



Differentiation between populations of a termite in eastern Africa: implications for biogeography

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ABSTRACT

Aim African forests are divided by an arid corridor which runs from the Horn of Africa to the Namib Desert. Several forest species occur in the forests of eastern Africa as well as in the Guineo-Congolian forest block. We evaluate the possibility that such species may have crossed the arid corridor along a route through the Kenyan Highlands and down the eastern drainages during climatologically favourable periods in the past.

Locations Eastern Africa, Ivory Coast.

Methods We used the termite species *Schedorhinotermes lamanianus* (Sjöstedt). This species occurs in lowland forests and woodland throughout Africa south of the Sahara. We sampled termites from 12 populations. We evaluated the differentiation between populations using amplified fragment length polymorphisms as well as morphometrical measurements.

Results Genetic and morphometrical analysis demonstrated substantial differentiation between populations west and east of the arid corridor in Kenya. To the east of this corridor we found an increase of morphological distance with geographical distance. *Schedorhinotermes lamanianus* occurs not only along the coast but also at isolated locations (e.g. ground-water forests in foothills) within the arid hinterland.

Main conclusions We interpret these populations as remnants of a wider distribution during wet climatic periods. At these times, populations of *S. lamanianus* were apparently able to establish along extensive gallery forests protruding into the arid belt of the Kenyan hinterland. There have been no connections between populations of this species east and west of the arid corridor across the Kenyan Highlands.

Keywords

AFLP, arid corridor, biogeography, coastal forests, Guineo-Congolian forests, Isoptera, Kenya, morphometry, *Schedorhinotermes lamanianus*.

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INTRODUCTION

An arid corridor runs throughout the African continent from the Horn of Africa in the north-east to the Namib Desert in the south-west (van Zinderen Bakker, 1969; Jürgens, 1997). The extent and importance of this corridor have varied over time in response to climatic change (for reviews see deMenocal, 1995, 2004). During the Pliocene and Pleistocene the climate shifted stepwise to more arid and variable conditions near 2.8, 1.7 and

1.0 Ma (deMenocal, 1995). Before 2.8 Ma African climate had been regulated by low-latitude insolation with a periodicity of 23–19 ka. From 2.8 Ma African climates varied primarily at a 41 ka periodicity. Additionally, the amplitude of these cycles increased. The next change in the variability occurred around 1.0 Ma (100 ka cycle; deMenocal, 1995). Both shifts were correlated with shifts of high-latitude ice sheets, probably driven by the variation of obliquity (41 ka cycle) and eccentricity (100 ka cycle).

This arid corridor had two important biogeographical consequences. First, it allowed the exchange of arid-adapted taxa between the arid belts of Africa. This is evident in the disjunct distributions of arid-adapted taxa in both southern and eastern Africa (e.g. Jürgens, 1997; Herron *et al.*, 2005) as well as in the phylogeography of some arid-adapted species (e.g. Nersting & Arctander, 2001; Muwanika *et al.*, 2003). Second, the arid belt was a barrier preventing the exchange of taxa between eastern and western forests in Africa (e.g. Burgess *et al.*, 1998; Roy *et al.*, 2001; Bowie *et al.*, 2004). The faulting and rifting in eastern Africa (the Rift Valley) accentuated the barrier. Thus, the origins and history of connections of eastern African forests constitute a central topic in African biogeography (Lovett & Wasser, 1993; Burgess *et al.*, 1998).

The separation of the Guineo-Congolian forest block in the west from the coastal and montane forests of eastern Africa may be as old as 10 Myr (Burgess *et al.*, 1998). During subsequent moist intervals in the climatic history, connections across the barrier could have been reopened, allowing for some exchange of taxa or gene flow within widely distributed species (Burgess *et al.*, 1998). In eastern Africa, two corridors have been suggested (Lovett & Wasser, 1993): a southern corridor along the riverine forests passing through the Tanganyika Rift and Ruka Rifts, as well as a northern route across the Kenyan Highlands. Further south, an exchange of taxa could have occurred along the woodlands of Zambia and Zimbabwe.

