Genetic Variation in Two African *Euprepis* Species (Reptilia, Scincidae), Based on Maximum-Likelihood and Bayesian Analyses: Taxonomic and Biogeographic Conclusions

Patrick Mausfeld-Lafdhiya[1], Andreas Schmitz[1], Ivan Ineich[2] & Laurent Chirio[2]

[1] Zoologisches Forschungsinstitut und Museum Alexander Koenig, Section Herpetology, Adenauerallee 160, 53113 Bonn, Germany

[2] Muséum national d'Histoire naturelle, Institut d'Ecologie et de Gestion de la Biodiversité, Laboratoire de Zoologie (Reptiles & Amphibiens), 25, rue Cuvier, F-75005 Paris, France

Abstract. In the present study we applied Bayesian and maximum likelihood methods of phylogenetic inference to mitochondrial 12S rRNA and 16S rRNA gene fragments to examine the degree of genetic variation within the West African *Euprepis affinis* and the widespread African *Euprepis maculilabris*. We found considerable genetic differentiation in *Euprepis affinis*, revealing a cryptic species. Similarly, we could show that *Euprepis maculilabris* is comprised of at least two distinct species, with the nominotypic form being distributed in West Africa, and a cryptic species in East Africa. We discuss biogeographical aspects and outline the relevant evolutionary processes, which probably led to allopatric speciation in *Euprepis maculilabris*. Evaluating the systematic status of *Euprepis comorensis* and *Euprepis casuarinae*, two species formerly recognized as subspecies of *E. maculilabris*, we underlined the need of further studies to clarify their taxonomic status.

Key Words: Africa – *Mabuya* – mtDNA – speciation – systematics

1. INTRODUCTION

1.1 General Remarks

Intercontinental relationships within the circumtropical genus *Mabuya* Fitzinger, 1826, are far more complex than previously thought (Mausfeld-Lafdhiya et al. 2002). Their molecular analysis has demonstrated that *Mabuya* consists of several separated evolutionary lineages, representing distinct and well-supported monophyletic radiations. To reflect the independent origins of the South American, Asian, Afro-Malagasy and Cape Verdian groups the genus *Mabuya* was partitioned into four genera, revalidating the name *Euprepis* for the Afro-Malagasy species (Mausfeld et al. 2002).

While the majority of species of the genus *Euprepis* occur in East and Southeast Africa, one can find several small high diversity centers in West and Central Africa. Probably the most important 'hotspot' seems to be Cameroon with at least 10 *Euprepis* species (LeBreton 1999; Chirio & Ineich 2000, unpubl. data). Cameroon is crossed by the Cameroon Mountain Chain, which offers a vast number of different ecological habitats, resulting in one of the most speciose herpetofaunas in Africa (LeBreton 1999). Despite extensive research done by a multitude of scientists (e.g. J.-L. Amiet, J.-L. Perret) in that country many species have not been studied in detail and in many cases consist of unresolved species complexes (e.g. Lawson 1993; Böhme & Schmitz 1996).

1.2. Taxonomic review of *Euprepis affinis*

There has been a lot of confusion about what should be regarded as the "true" *Euprepis affinis*. In 1838 Gray published a short description of *Tiliqua affinis*, based on a single British Museum specimen of unknown origin. In 1844 Hallowell described *Euprepes blandingii*. Gray (1845) described *Euprepis raddoni* from West Africa. In 1857 Hallowell described *Euprepes frenatus* from Liberia and *E. albilabris* from Gabon, but noted that the former was perhaps a variety of *E. blandingii*. Peters (1864) described *Euprepes* (*Euprepis*) *aeneofuscus* from Elmina (Ghana), du Bocage (1872) described *Euprepes gracilis* from Bissau and Fischer (1885) described *Euprepes* (*Euprepis*) *pantaenii* from Sierra Leone. Boulenger (1887) regarded *Tiliqua* and *Euprepis* as synonyms of *Mabuya*. He recognised *M. affinis* (Gray) (illustrating the type, which he indicated was in a bad state, being discoloured and without the tail). He placed all the above-mentioned forms as synonyms of *M. raddonii* (Gray), which he also illustrated (Appendix 1).

