of the mechanism and tempo of speciation in the African rainforest.

The aim of this paper is to review our current knowledge of the evolution of continental African rainforests, primarily those of the main Guineo–Congolian block, and focusing on *in situ* evolution of lineages rather than their ultimate origin. The approach was to study evidence from species-level phylogenies of either Guineo–Congolian organisms, or other studies in which such information has been included. It was found that only a very small number of studies have focused on African rainforest groups: most of the data sample few species, are biased towards East Africa and savannah species, or have a taxonomic aim with no biogeographic discussion. Although an in-depth analysis of the evolution and origins of African rainforests is impossible owing to the paucity of suitable datasets, the studies reviewed here go some way to answering when and how the African forest biome developed.

2. THE AFRICAN RAINFOREST

The main African rainforest block (Lower Guinea Region) is centred in the Congo Basin and extends from the East African Albertine Rift mountains to the Atlantic Ocean in the West (figure 1). A smaller western block is found in the Upper Guinea Region, from Sierra Leone to Ghana. Small patches of rainforest also occur in the East African mountains between about 1200 and 2500 m altitude (White 1983). These forests however, although similar in physiognomy to the Guineo–Congolian rainforest, have a related, although different, species composition (White 1983) and are not discussed in this review.

The estimate for the number of flowering plant species in tropical Africa (mainland Africa from approximately the Tropic of Cancer to the Tropic of Capricorn) is 26 274 (Lebrun 2001; Lebrun & Stork 2003), which compares with *ca.* 90 000 for South America (Thomas 1999) and *ca.* 50 000 for Southeast Asia (Whitmore 1998). The species richness estimate for White's (1983) Guineo–Congolian region, which accommodates the two main rainforest blocks is some 8000 species (White 1983; Lebrun 2001). The main centres of species richness are in western Cameroon, around Mount Cameroon and the Cameroon highlands, the Kivu centre, and the Upper Guinea centre (Bentje *et al.* 1994; Linder 2001). These centres coincide with areas of greater rainfall (Linder 2001) and, in the case of the Kivu and Lower Guinea centres, also with mountain formations and altitudinal variation. Species endemism is estimated at 80% for the Guineo–Congolian region (White 1983). Centres of endemism coincide with areas of species richness, but rank differently, with the Kivu centre showing the highest levels of endemism followed by the area including Cameroon and Gabon (Linder 2001; Jetz & Rahbek 2002).

In terms of floristic composition, the African rainforest differs from other tropical floras in three ways (Richards

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Figure 1. Estimated distribution of African Guineo–Congolian evergreen rainforest (after Mayaux *et al.* 2004).

1973; Brenan 1978; Gentry 1993). First, at the continental level, it has fewer families, genera and species than other continents. Second, in contrast to South America for example, a larger proportion of the species have a wide, although sometimes discontinuous, area of distribution and there are therefore less local endemics (Gentry 1993). Third, African rainforests are poorer in some families that are very well represented in wet tropical forests elsewhere such as Lauraceae, Myrtaceae, Myristicaceae and Palmae (Arecaceae). The question of Africa's floristic poverty is relative. First, at the local or community level, a hectare of African rainforest will contain the same levels of alpha diversity as many equivalent areas in the neotropics (Gentry 1993). The difference lies in the fact that the neotropical flora has higher levels of species with restricted distributions, so a comparison of geographically widely spaced inventory plots in South America would show fewer species in common than a similar number in Africa. The abundant locally endemic species found in South America are mostly montane and submontane species found throughout the Andes (Gentry 1993). This endemic richness has been interpreted as the result of a speciation explosion associated with the Andean orogeny (Gentry 1989). Africa has fewer mountains and a lower associated complexity of vegetation types than South America, explaining, at least partly, the comparatively lower number of species.

The comparative floristic poverty of African rainforests has also been attributed to the degrading effect of significant climatic changes during the Cenozoic, and more recently to Pleistocene climatic fluctuations, resulting in a drier climate throughout most of equatorial Africa (Raven & Axelrod 1974). Although historical climatic oscillations may dominate the interpretation of African rainforest species composition and distribution, alternative explanations have been proposed, such as the effects of human impact (Richards 1973), the reflection of current ecological conditions (i.e. most African forests are drier than most neotropical ones (Richards 1973; Gentry 1993)) or the result of different patterns of evolutionary radiation rather than mass extinction (Gentry 1993).