We evaluate the importance of the northern route for eastern Africa by analysing the genetic and morphometrical differentiation between populations of a forest-adapted species east and west of the arid corridor. If this corridor was closed for an exchange between populations, we would expect major genetic and morphological differentiations between populations. We use the damp-wood termite *Schedorhinotermes lamanius* (Isoptera: Rhinotermitidae) as a model species. This species is widely distributed in the lowland forests and woodlands of the Ethiopian region (Harris, 1968; see also Fig. 1). It is also found in patches of semi-evergreen vegetation, gallery forests and plantations (e.g. cashew plantations). East of this arid corridor, *S. lamanius* is found in coastal forests and in scattered locations in the arid hinterland of the coast (Taita Hills, or in ground-water forests in the foothills). West of the arid corridor, this species exists in the Guineo-Congolian forests with eastern outposts in western Kenya (Brandl *et al.*, 1996). *Schedorhinotermes lamanius* shows life-history characteristics that have been interpreted as favouring long-term survival even in small forest fragments (Brandl & Kaib, 1995; Brandl *et al.*, 1996; Husseneder *et al.*, 1998). Thus, the currently isolated populations of *S. lamanius* in the hinterland of the Kenyan coast have been hypothesized to represent remnants of a wider distribution found during humid periods (Kaib & Brandl, 1992; Brandl & Kaib, 1995). During these periods, extensive gallery forests may have allowed forest species to extend into the arid corridor (Fjeldså & Lovett, 1997). Along these gallery forests species may have reached the forests of the Kenyan Highlands and finally the eastern outposts of the Guineo-Congolian forest

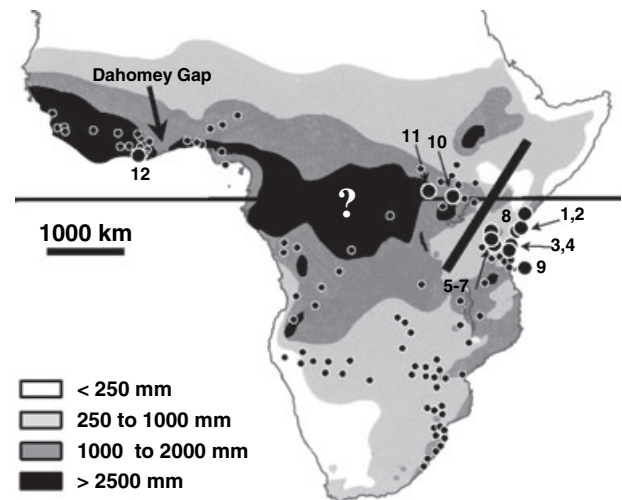


Figure 1 Rainfall modified after Kingdon (1999), as well as the distribution of *S. lamanius* in Africa (small circles) modified after Harris (1968), and completed with records from Angola (Weidner, 1974), Kenya (Brandl *et al.*, 1996), Zaire (Ruelle, 1994), Zimbabwe (Mitchell, 1980) and southern Africa (Coaton & Sheasby, 1973). The question mark indicates an area of suitable habitat but no records of sampling, which can be attributed to a lack of surveys. The black bar marks the Rift Valley complex. The arrow marks the Dahomey Gap, which is a non-rain forest region and separates the rain forest belt along the West African coast. Large circles indicate sampled populations. For population numbers and locations see Table 1.

block. The goal of this study is to elucidate the degree of population differentiation in *S. lamanius* east and west of the arid corridor. The amount of differentiation can be interpreted to give an indication of the antiquity of the separation between present populations east and west of the arid corridor.

MATERIALS AND METHODS

To study the genetic and morphometrical differentiation of *S. lamanius*, individuals were sampled from nine populations east and three populations west of the arid corridor. Six populations were sampled along the Kenyan coast (Mrima Forest, Shimba Hills, Arabuko Sokoke Forest, Gedi, Tana River) as well as from Zanzibar. Additionally, three isolated populations were collected from the Kenyan hinterland (Kibwezi Forest, Mzima Springs, Taita Hills). The three populations west of the arid corridor were sampled in Uganda (Masindi and Mabira Forest) and near Abidjan (Ivory Coast; Fig. 1, Table 1). Genetic and morphometrical data stem from different colonies (except for some populations west of the arid corridor). Species identification is based on the key, as well as on further details, provided by Harris (1968).