According to Loveridge (1936), Boulenger erroneously thought that both Gray's and Hallowell's papers appeared in 1845. However, it seems that Hallowell's paper appeared "on or before July 19, 1844" (Loveridge 1936). Consequently he re-established the name *blandingii*, a name that has been used by most authors since then (Mertens 1941; Loveridge 1941; de Witte 1953; Grandison 1956; Mertens 1964;

DUNGER 1972; BARBAULT 1974). But not all authors followed Loveridge's taxonomic conclusion and still used *raddoni* (MANAÇAS 1951; MONARD 1951; HELLMICH 1957). 128 years after its first description, DE WITTE (1966) used the name *affinis* (Gray) again; interestingly, he listed both *affinis* and *blandingii* from the Democratic Republic of Congo (DR Congo) (Appendix 1). Due to the fact that he could "find no characters that consistently distinguish between the West African *maculilabris* and *blandingi* (= *raddoni*)" HORTON (1973) even considered *E. blandingii* Hallowell and *E. raddoni* (Gray) as synonyms of *maculilabris*. In 1974 HOOGMOED published the only comprehensive taxonomic revision of *affinis*. He completely agreed with GRANDISON (1956), who examined the type of *affinis* (BM 1946.8.18.21/XIV 929), and who concluded that it was conspecific with the nominal species *blandingii*. Thus, HOOGMOED (1974) considered all *E. blandingii* (Hallowell, 1844) and *E. raddonii* (Boulenger, 1887) and *E. affinis* (Boulenger, 1887) as synonyms of *E. affinis* (Gray, 1838). Moreover, he regarded *E. raddonii* (Boulenger, 1887) partly as a synonym of *E. albilabris* (Hallowell, 1844). Except for LAWSON (1993), who again used the name *blandingii* Hallowell, subsequent authors followed HOOGMOED (1974) and used *E. affinis* (e.g. BÖHME & SCHNEIDER 1987; BÖHME et al. 1996; AKANI & LUISELLI 2001; BARNETT et al. 2001; HALLERMANN 2001).

1.3. Taxonomic review of *Euprepis maculilabris*

Since GRAY (1845) described *Euprepis maculilabris* from "West Africa", the taxonomy of the "*Mabuya*" *maculilabris*-group (sensu BROADLEY 1974) has been in a dynamic, unstable state (Appendix 2). The following taxa can be assigned to the *maculilabris* group: *Euprepis maculilabris*, *E. maculilabris albotaeniata*, *E. comorensis*, *E. casuarinae*, *E. boulengeri* and *E. infralineata*.

PETERS (1854) described *Euprepes comorensis* from Anjouan, Comoros and in 1882 named a variant of it from Grand Comoro *E. angasijanus*. In 1866 DU BOCAGE described *Euprepes anchietae* from Cabinda and PETERS (1879) described *E. notabilis* from Chinchixo and Pungo Androngo (Angola). In 1887 BOULENGER recognized *Mabuia comorensis* (Peters), but placed all the other described taxa in the synonymy of *M. maculilabris* (Gray). DU BOCAGE (1895) accepted Boulenger's findings and also recorded *M. maculilabris* from the islands of Principe and Sao Tome. In 1911 STERNFELD described *Mabuia boulengeri* from the Makonde Plateau in Tanzania. STERNFELD (1912) described a first subspecies of *Mabuia maculilabris* from the DR Congo, *M. m. major* and six varieties (Appendix 2). BOETTGER (1913) described *Mabuia comorensis* var. *infralineata* from Europa Island in the Mozambique

Channel, recorded typical *M. comorensis* from Mafia, Songo Songo and Zanzibar islands, and described *M. albotaeniata* from Pemba Island. In 1917 STERNFELD recorded additional material of *M. maculilabris major* from DR Congo and one specimen of the typical form without precise locality.

The first comprehensive analysis of variation in a long series of *Mabuya maculilabris* (Gray) was done by SCHMIDT (1919). He considered *Mabuia maculilabris major* and *M. m. bergeri* as synonyms of *E. maculilabris* Gray. In his view "*Mabuya maculilabris* does not seem at present divisible into subspecies. Either it has reached its present range too recently to be influenced by the environmental differences or these differences have recently been superimposed on a long established range".