3. VEGETATION AND CLIMATIC HISTORY OF TROPICAL AFRICA

Since the break-up of Gondwana, starting in the Mid-Cretaceous, Africa has moved north some 15° (Axelrod & Raven 1978), reaching its present-day position in the Mid-Tertiary (Maley 1996). There are numerous reviews on the geological and climatological history of Africa (Axelrod & Raven 1978; Coetzee 1993; Sosef 1994; Maley 1996; Wieczorek *et al.* 2000). This synopsis is based mainly on the descriptions of Axelrod & Raven (1978) and Morley (2000), which will not be repeatedly cited (citations are given only for additional authors). An excellent review of the Tertiary palaeobotanical history of African rainforests is provided by Jacobs (2004).

From the Late Cretaceous to the Early Palaeocene (77–55 Myr ago) Africa was isolated from other land masses and climatic conditions were stable. Because Africa was situated *ca.* 15° south of its present latitude, a large proportion of northern Africa was covered by rainforest, which extended from the east to west coast and from the Gulf of Guinea north to the Tethys Sea. Savannah-type woodland would have flanked the rainforest to the south, with subtropical rainforest dominating South Africa and the southern half of East Africa. Montane forests were restricted to small areas between 0 and 10° north. The terminal Cretaceous event brought about widespread extinctions throughout Africa, as is evidenced in the pollen record by a 50% fall in gymnosperm diversity.

In the Palaeocene to Early Eocene (65–46 Myr ago), the West African flora diversified almost without interruption. Climate was probably more seasonal, and diversification occurred during the change in lowland vegetation to a mosaic of rainforest and savannah extending over what is today the Congo Basin (Coetzee 1993). Grass pollen was common in Cameroon, together with that of forest elements (Salard-Cheboldaeff 1990). The end of the Eocene was once again marked by global cooling, most notably tracked in Africa by the extinction of many palms and an overall species diversity decrease, although this episode did not drastically alter the biotic composition of the continent.

The Early Oligocene (33 Myr ago) was characterized by a short sharp cooling event that may have been related to the main extinction event at the end of the Eocene. The remainder of the Oligocene was clearly characterized by widespread rainforests throughout much of the equatorial region and which probably extended from coast to coast.

The Miocene (23–5 Myr ago) was one of the most defining periods of Africa's geological and climatological history, and the biotic composition of Africa today was very much determined by Miocene events. The Early Miocene was warm, and more humid than the Late Eocene, but the drastic cooling of global temperatures and the closure of the Tethys Sea in the Mid-Miocene resulted in ever greater aridification throughout this period. Lowland rainforest in the central and northern Sahara and in parts of South Africa was gradually replaced by savannah woodland, while at the same time, the lowland rainforest belt shifted southwards almost to its present-day latitude, but probably extended continuously from the west to the east coast of Africa (Coetzee 1993). Uplift and accompanying warping and vulcanism started in the Late Oligocene–Early Miocene, together with the opening of the Great Rift Valley. By the Late Miocene (7 Myr ago), the Eastern Arc mountains were uplifted, uplands produced by volcanic activity in West Central Africa were present, and the Gulf of Guinea islands had emerged. Therefore, by the end of the Miocene, most of the present topology of Africa was in existence.

By the Late Miocene, rainforests were limited to small patches in upland areas and possibly along lowland river systems ('refugia'). There is evidence in Ethiopia of dense evergreen forest occurring at altitudes of between 900 and 1000 m during the Late Miocene (8 Myr ago), when these upland areas served as rainforest refugia (Yemane *et al.* 1987 in Coetzee 1993). Under the moister conditions of the Middle and Late Tertiary, the African rainforest was probably very species rich, especially into the Miocene, but the subsequent progressively drier climates eliminated much of the floristic diversity. Although the result of tropical Africa's aridification was overall impoverishment of the rainforest flora at the species-level in particular, few extinctions of rainforest plant lineages have been noted during the Late Miocene (10–5 Myr ago) (Maley 1996), suggesting that many present-day African lineages may date from the Early Miocene.