Amplified fragment length polymorphism (AFLP) analysis (Vos *et al.*, 1995) followed the procedures of Kaib *et al.* (2004). In brief, we extracted total DNA from the head and thorax of workers using a commercially available kit (DNAeasy® tissue kit, Qiagen, Hilden, Germany). *EcoRI* and *MseI* were employed

Table 1 List of sample locations and mean geographic coordinates of sample sites. Population numbers (No.) correspond to Figs 1 and 2. The numbers of colonies used for genetic (AFLP) and morphometrical analyses (Morph.) are also stated. Genetic and morphometrical data stem mostly from different colonies and are thus almost independent data sets. The broken line separates populations east and west of the arid corridor.

No.	Sample location	Country	Coordinates	AFLP	Morph.
1	Arabuko Sokoke Forest	Kenya	3°19' S, 39°56' E	1	4
2	Gedi	Kenya	3°16' S, 40°00' E	4	5
3	Shimba Hills	Kenya	4°11' S, 39°25' E	15	15
4	Mrima Forest	Kenya	4°28' S, 39°16' E	1	5
5	Taita Hills	Kenya	3°23' S, 38°22' E	4	6
6	Kibwezi Forest	Kenya	2°24' S, 37°57' E	2	3
7	Mzima Springs	Kenya	3°00' S, 38°01' E	2	5
8	Tana River	Kenya	1°59' S, 39°56' E	2	0
9	Zanzibar	Tanzania	6°08' S, 39°16' E	2	2

10	Mabira Forest	Uganda	0°42' N, 33°55' E	2	2
11	Masindi	Uganda	1°44' N, 31°42' E	3	3
12	Abidjan	Ivory Coast	5°19' N, 4°04' W	1	4

Table 2 List of AFLP primers used for this study with specific extensions (bold)

Joe 1 (<i>EcoRI</i>)	5'-Joe-G ACT GCG TAC CAA TTC ACG -3' 5'-G ATG AGT CCT GAG TAA CAG -3'
Tamra 1	5'-Tamra-G ACT GCG TAC CAA TTC ACC -3' 5'-G ATG AGT CCT GAG TAA CAC -3'
Tamra 2	5'-Tamra-G ACT GCG TAC CAA TTC ACC -3' 5'-G ATG AGT CCT GAG TAA CAG -3'

as restriction enzymes. Amplified DNA fragments were separated on an ABI PRISM 310C genetic analyser (Applied Biosystems, Foster City, CA, USA) and banding patterns were recorded using the ABI PRISM GeneScan analysis software (Applied Biosystems). Individual runs were aligned via an internal size standard. Thirty-nine different primer combinations were tested. Based on the number and size distribution of the polymorphic fragments, three primer combinations (selective bases ACG/CAG (Joe), ACC/CAC (Tamra 1), ACC/CAG (Tamra 2); see Table 2) were chosen for further analysis. Selected primers amplified 427 dominant loci consistently (114 monomorphic loci). Four individuals from each of the 39 colonies were genotyped. For distribution of colonies across populations see Table 1.

Genetic similarities between individuals were calculated from the presence/absence matrix of aligned fragments using the Jaccard index (using *NTSYS-PC* 2.02k; Rohlf, 1990). In a first step we extracted the first two principal coordinates of a matrix of 12,090 similarities between all possible pairs of the 156 individuals. As the assumptions of the Hardy–Weinberg equilibrium are obscure with dominant markers, we used a phenetic approach to estimate population genetic structure from the total data matrix (*AMOVA* within *ARLEQUIN* 2.00; Excoffier *et al.*, 1992, see also Keiper & McConchie, 2000). Only loci that matched the criterion of Lynch & Milligan (1994); bands with a frequency of less than $1 - (3/N)$, N being the total sample size) were included in the *AMOVA*. In a second step, we calculated a similarity matrix between the 12 populations. For this we calculated the mean similarities between each pair of populations using all possible pairs of individuals of the two selected populations. This new similarity matrix (66 mean similarity

indices) was subjected to a cluster analysis (*UPGMA* as implemented in *NTSYS-PC*; Rohlf, 1990). Furthermore, we plotted mean similarities between populations vs. geographical distance. The correlation between the two matrices was tested using matrix permutations (as implemented in *NTSYS-PC*).