BARBOUR & LOVERIDGE (1928), listed both *M. comorensis* and *M. maculilabris* for the Uluguru and Usambara Mountains, Tanzania, with *M. c. infralineata* a synonym of the former and *M. boulengeri* and *M. albotaeniata* synonyms of the latter. They hypothesized that "*maculilabris* is undergoing evolutionary differentiation, but these variations have not progressed far enough, or become sufficiently standardized, to merit racial recognition". One year later LOVERIDGE (1929) listed 11 *Mabuya maculilabris* from Uganda and one from western Kenya. He tentatively referred those USNM specimens to *maculilabris*, "for it occurs to me that they are more closely related to *comorensis* than to *maculilabris*, at the same time they are undoubtedly identical to what Boulenger called *maculilabris* from Ruwenzori". In addition, he mentioned that "they are the same as Stenfeld's [sic] *M. maculilabris major* from the Central Lake region and agree with specimens in the Museum of Comparative Zoology from Mutea on the White Nile; Rutshuru and Bumba, Belgian Congo, and Sao Thome Island, West Africa". He also recorded one specimen of *M. comorensis* from Kenya and stated that "true Cameroon *maculilabris* have 33 to 36 scale rows, while East African examples more usually have 30" (see also MERTENS 1955). In 1933 LOVERIDGE concluded that "at most *comorensis* appears to be a race of *maculilabris*", and in 1942 LOVERIDGE for the first time mentioned the subspecies *M. maculilabris comorensis* from Magrotto Mountain, northeast Tanzania, differing from "typical *maculilabris* in having 34-36 midbody scale-rows, together with a more robust build and shorter tail". LOVERIDGE (1957) tentatively placed *M. maculilabris major* with all its taxonomically recognized variations in synonymy with *M. maculilabris maculilabris* Gray (Appendix 2). He listed four subspecies: *Mabuya maculilabris maculilabris*, *M. m. albotaeniata*, *M. m. boulengeri* and *M. m. comorensis* (with *Euprepes angasijanus* and *Mabuia comorensis* var. *infralineata* as synonyms). BROADLEY (1974) published a first com-

prehensive review of the *Mabuya maculilabris* group. He refuted the subspecies status of *M. m. boulengeri*. He reinstated *M. boulengeri* as a full species, sympatric with *M. maculilabris* in southeastern Tanzania and southern Malawi. Besides listing the subspecies *M. m. comorensis*, *M. m. albotaeniata* and *M. m. infralineata*, he herein described the subspecies *Mabuya maculilabris casuarinae* from Casuarina Island off the coast of north Mozambique, which is "distinguished from all other races except *comorensis* by its high count of lamellae beneath the fourth toe (23-24) and numerous supraciliaries (6-7). It is distinguished from *comorensis* by its lower count of midbody scale rows (31-32 compared with 34-38)". According to BROADLEY (1974) "the northeast Tanzanian populations of *maculilabris*, with 34-38 midbody scale rows, previously included with *comorensis*, lack the high counts of subdigital lamellae found in true *comorensis* and are now included with typical *maculilabris*". BRYGOO (1981) reinstated *M. comorensis* as a full species, with *E. angasijanus* Peters remaining in synonymy. Additionally, mainly based on coloration differences, he elevated *M. comorensis infralineata* to species rank. Recently, BROADLEY (2000) published a review of the southeast African *Mabuya* species in which he elevated *M. casuarinae* and *M. albotaeniata* to species rank on a par with the other insular forms. For *Mabuya maculilabris* BROADLEY (2000) mentions a distribution area from "Guinea, east to Somalia, south to Angola, northern Zambia, Malawi and the northern half of Mozambique".

In the present study we apply Bayesian and maximum likelihood methods of phylogenetic inference to our data consisting of two mitochondrial gene fragments (12S and 16S) to examine the genetic differentiation within *Euprepis maculilabris* and *Euprepis affinis*. We intend to give evidence for the existence of full species complexes under the name of these two *Euprepis* taxa without the claim of a comprehensive systematic revision, which will be done separately.

2. MATERIAL AND METHODS

We obtained DNA sequence data from nineteen *Euprepis* specimens representing seven nominal species. Considering the broad distribution area of *Euprepis affinis* in Central and West Africa and of *Euprepis maculilabris* from Sao Tome in the West to Kenya and Mozambique in the East, we here concentrate on selected populations emphasizing the degree of variability in the corresponding species, without covering populations over the entire distribution area. Thus, in order to elucidate phylogenetic affinities and the degree of genetic variation within *Euprepis affinis* we included five *E. affinis* specimens (one from Guinea-Bissau and four from Cameroon). Additionally, two cf. *affinis* from Cameroon were also included in the analysis. As many authors considered *E. albilabris* a synonym of *E. af-*

finis (e.g. BOULENGER 1887; SCHMIDT 1919; MANAÇAS 1951), we included two *albilabris* specimens in the analysis, one from Cameroon and one from Uganda. To assess the degree of genetic variation within *Euprepis maculilabris* we included four *maculilabris* specimens, two from Cameroon and two from Tanzania. Additionally, we included *Euprepis comorensis* (Nosy Tanikely, Madagascar), formerly considered a subspecies of *maculilabris*. Furthermore, we added three *Euprepis perroteti* specimens, *E.* cf. *irregularis* (Uganda) and *E.* sp. nov. (Cameroon) to the data set. *Mabuya agilis* and *Scelotes mirus* were used as outgroups.