The Early Pliocene (5–3.5 Myr ago) was characterized by moist climates, the expansion and diversification of rainforests and the retraction of savannah. Pollen assemblages from this time show increased species diversity; the Late Miocene rainforest taxa are joined by many other species. Diversity peaked just before the end of the Pliocene (3.5 Myr ago), when rainforest extended to 20° north. At 3.48 Myr ago there is evidence for a change to a much drier climate, marking a change during the Late Pliocene (3.5–1.5 Myr ago) to much more pronounced climatic changes, with marked drying and cooling cycles. The Great Rift Valley developed in the Pliocene and Early Pleistocene, as did the Congo Basin (Coetzee 1993). Late Tertiary–Early Quaternary floras from five localities in the mountains of Cameroon show a rich environment where *ca.* 230 species were identified, most of them very similar or equal to extant species. Later, this flora was affected by episodes of ice-age aridity. The first appearance of West African gymnosperm pollen since the Cretaceous occurs 2.7 Myr ago. Major arid phases during the Late Pliocene occurred at 3.2 and 3.0 Myr ago, resulting in a reduced expanse of grasses and numerous regional extinctions.

The Quaternary (1.8 Myr ago to the present) is characterized by marked glacial variations, particularly from 800 000 years BP onwards. The most arid periods, coinciding with glaciations, resulted in fragmentation of forests and formation of forest refugia. The lowering of temperatures resulted in the extension of montane and submontane floras to lower altitude, more or less replacing lowland rainforest, and allowing the migration of montane floras and faunas between mountain ranges. With subsequent warming these montane floras would then be once again isolated on mountains. Since 2.5 Myr ago there have been 21 glacial cycles, 9 major and 12 minor (Hamilton 1982; Hamilton & Taylor 1991; Sosef 1994). The last period of maximum global warming occurred in the Holocene (last 11 000 years), while the last glacial maxima resulting in forest fragmentation occurred in the Pleistocene, from 160 000–130 000 years BP and from 24 000 to 12 000 years BP (Maley 1996).

These continual cycles of climatic change had a significant impact on the diversity and distribution of the African flora and fauna. The narrowing of forest habitat ranges during glacial maxima limited forest organisms to areas with continually high degrees of humidity and shade, such as crevasses and gallery forests in lowland areas and along mid-altitude regions of Africa's montane regions. Glacial maxima would often have meant large numbers of local extinctions, and in some cases would eliminate entire lineages, or leave a few representatives of once species-rich groups.

Figure 2. Postulated distribution of African rainforests during glacial maxima and the location of postulated glacial lowland refugia (after Maley 1987).

4. MODELS OF RAINFOREST SPECIATION IN AFRICA

Several models have been suggested to explain the patterns of species distribution and radiation observed in African rainforests. Moritz *et al.* (2000) provided an insightful review of different speciation models that have been at work in rainforests. Here, speciation models for which there is African evidence are assessed.

(a) *Refugial speciation model*

The refugial speciation model is a speciation mechanism often invoked in the Pleistocene refuge theory (Prance 1982). The Pleistocene refuge theory states that climatic oscillations during the Pleistocene fragmented the previously continuous rainforest into islands or refuges, often coinciding with mountain areas, that were separated by areas of savannah. The high frequency of climatic oscillations during the Pleistocene would have caused lowland forests (below 1500 m) to contract and expand repeatedly. Therefore, during periods of glacial maxima, when conditions were markedly drier and cooler, lowland rainforest would have persisted only in restricted areas. These postulated refugia would 'trap' species until more favourable conditions (i.e. wetter and warmer) allowed them to re-expand their ranges (Sosef 1994, 1996). Several workers have attempted to identify or give evidence for the location of these putative Pleistocene refugia based on either high species richness or high levels of endemism (figure 2; Aubréville 1962; Diamond & Hamilton 1980; Endler 1982; Grubb 1982; Mayr & O'Hara 1986; Colyn *et al.* 1991; Sosef 1994, 1996; Robbrecht 1996). Refuge theory has wide acceptance in an African context, but, as for South America (Colinvaux *et al.* 1996, 2001; Pennington *et al.* 2000), still remains contentious for some authors (Fjeldså 1994; Fjeldså & Lovett 1997). However, successive studies continue to identify local centres of endemism, and to refine or suggest slight modifications to the location and extent of established African montane rainforest refuge centres (Rietkerk *et al.* 1996; Robbrecht 1996; Leal 2001).