Fourteen linear morphometrical variables from the head, thorax and forelegs of minor soldiers were measured (see Appendix S1 in Supplementary Material). Measurements were taken from 10 to 17 individuals from 54 colonies across 11 of the 12 studied populations (861 individuals). No colonies from the Tana River population were available for morphometrical analyses. Prior to further analyses, all variables were \log_{10} -transformed to minimize the effect of differences in body size (see also Husseneder *et al.*, 1998). Analogous to the analyses of the AFLP data, we followed a three-step procedure to evaluate morphometrical differentiation. In the first step, we projected all sampled colonies into a two-dimensional ordination diagram using a canonical variates analysis. Individuals were grouped according to colonies. In the second step, we calculated a matrix of Mahalanobis distances between populations and performed a *UPGMA* cluster analysis using *SPSS* 10.0 for Windows. Finally, we plotted the morphometrical distance between populations vs. geographical distance and tested the correlation by matrix permutations.

We correlated genetic similarity vs. morphometrical distance using matrix permutations to evaluate significance. Furthermore, we tested for similarities in the phylogeographical tree generated from the AFLP and morphometrical data using procedures implemented in the program *COMPONENT* (Page, 1993). We selected the nearest-neighbour interchanges (NNI distance) and compared this index with a distribution generated from 1000 pairs of random trees. Given two unrooted binary trees, the NNI distance between those trees is the smallest number of nearest-neighbour interactions required to transform one tree into the other.

RESULTS

The three primer combinations produced 427 AFLP fragments. The size of these fragments ranged from 49 to 451 bp

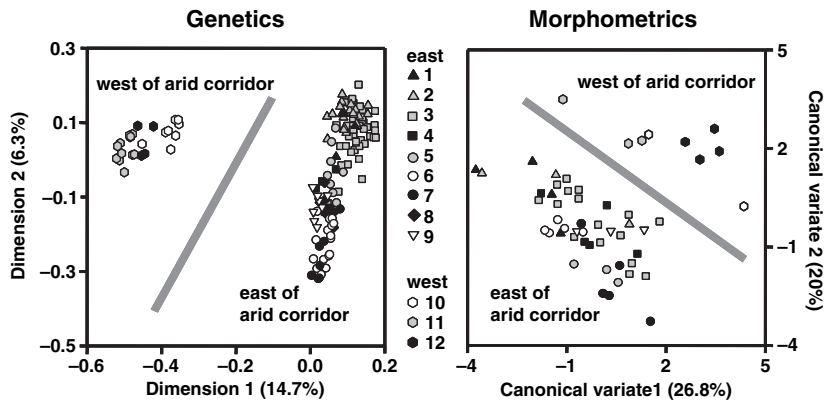


Figure 2 Principal coordinates analysis of the similarity matrix (Jaccard) between 156 individual workers using AFLPs (left). The two dimensions summarize 21% of the total variation. Symbols represent individuals. The first two axes of a canonical variates analysis using 14 linear morphometrical measurements (\log_{10} -transformed) of minor soldiers (right). Individuals were grouped according to colonies. The two dimensions summarize 46.8% of the total variation. Symbols represent centroids of colonies. For numbers of populations see Table 1. Note the clear differentiation between populations east and west of the arid corridor.

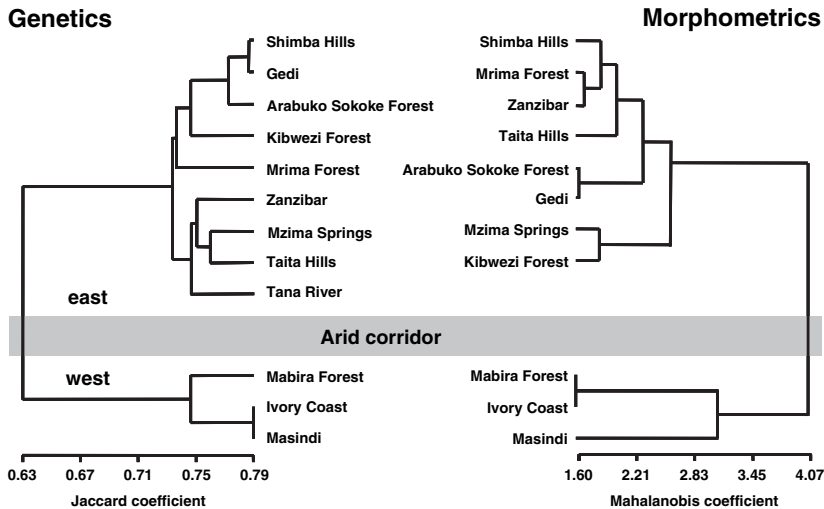


Figure 3 Cluster diagrams using the UPGMA algorithm on the matrix of the mean genetic similarity (left) and the Mahalanobis distance (right) between populations. Note the clear differentiation between populations east and west of the arid corridor.