All voucher specimens used in the present study, with their localities, collection numbers and accession numbers are listed in Tab. 1. A map indicating the localities of the specimens included in our study is shown in Fig. 1. DNA was extracted from the tissue samples using QuiAmp tissue extraction kits (Quiagen). The primers 16sar-L (light chain; 5' – CGC CTG TTT ATC AAA AAC AT – 3') and 16sbr-H (heavy chain; 5' – CCG GTC TGA ACT CAG ATC ACG T – 3') of PALUMBI et al. (1991) were used to amplify a section of the mitochondrial 16S ribosomal RNA gene. PCR cycling procedure was as follows; an initial denaturation step of 90 s at 94°C followed by 33 cycles of denaturation for 45 s at 94°C, primer annealing for 45 s at 55°C and extension for 90 s at 72°C. Additionally, a section of the mitochondrial 12S ribosomal RNA gene was amplified using the primers 12SA-L (light chain; 5' – AAA CTG GGA TTA GAT ACC CCA CTA T – 3') and 12SB-H (heavy chain; 5' – GAG GGT GAC GGG CGG TGT GT – 3') of KOCHER et al. (1989). Cycling procedure was as follows: 35 cycles of denaturation 45 s at 94°C, primer annealing for 60 s at 50°C and extension for 120 s at 74°C (12S).

PCR products were purified using Qiaquick purification kits (Qiagen). Sequences were obtained using an automatic sequencer (ABI 377). The obtained sequences (lengths referring to the aligned sequences including gaps) comprised 550 bp (16S), and 398 bp (12S). Sequences have been submitted to GenBank.

Sequences were aligned using ClustalX (THOMPSON et al. 1997; default parameters). The alignment was subsequently adjusted manually using the program Se-Al 1.0a1 (RAMBAUT 1996). We explored the quality of our alignment by varying alignment gap opening cost (6, 9, 15) and comparing alignments. In the 12S data no ambiguously aligned regions could be detected, while in the 16S data set three ambiguously aligned regions of a total of 55 bp were found; these sites were excluded from further analyses (GATESY et al. 1993; MILINKOVITCH & LYONS-WEILER 1998). The complete alignment is available from the authors upon request.

To determine the statistical validity of combining the 16S and 12S data sets for phylogenetic analyses, we performed the partition homogeneity (PH) test. We used PAUP*4.0b10 (SWOFFORD 2002) to generate a null-distribution of length differences using 1000 same-sized, randomly generated partitions from the original data with replacement.

Tab. 1. List of voucher specimens included in the present study, with their respective localities, collection numbers and accession numbers (12S, 16S)