The refugial speciation model invokes allopatric genetic differentiation between populations fragmented by the spreading of savannah vegetation and trapped in refuges during glacial maxima in the Quaternary. This speciation model suggests a geologically recent origin for rainforest species (Hamilton 1976). This hypothesis is only one interpretation of the high levels of diversity observed in these areas. An alternative hypothesis suggests that refuge areas acted as 'museums' or 'sinks' by remaining climatologically stable through time, accumulating species gradually and experiencing low rates of extinction (Stebbins 1974; Lovett & Friis 1996). Linder (2001) found that although centres of species richness are strongly linked to increased levels of rainfall, endemism is not. This supports suggestions that centres of endemism could be in places that have shown climatic stability over longer periods of time, regardless of whether they remained wet or dry (Lovett & Friis 1996; Fjeldså & Lovett 1997). Endemism is often correlated with montane regions where there is altitudinal variation and geological dissection sustaining a greater range of habitats. Authors who dispute the refuge hypothesis suggest that refuge species are simply the result of recent montane speciation. It is unquestionable that much of the floristic diversity in African highland areas are the result of recent speciation, as exemplified by *Begonia* (Plana *et al.* 2004). The montane refuge speciation model describes speciation in response to the availability of new montane habitats during orographic uplift, which in Africa began in the Late Oligocene–Early Miocene and which to some extent (e.g. Mount Cameroon) continues today (Roy 1997). Montane speciation invokes refuge theory because this rapid expansion into new montane areas was followed by subsequent isolation and divergence of populations amongst refugial areas in the Plio–Pleistocene (Roy 1997). Therefore, whether for new or ancient species, these montane mosaics have acted, or are currently acting as, climatic refuges. Although the refuge speciation model itself envisages ‘refuges’ as speciation ‘engines’, there is little empirical data dating the time of origin of species endemic to these refuge areas.

A variation of the refuge model, which in Africa tends to function in mountain regions, is termed the ‘fluvial refuge model’, which stipulates that gallery forests acted as refugia during glaciations . This model is well developed to explain some patterns of speciation in wet tropical America (Pennington *et al.* 2000). In Africa, the suggestion that lowland forest patches remained near rivers in the Central Congo Basin is supported by the distribution and systematics of primates (Colyn *et al.* 1991). Within this area, well differentiated primate subspecies are found within interfluvial forest blocks, suggesting that the river network could have had a defining role in promoting primate speciation during the last glacial maxima. A similar conclusion was reached based on the distribution of Rubiaceae genera (Robbrecht 1996) and Caesalpiniaceae species (Wieringa 1999), where the restricted range of some species in riverine communities was observed. These riverine areas coincide with areas of plant species endemism in the Congo Basin (Ndjele 1988).

(b) *Ecotonal or gradient model*

This mode of speciation, in which the transition zones between forest and savannah play an important role in species generation, has been observed in African vertebrates but remains to be demonstrated in plants. This model, as presented by Smith *et al.* (1997), stipulates that populations inhabiting forest patches in ecotones, which are characteristically drier and more prone to abiotic fluctuations, experience selection pressures that lead to phenotypic divergence. Smith *et al.* (1997) compared populations of the little greenbul, small forest-dwelling birds that occur within the main rainforest block and in small forest patches within the savannah–forest boundary. He found a high degree of morphological variation between forest and ecotonal populations, but surprisingly less genetic diversity than expected, demonstrating that selection pressures can be strongly active, even in the presence of considerable gene flow. The importance of ecotones in bird speciation, however, had already been highlighted by Fjeldså (1994), who concluded that the forest–savannah transition zone played the most important role in recent species diversifications on the basis of the distributions of species inferred as new and relict, and the dominant presence of new species in ecotonal habitats.