(including primers, 2×19 bp). In 73% of all scored fragments (313 from 427) we found variation within or between populations. We found no difference in the percentage of polymorphic loci between populations (percentage of polymorphic loci within populations is between 56% and 67%; $G = 18.4$, d.f. = 11; $P > 0.05$).

The ordination of individuals showed a clear separation between individuals sampled east and west of the arid corridor (Fig. 2, left). However, within these two groups some populations overlapped. When grouping individuals according to the two clusters apparent in the ordination (Fig. 2, left) and into populations within these two clusters, more than a third (37%) of the genetic variability can be attributed to differentiation between east and west of the arid corridor and 17.5% to variation between populations within the two clusters. The cluster diagram generated from the mean Jaccard similarities between populations also showed a clear separation of populations east and west of the arid corridor (Fig. 3, left;

co-phenetic correlation coefficient = 0.98). Within the eastern group of populations the clustering shows little agreement with the geographical location. Nevertheless, across the eastern populations the correlation between genetic similarity and geographical distance was significant (Fig. 4, left). However, western populations showed a lower genetic similarity than expected from the regression line across eastern populations (Fig. 4, left). Thus, the clear genetic difference between the populations east and west of the arid corridor is not just a function of geographical distance.

Similar to the AFLP data, our morphometrical data revealed a clear separation of populations east and west of the arid corridor (Fig. 2, right), which was also evident in the UPGMA diagram (Fig. 3, right; co-phenetic correlation coefficient = 0.91). However, contrary to the AFLP data the relationships among eastern populations showed a pattern of similarity consistent with geography (compare Fig. 1 and Fig. 3, right). Morphometrical distance increased with geo-

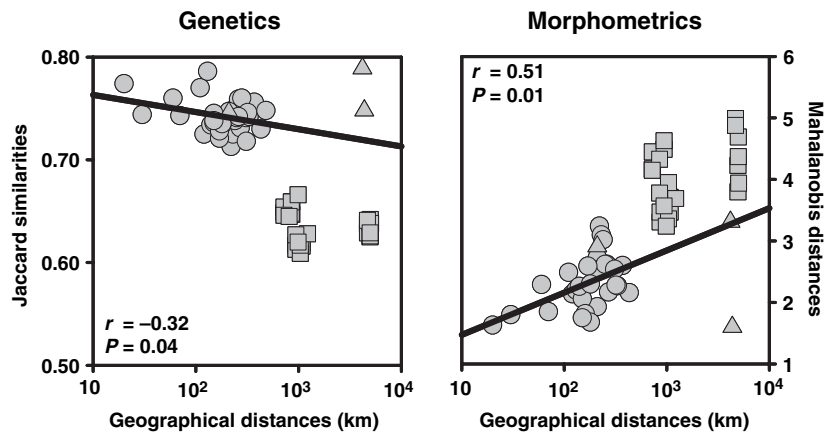


Figure 4 Relationship of geographical distance (\log_{10} -transformed) vs. mean genetic similarity (Jaccard, left) and morphological distance (Mahalanobis, right) across all pairwise comparisons (circles: between populations east of the arid corridor; triangles: between populations west of the arid corridor; squares: comparison of populations east and west of the arid corridor). The regression line was calculated using populations east of the arid corridor (matrix correlations refer to the regression lines; 999 permutations; one-tailed error probabilities). Note the clear deviation of the comparisons between populations east and west of the arid corridor from the regression line. Only eight populations were used for the morphometrical data (without Tana River; see Table 1).

graphical distance for populations east of the arid corridor (Fig. 4, right). We found a clear deviation of the morphological distance between populations east and west of the arid corridor from the expectation derived from eastern populations (Fig. 4, right; sufficient populations were only sampled east of the arid corridor). All these results parallel the genetic data.