Species	Locality	Collection number	Accession number
Scelotes mirus	Malolotja Reserve, Swaziland	Voucher not collected	AF153559, AF153586
Mabuya agilis	Maricá, Rio de Janeiro, Brazil	MNRJ 9561	AF548796, AF549184
Euprepis affinis	Ilha Bubaque, Guinea Bissau	ZFMK 62376	AF202622, AF202627
affinis	Benakuma, West of Wum, Cameroon	MNHN 2002.742	AY159105, AY159118
affinis	Benakuma, West of Wum, Cameroon	MNHN 2002.743	AY159106, AY159119
affinis	Bridge over River Bagwor, Fontem, Cameroon	MNHN 2002.746	AY159107, AY159120
affinis	Jully Hotel, North of Kribi, Cameroon	MNHN 2001.108	AY159109, AY159122
cf. *affinis*	Ngoulemakong, NE of Ebolowa, Cameroon	MNHN 2002.745	AY159103, AY159116
cf. *affinis*	Benakuma, West of Wum, Cameroon	MNHN 2002.744	AY159104, AY159117
albilabris	Mt. Ruwenzori, Semliki NP, Uganda	ZFMK 63296	AY070331, AY070350
albilabris	Kika, East of Moloundou, Cameroon	MNHN 2001.103	AY159102, AY159115
perroteti	Abuko Wildlife Reserve, Gambia	ZFMK 51844	AY159101, AF153578
perroteti	Crossroads Hina-Moufou, Cameroon	MNHN 2001.110	AY159100, AY159114
cf. *perroteti*	Tchabal Mbabo, Cameroon	Voucher not collected	AY159099, AY159113
spec. nov	Hossere Ngang-Ha , Cameroon	MNHN 2002.0747	AY159108, AY159121
cf. *irregularis*	Mt. Elgon, Uganda	ZFMK 66631	AY070329, AF153571
cf. *maculilabris*	Amani, Usambara Mts., Tanzania	ZFMK 74514	AY070338, AY070356
cf. *maculilabris*	Tanzania	Voucher not collected	AY159112, AF153574
maculilabris	Afan, NE of Ma'an, Cameroon	MNHN 2000.5199	AY159110, AY159123
maculilabris	Benakuma, West of Wum, Cameroon	MNHN 2000.5200	AY159111, AY159124
comorensis	Nosy Tanikely, Madagascar	ZFMK 62192	AY070328, AF153565

Codens: ZFMK for Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, MNHN for Muséum national d'Histoire naturelle, Paris, and MNRJ for Museu Nacional, Rio de Janeiro.

Prior to phylogenetic reconstruction, we tested for homogeneity of base frequencies among taxa using the χ^2 test as implemented in PAUP*4.0b10 (which ignores correlation due to phylogenetic structure): (1) over all sites, (2) over parsimony-informative sites only, (3) without constant sites (parsimony-uninformative and constant sites will mislead the χ^2 test (MISOF et al. 2001). All phylogenetic reconstructions were conducted with the combined data set of the 16S and 12S gene fragments.

Maximum likelihood analysis. – All maximum likelihood analyses (FELSENSTEIN 1981) were performed with PAUP*4.0b10 (SWOFFORD 2002). In order to compare the results obtained via maximum likelihood and Bayesian analyses, a hierarchical likelihood-ratio test was carried out using MRMODELTEST 1.1b (NYLANDER 2002), a simplified version of MODELTEST (POSADA & CRANDALL 1998, 2001), selecting the best-fit model of nucleotide substitution for our data set. The model parameters (substitution parameters, shape of gamma distribution, proportion of invariable sites) were estimated from the data set, without sites containing gaps (AGUINALDO et al. 1997). The ML tree was calculated with the parameter estimates obtained under the best-fit model. A heuristic search was made with 10 replicates of random stepwise addition and tree bisection-reconnection (TBR) branch-swapping. The

relative branch support of the phylogenetic analyses was evaluated with 100 bootstrap pseudoreplicates (gap-sites excluded, heuristic search, random addition of taxa with 10 replicates, TBR branch-swapping).

The existence of phylogenetic signal was assessed by calculating the skewness, or g1 statistic (implemented in PAUP*), which provides a measure of phylogenetic information content (HILLIS & HUELSENBECK 1992). We produced 1000 randomly generated ML trees for (with outgroup excluded; settings for ML identical to the one described above).

A matrix of pairwise sequence differences for the combined 16S and 12S rRNA genes was calculated using the p-distance.