5. TEMPORAL SPECIATION PATTERNS IN AFRICAN RAINFORESTS

(a) *Evidence from distribution data*

It has been common practice to analyse species distribution data in the light of past climatological and geological events, thus revealing spatio-temporal processes of speciation. This has been carried out with plant and animal distributions for Africa as it has for other continental floras. As one would expect, the pattern and time-frame of speciation varies depending on the organism studied.

Numerous historical studies have invoked past-climatic fluctuations, particularly during the Pleistocene, to explain present-day plant distributions, and these are commonly the same studies used to support refuge theory (e.g. Diamond & Hamilton 1980; Sosef 1994, 1996). In general, the mechanism inferred to generate observed species distributions has been that of allopatric speciation in different refuge areas. In 1994, Sosef published a study of the distribution of 40 species of African rainforest *Begonia*. The distributions were used to indicate the position of postulated African Pleistocene rainforest refugia. Sosef (1994, 1996) argued that the location of former refuges could be deduced from the present-day distribution of this group of begonias because of the high degree of species endemicity and the inability of the seeds to disperse effectively: usually dropping to the ground below the mother plant. He interpreted the pattern of distribution of these species as representing not only rainforest refuges but also as a product of a Pleistocene montane refuge model of speciation. Therefore, many of the species in these sections would have arisen during the late Pleistocene when continuous large-scale climatic oscillations may have driven speciation. Although other studies have pinpointed refugia based on organismal distributions, the *Begonia* study was one of the first to specifically interpret refuges as speciation engines, expanding and contracting as the result of recent global climatic turbulence.

Since then, other studies have come to similar conclusions and have presented the refuge model as the prime speciation mechanism. A study on African primate distributions found several distinct taxa within interfluvial blocks and concluded that a Major Fluvial Refuge in the Congo Basin, consisting of several independent centres would have persisted during glacial maxima in the Quaternary (Colyn *et al.* 1991). This study is the primary exponent of the fluvial refuge model. However, the important role of river systems during periods of aridification has also been identified in caesalpinioid legumes (Wieringa 1999) where the distribution of some species of *Bikinia* and *Aphanocalyx* are held as indicators of riverine refugia in West Central Africa. Similarly, distributions of African Rubiaceae genera not only gave support for established refuge areas, but also demonstrated the importance of fluvial refugia in some taxa (Robbrecht 1996).

In contrast to the suggested recent origin of some West Central African groups, comparative studies based on other taxa have reached alternative conclusions. Fjeldså & Lovett (1997) studied distributions of what they hypothesized as old and new species of forest plants and birds. To represent recently evolved plant groups they chose *Impatiens* (Balsaminaceae) and *Crotalaria* (Leguminosae), two genera that form aggregates of closely related herbaceous species. To represent old lineages they chose forest trees known to be poorly dispersed and which are found west and east of the arid corridor, indicating that the generic distributions predate Miocene uplift of the central African plateau (e.g. *Allanblackia* (Guttiferae (Clusiaceae)), *Zenkerella* (Leguminosae (Fabaceae)) and *Mammea* (Guttiferae)). They concluded that lowland areas which have been postulated as Pleistocene refugia are dominated by species that represent lineages of pre-Pleistocene age, while recently diversified taxa are found mainly at the edges of the main rainforest blocks and inhabitat islands outside them. Furthermore, they refuted the hypothesis advocated by Sosef (1994, 1996) that rainforest refuges acted as speciation centres, but supported their role as 'museums' or 'sinks' (Stebbins 1974), where species accumulate gradually and experience low extinction rates as a result of stable climatic conditions.

The competing hypotheses of putative refuge areas acting as engines of speciation and repositories of Pleistocene neoendemics, or as museums where species have accumulated over long periods as a result of low extinction rates, can be tested by dated molecular phylogenies.

(b) *Evidence from molecular data*

Molecular phylogenies of birds, mammals, lizards, frogs and salamanders from tropical regions of the neotropics, Africa and Australia suggest that most speciation events in tropical rainforests pre-date the Pleistocene (Moritz *et al.* 2000). If, however, we add plant data to our perspective of African rainforest evolution, the picture increases in complexity.