Across all 11 populations for which we have genetic and morphometrical data, genetic similarities and morphometrical distances are correlated ($r = -0.84$, $P < 0.01$, 999 permutations). However, this correlation dropped considerably when we restricted the analysis to the eastern populations ($r = -0.29$, $P < 0.1$, 999 permutations). The NNI distance between the two trees shown in Fig. 3 is 11. Only 8% of NNI distances between pairs of random trees are less than or equal to this value. Hence the two trees in Fig. 3 are marginally more similar than expected by chance. However, analysing only the eastern populations, the NNI distance (7) of the genetic and morphometrical tree is within the expectation derived from random trees. These results confirm the deep split between *S. lamanius* populations east and west of the arid corridor.

DISCUSSION

Genetic and morphometrical data reveal a clear separation of populations east and west of the arid corridor, which cannot be explained by geographical distance alone. Hence, the two independent data sets (note that we sampled mostly different colonies for genetic and morphometrical analyses) suggest that there was no connection between populations of *S. lamanius* across the Kenyan Highlands during recent times.

Schedorhinotermes lamanius builds conspicuous and characteristic galleries, and the distribution of this species is well documented for most regions in Africa south of the Sahara

(Harris, 1968). At present, there are no records from the Central Kenyan Highlands and the most westerly Kenyan record is located close to the Ugandan border (Ramogi Forest; Brandl *et al.*, 1996), west of the arid corridor. There are no distributional records of *S. lamanius* in eastern Africa between western Kenya and the coast and adjacent low-land forest remnants. Apparently this gap was not crossed by *S. lamanius* during climatically favourable periods during the more recent past. A more precise estimate of the separation time may come from sequence data. Our own preliminary data suggest a sequence divergence of a mitochondrial gene of 2–3% between populations east and west of the arid corridor. This points to a separation time of 1–1.5 Ma (standard molecular clock; Avise *et al.*, 1998).

This conclusion is corroborated by the distribution of the tineid moth, *Paraclystis*, a common inquiline in *S. lamanius*. Inquilines are distant insect taxa which break the social insect colony's recognition system and are thus tolerated in the colony and can even be treated like nestmates. The biological role of *Paraclystis* in termite colonies is not yet understood. Two species of *Paraclystis* are known to exist. While the species *Paraclystis divisus* (Silvestri) is found west of the arid corridor from the Atlantic coast to Ramogi Forest in western Kenya, only *Paraclystis integer* (Silvestri) has been recorded from *S. lamanius* colonies along the Indian Ocean (including the Mzima and Kibwezi forests; Brandl *et al.*, 1996). Hence, the clear gap in the differentiation between populations of *S. lamanius* is confirmed by the distribution of two congeneric inquilines.

A separation of populations east and west of the arid corridor has also been found in a number of other species. Particularly relevant is the population structure of the *Anopheles gambiae* complex, an important vector of malaria (Lehmann *et al.*, 1999, 2000, 2003). Similar to our study, Lehmann *et al.* (2003) demonstrated a close genetic relation-

ship between populations from western African and western Kenya as well as a clear separation of eastern and western populations in Kenya using microsatellite data. A similar population genetic structure across Kenya was shown in *Anopheles funestus* Giles by Braginets *et al.* (2003), and in the tsetse fly, *Glossina pallidipes* Austen (Krafsur, 2002). A general distribution across Africa similar to *S. lamanius* is also found in the sunbird complex, *Nectarinia olivacea* (A. Smith) and *Nectarinia obscura* (Jardine) (Bowie *et al.*, 2004). For this bird species the authors found a clear genetic difference between individuals from the east African coast and individuals from the Guineo-Congolian forests. The eastern outpost of the Guineo-Congolian forest occurred in the Kakamega Forest in western Kenya (for the distribution of this sunbird in Kenya see Lewis & Pomeroy, 1989). In contrast to the situation in eastern Africa, the authors found little differentiation from Ghana to South Africa and to western Kenya. The study of Bowie *et al.* (2004) suggested that the dominant evolutionary mechanism shaping genetic variation within the *N. olivacea/obscura* complex was range expansion out of eastern Africa during a period of forest expansion in the mid-Pleistocene. But during the expansion of the range the species was not able to cross the Rift Valley system. Donnelly *et al.* (2001) also found indications of a recent expansion in eastern Africa for *Anopheles*. Thus the available data for termites, diptera and birds point to concordant phylogeographical patterns in eastern Africa. Nevertheless, we need reliable time estimates for the different taxa to evaluate whether the same processes generated the concordant patterns.