Bayesian analyses. – All Bayesian analyses (RANNALA & YANG 1996; LARGET & SIMON 1999; MAU et al. 1999; LI et al. 2000; HUELSENBECK et al. 2001) were performed with MRBAYES, version 3.0b1 (HUELSENBECK & RONQUIST 2001), which approximates the posterior probabilities (PP) of trees. The program uses a variant of Markov chain Monte Carlo (MCMC), Metropolis-coupled MCMC (GEYER 1991), which is less prone to entrapment in local optima than is normal MCMC (METROPOLIS et al. 1953; HASTINGS 1970; GREEN 1995).
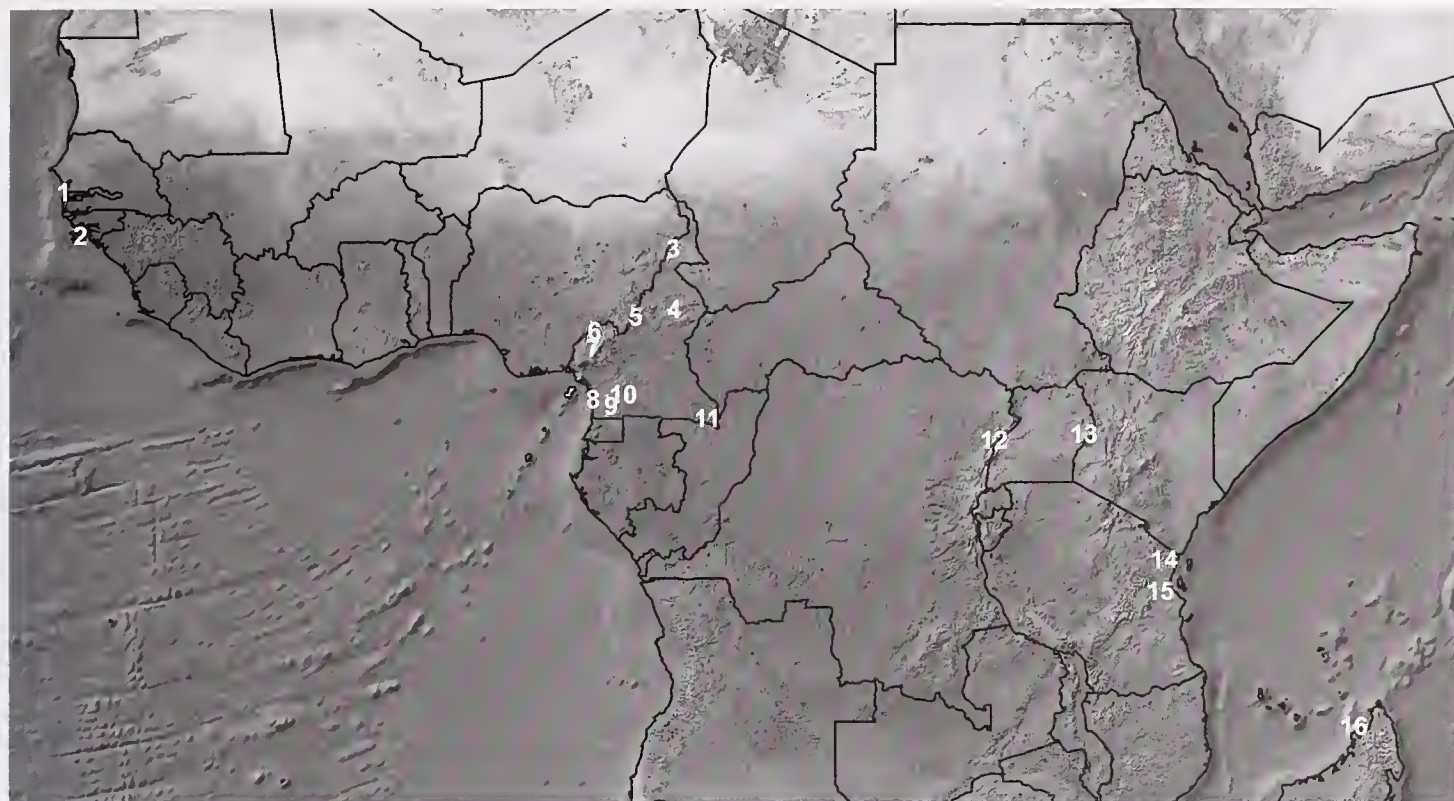
Fig. 1. Map showing the localities of the ingroup-specimens included in the present study. Locality names are as follows: (1) Abuko Wildlife Reserve (*Euprepis perroteti*), Gambia, (2) Ilha Bubaque (*Euprepis affinis*), Guinea Bissau, (3) Crossroads Hina-Moufou (*Euprepis perroteti*), Cameroon, (4) Hossere Ngang-Ha (*Euprepis* spec. nov.), Cameroon, (5) Tchabal Mbabo (*Euprepis* cf. *perroteti*), Cameroon, (6) Benakuma (*Euprepis affinis, Euprepis* cf. *affinis*), Cameroon, (7) Bridge over River Bagwor (*Euprepis affinis*), Cameroon, (8) Jully Hotel (*Euprepis affinis*), North of Kribi, Cameroon, (9) Afan, Cameroon, (10) Ngoulemakong (*Euprepis* cf. *affinis*), Cameroon, (11) Kika (*Euprepis albilabris*), Cameroon, (12) Semliki NP (*Euprepis albilabris*), Mt. Ruwenzori, Uganda, (13) Mt. Elgon (*Euprepis* cf. *irregularis*), Uganda, (14) Amani (*Euprepis* cf. *maculilabris*), Usambara Mts., Tanzania, (15) Tanzania (*Euprepis* cf. *maculilabris*), without exact locality given, (16) Nosy Tanikely (*Euprepis comorensis*), Madagascar.