(i) *Plants*

The first phylogenetic study of an African plant genus restricted to rainforest was carried out on *Aframomum* (Harris *et al.* 2000). *Aframomum* is the largest genus of African gingers (Zingiberaceae) comprising *ca.* 80 species of rainforest understorey herbs. The authors sequenced the ITS of nrDNA for 28 species of *Aframomum*. The resulting phylogeny showed remarkably short branch lengths, evidence of a significant lack of molecular sequence divergence in contrast to the high levels of morphological variability (Harris *et al.* 2000). The authors postulated that the genus *Aframomum* as seen today is the result of a rapid radiation which probably took place during the Pleistocene. This strong support for a Pleistocene model of recent speciation is exceptional and unusual.

By contrast, a molecular study on African begonias found significantly different results. There are 158 species of *Begonia* in Africa, of which the majority are rainforest understorey terrestrial herbs or epiphytes. Only a very small number are adapted to xerophytic or seasonal conditions in East and South Africa. Sequences from both ITS and the *trnL* intron region of cpDNA were generated for 53 species of African *Begonia* (Plana *et al.* 2004). The phylogeny was then dated by non-parametric rate smoothing (Sanderson 1997) and using the ages of Reunion (2 Myr ago) and Mayotte (5.4 Myr ago) (Emerick & Duncan 1982), which are home to the island endemic species *Begonia salaziensis* and *B. comorensis*, respectively. The authors found that much of the deeper variation in the genus, as well as key biological innovations, such as the evolution of fleshy fruits (*ca.* 9 Myr ago) or dispersal to Madagascar (13.5 Myr ago), occurred in the Mid- to Late Miocene, coinciding with widespread aridification in Africa (Plana *et al.* 2004). The same study, however, found that just under 40% of species were of recent Plio–Pleistocene origin, and were concentrated in larger, morphologically homogeneous groups. This supports a recent origin for some begonias. Although the numbers of species sampled was low, the same study showed that a number of the species that Sosef (1994) suggested had a Pleistocene origin did indeed date to the Late Pleistocene. Even the basal node of Sosef's study group was dated only to 3.4 Myr ago, suggesting that additional sampling would place the origin of more of these rhizomatous rainforest species as recent. Similar results have been found for the species-rich legume genus *Inga* in South America: the *ca.* 300 tree species were found to have low levels of sequence divergence (Richardson *et al.* 2001). The authors concluded that diversification in this genus occurred within the last 10 Myr, *ca.* 30% of the genus dating from the Pleistocene.

While the above mentioned studies placed dated phylogenies within a historical geological and climatological context, other phylogenetic studies have not yet applied molecular dating methods, although some preliminary observations are possible. The legume genera *Bikinia*, *Aphanocalyx* and *Tetraberlinia* (Caesalpinioideae) are a group of closely related genera consisting of primary evergreen forest trees with their centre of diversity in Gabon (Wieringa 1999). An examination of the phylogenetic relationships among species in these groups was carried out by sequencing the ITS region for 16 species in these genera (Wieringa & Gervais 2003). The authors found evidence of rapid speciation in *Tetraberlinia* and *Bikinia*, and somewhat slower rates in *Aphanocalyx*, and concluded that this pattern could be interpreted as the result of Quaternary refuge speciation. A preliminary study on the related legume genus *Berlinia* reached similar conclusions (Mackinder 2000). *Berlinia* is a group of large tropical African trees with their greatest diversity in the Guineo–Congolian region (Mackinder 2000). Although the study was small, an analysis of ITS and *trnL* sequence data found low levels of sequence divergence.