East of the arid corridor, *S. lamanius* is distributed within coastal lowland forests. These forests are fragmented and the morphometrical analyses suggest some differentiation between these coastal populations, which parallels the distribution of forest fragments. Taking into account the large geographical distance between the Ivory Coast and Uganda, the low genetic and morphometrical differentiation between samples from the Ivory Coast and Uganda is surprising. The Ivory Coast is located west of the Dahomey Gap (Fig. 1). No records of *S. lamanius* are available for the Dahomey Gap. However, during the Holocene climate optimum there was no Dahomey Gap (Salzmann & Hoelzmann, 2005). Hence, opportunities for dispersal may have occurred in the past. Moreover, the close similarity of populations from western Africa to Uganda illustrates that the species has sufficient dispersal capacity to migrate across vast distances as long as suitable habitats are available.

The populations in the Mzima and Kibwezi forests are differentiated from the coastal populations, although the genetic data are not as clear-cut as the morphometrical data. From the morphometrical point of view, individuals from the Mzima and Kibwezi forests are similar. One may argue that this is due to similar environmental conditions. But termites live in colonies and individuals of the investigated species search within galleries for food. Hence, individuals are not directly exposed to fluctuating weather conditions. Furthermore, Husseneder *et al.* (1998) found a clear correlation

between genetic and morphometrical similarity on a small spatial scale, an indication that morphology matches genetics. Therefore, populations of *S. lamanius* from the Mzima and Kibwezi forests may have a common origin.

Schedorhinotermes lamanius is a termite species in which replacement reproductives (progeny of the colony-founding sexual pair and hence related) are common (Husseneder *et al.*, 1999). A strong influence of the sociogenetic organization on dispersal and the degree of population genetic structure has been documented for several ant species (Seppa & Pamilo, 1995; Pamilo *et al.*, 1997; Goropashnaya *et al.*, 2001). Monogynous species usually show marked dispersal and little or no genetic differentiation. Polygynous species, in contrast, exhibit marked population differentiation. Restricted dispersal and gene flow is supposed to be a common characteristic in termites (Brandl *et al.*, 1996; Thompson & Hebert, 1998; Goodisman & Crozier, 2002). Nevertheless, the production of many replacement reproductives allows large colonies to separate into daughter colonies (budding). Colonies can thus not only multiply by nuptial flights but also via budding. Husseneder *et al.* (1998) found isolation by distance up to a spatial scale of 1 km, which is consistent with the importance of budding for local populations. Budding may be regarded as a strategy for an effective exploitation of small patches of resources.

Schedorhinotermes lamanius occurs within gallery forests along the Tana River. Distributional records from Tanzania also show that *S. lamanius* may protrude along gallery forests into arid regions (Kemp, 1955). During more humid periods extensive gallery forests may have allowed *S. lamanius* to follow these forests deep into arid regions. However, these dispersal corridors were not open for an exchange between populations east and west of the arid corridor during the last million years.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online from <http://www.Blackwell-Synergy.com>:

Appendix S1 Differentiation between populations of a termite in eastern Africa: morphometrical parameter and Mahalanobis distances between population centroids.

BIOSKETCHES

Lena Wilfert graduated from the University of Bayreuth and is now a PhD student at the ETH Zurich. Her current research focuses on the genetic basis and evolutionary dynamics of host–parasite interactions and on the adaptive value of recombination.

Manfred Kaib is a senior researcher at the Department of Animal Physiology, University of Bayreuth. His research interests focus on the physiology, sociobiology and biodiversity of termites in eastern Africa.

Walter Durka is a research scientist at the Department of Community Ecology of the Environmental Research Centre. In his research molecular genetic methods are applied to a range of problems in ecology and conservation.

Roland Brandl is a Full Professor at the Department of Animal Ecology, Philipps-University of Marburg. His main research fields are community ecology, population genetics and biodiversity.

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