Species in *Aframomum*, *Begonia* and possibly Leguminosae, all primarily rainforest groups, are the result of Miocene and Pleistocene diversification, but genera which have both xerically-adapted and mesophytic species may well tell a different story. The genus *Acridocarpus* (Malpighiaceae) is comprised of 30 tree species widely distributed across Africa and Madagascar, with a single species in New Caledonia. *Acridocarpus* species grow in a wide range of habitats, from rainforest to savannah. In a study of 14 *Acridocarpus* species, of the mainland African species sampled, four were East African and seven were West African (Davis *et al.* 2002*a*). Of the latter, three are rainforest species and the rest are adapted to increasingly xeric conditions, from forest margins to the forest–savannah ecotone. The authors calibrated divergence-time estimates for the

Acridocarpus phylogeny using estimates for the split between *Acridocarpus* and *Brachylophon* determined in a global Malpighiaceae phylogeny (Davis *et al.* 2002*b*). The results showed that the start of diversification of the rainforest species dated to the very beginning of the Miocene when conditions were favourable for rainforest expansion and that xerophytic species were more recently derived. In an examination of the phylogenetic relationships within *Streptocarpus* (Gesneriaceae) the authors also found that species adapted to mesophytic habitats tended to be phylogenetically basal, with derived species not only showing increasing drought-tolerance but also a clear southern migration route down eastern Africa (Möller & Cronk 2001).

(ii) *Animals*

For vertebrates, the main studies examining speciation in African forests have been carried out on birds. These have concentrated on small groups with a prominent East African presence, although a small number of Guineo–Congolian rainforest species have been sampled, allowing some interpretation of rainforest vertebrate evolution. Using published DNA hybridization data, Fjeldså (1994) and Fjeldså & Lovett (1997) found that recently diverged Plio–Pleistocene groups inhabit montane regions and are derived from pre-Pleistocene ancestral lineages inhabiting lowland rainforests. Roy *et al.* (2001) used mtDNA sequence data to investigate phylogenetic relationships in the passerine bird genus *Sheppardia* in a historical biogeographic context. The genus *Sheppardia* is represented by eight forest-dwelling species known commonly as African forest robins or akalats. They found that all species evolved rapidly from a common ancestor around the end of the Miocene to the Early Pliocene, coinciding with the final major uplift of the East African Highlands. Intraspecific variation, however, is dated to the Pleistocene, even among widely disjunct populations. An earlier examination of relationships among African greenbuls (*Andropadus*) also showed montane species to be a derived monophyletic group of Plio–Pleistocene age, whereas the lowland species were dated to the Miocene (Roy 1997).

Wieczorek *et al.* (2000) used mtDNA sequence data to interpret the phylogeny of African *Hyperolius* frogs from a historical vegetation and climatic perspective. Again the majority of species in this group are East or South African and are either adapted to savannah environment or are generalists. A small number, however, do occur in West African and West Central African rainforests. The basal taxa in *Hyperolius* tend to be generalists or adapted to rainforests, with the genus believed to have begun its diversification in Africa in the Late Oligocene and Early Miocene (Wieczorek *et al.* 2000).

More recently, a phylogeny of African genets (*Genetta*) was generated based on cytochrome *b* sequence data representing 15 species of genet (Mayaux *et al.* 2004). The authors estimated divergence times assuming a molecular clock and calibrating their phylogeny based on a divergence date between *Genetta* and *Poiana*, another genus in the Viverridae. The authors found that although the basalmost branch (*Genetta thierryi*) corresponded to a species of moist and dry savannahs and therefore of an open habitat, the subsequent series of basal branches corresponded to rainforest species estimated to have diverges during the Late Miocene–Early Pliocene. Again, within this phylogeny, the bulk of savannah species are found within a derived clade, with an origin dated at 3.5–3.4 Myr ago. In this example the biogeographic pattern increases in complexity because nested within the savannah clade are two rainforest species, and this habitat reversal is dated to the Pleistocene.

(c) ***Lowland rainforests: old or new?***

The influential review of Moritz *et al.* (2000) suggested that the pre-Pleistocene origin of rainforest species was a global phenomena. As discussed above, this has certainly been demonstrated in African rainforest vertebrates where rainforest taxa are commonly placed basally to more derived montane or sclerophyllous species in molecular phylogenies. Plant groups where the greatest proportion of species belong to seasonal forest or savannah environments have a similar diversification sequence. In *Acridocarpus* (Malpighiaceae) rainforest species hold a phylogenetically basal position with a pattern of increasing drought tolerance among the derived taxa (Davis *et al.* 2002*a*). Similar results have been found for *Streptocarpus* (Gesneriaceae) (Möller & Cronk 2001), although unfortunately this phylogeny is not dated. For *Acridocarpus* and very possibly for *Hyperolius* frogs, although the latter are not part of a dated phylogeny, the diversification of basal rainforest taxa is estimated at between 27 and 23 Myr ago when the climate was wetter and more humid and rainforest extended from coast to coast. *Hyperolius*, like *Acridocarpus*, is not a ‘true’ rainforest group, having only a small subsample of species restricted to lowland rainforests. True rainforest genera, which occur only in rainforest environments, do not show this temporal pattern. *Begonia*, *Aframomum* and some rainforest caesalpinioid legumes show speciation occurring mainly within the last 10 Myr.

If this pattern is true, and not a result of deficient species sampling, then we may postulate that genera such as *Acridocarpus* and *Hyperolius* represent rainforest lineages that survived successfully through periods of widespread aridification by speciating into xeric environments. These groups rarely, if ever, have strict rainforest species within their more derived lineages, lending credence to the hypothesis that there have been equivalent savannah refuges and that the Pleistocene functioned as much as an engine for savannah as for rainforest speciation. Many species or lineages that are found in present-day rainforests, and which may or may not have savannah relatives, appear to have been either absent from Africa in the Mid- to Late Miocene or, in the case of some lineages, lacked the physiological capacity to adapt to early global glacial environments, surviving precariously until favourable mesophytic conditions allowed varying degrees of speciation.

6. CONCLUSIONS

Crame (2001, p. 182) explained that the diversity we see today is the result of a ‘. . .modified form of the refuge hypothesis, stretching back over longer periods of time. . . ’. The issue of whether rainforest centres of endemism or refugia acted as engines or sinks is commonly presented as two conflicting hypotheses. As evidenced from distribution data and from molecular phylogenies, these hypotheses are not mutually exclusive and these centres of diversity contain both recent and relict species or lineages. In areas where these postulated refuge areas coincide with mountain regions (the majority, in the Guineo–Congolian region) this probably reflects both the role of these mountains in speciation by providing a wide range of new habitats, and these same peaks and valleys providing refugia for species during periods of climatic turmoil.

An examination of the literature discussing speciation events in African rainforests provides one clear result: species that constitute African rainforests are of varying age, and it is the contraction and expansion of forests throughout history, in response to global climatic fluctuations, that have driven their composition. From the available data it is apparent that African rainforests (and possibly rainforests worldwide) are an assemblage of relict species from a once widespread Mid-Tertiary (Late Oligocene–Early Miocene) rainforest and species of recent Plio–Pleistocene origin, born as a result of multiple consecutive glaciations. The Mid–Tertiary element of relict rainforest species is represented by genera or groups of species that are more drought tolerant, ranging from savannah to the more seasonal rainforests of the East African highlands. These groups tend to have fewer West and Central African rainforest representatives, which commonly occupy basal phylogenetic positions. These phylogenies show an increase in drought tolerance among derived taxa, with rare switches back to rainforest. Just as the Plio–Pleistocene may have been an important instigator of species diversification in rainforests, it also impacted savannah environments with the same result of driving species production. The Plio–Pleistocene element are largely genera of rainforest species (which may or may not have some sclerophyllous representatives) of Recent, Late Miocene to Pleistocene origin. These are monophyletic groups with their closest relatives occurring either outside Africa or in more seasonal habitats.

It is evident, however, that datasets for wet tropical African groups are seriously under-represented. There are, for example, no dated phylogenies for rain forest trees or for strictly African rainforest vertebrates. Remarkably, refuge theory in Africa has never been explicitly tested with molecular data, and there is a real need for more phylogenetic studies that look at relationships between species endemic to proposed refuge areas, or population genetic studies among populations of individual species occurring both in and out of postulated refugia. The montane and ecotonal speciation models have never really been specifically tested, particularly in plants. Without these kinds of studies it will be impossible to achieve an accurate estimate of speciation in the African rainforest biome.

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GLOSSARY

cpDNA: chloroplast DNA
ITS: internal transcribed spacer
mtDNA: mitochondrial DNA
nrDNA: nuclear ribosomal DNA