To select the best-fit model of nucleotide substitution for our data set (with all gaps excluded from the analysis), the hierarchical likelihood-ratio test was carried out using MRMODELTEST 1.1b (NYLANDER 2002). Consequently, the settings of MRBAYES were specified according to the results of MRMODELTEST. Besides the specific parameters calculated by MRMODELTEST, the default settings of MRBAYES were used. We ran two MCMC analyses for 10^6 generations each. Each chain consisted of one cold and three heated chains and the Markov chains were started from a random tree. The Markov chains were sampled every 100th generation, resulting in 10,000 sampled trees from each chain. The initial 1,000 (10%) trees were disregarded as "burn-in" (the portion of the chain that was sampled before stationarity was reached). Inferences, then, were based on the 9,000 trees samples from each chain. The topologies were used to generate a strict-consensus tree, with the percentage of samples recovering any particular clade representing that clade's posterior probability (HUELSENBECK & RONQUIST 2001). Unlike the non-parametric bootstrap values of the ML analysis, these are the true probabilities of the clades under the assumed model (RANNALA & YANG 1996). Consequently, we consider probabilities of 95% or greater to be significantly supported.

3. RESULTS

The PH test failed to detect significant incongruence between the two data sets (p = 0.16), suggesting the two mtDNA fragments could be combined. The resulting combined data set (16S and 12S rRNA gene fragments) included a total of 865 characters. The matrix for the uncorrected p-distances for all nucleotide sites is presented in Appendix 3.

In the data set a phylogenetic signal is clearly present (ML: g1 = − 1.1169, p = 0.01). When all characters were included, we found no significant deviation from the homogeneity of base frequencies among taxa (χ^2 = 12.8664, p = 1.0000, df = 60). The same was true for the parsimony-informative sites only (χ^2 = 53.8529, p = 0.6985, df = 60) and without constant sites (χ^2 = 39.5078, p = 0.9811, df = 60).

The comparison between the different likelihood scores for each model showed that the GTR + I + G model (YANG 1994) was the most appropriate model that fit our data set. This model incorporates unequal base frequencies [$\pi_{(A)}$ = 0.3468, $\pi_{(T)}$ = 0.2053, $\pi_{(C)}$ = 0.2590, $\pi_{(G)}$

= 0.1889], and takes into account the proportion of in-variable sites (I = 0.5181), and the gamma distribution shape parameter (α = 0.6781).

Tab. 2. Parameter estimates of the substitution model (GTR + I + Γ), sampled after the burn-in phase of the chain. The columns indicate the parameter, mean and 95% credible interval for the parameter. The parameters are TL, the tree length; r_{ij}, rate of substitution between nucleotides i and j measured relative to the rate between G and T (r_{GT} =1); π_i, base frequencies; α, gamma shape parameter for among-site variation; and *Pinvar.*, proportion of invariable sites. Upper values in each pair correspond to the 1. run; lower values correspond to the 2. run.

Parameter	Mean	95% Credity Interval
TL	1.15	(0.92, 1.47)
	1.16	(0.93, 1.46)
r_{GT}	1.00	
	1.00	
r_{CT}	38.58	(20.41, 49.58)
	38.38	(20.53, 49.63)
r_{CG}	0.84	(0.11, 2.16)
	0.81	(0.10, 2.03)
r_{AT}	3.71	(1.62, 6.47)
	3.62	(1.69, 6.11)
r_{AG}	14.44	(7.09, 23.59)
	13.95	(7.23, 26.28)
r_{AC}	4.47	(2.15, 7.24)
	4.49	(2.18, 7.58)
π_A	0.338	(0.310, 0.367)
	0.339	(0.310, 0.368)
π_C	0.262	(0.237, 0.287)
	0.261	(0.235, 0.287)
π_G	0.192	(0.170, 0.218)
	0.193	(0.168, 0.219)
π_T	0.208	(0.185, 0.232)
	0.208	(0.184, 0.233)
α	0.593	(0.292, 1.155)
	0.574	(0.278, 1.097)
Pinvar.	0.499	(0.327, 0.623)
	0.492	(0.306, 0.619)

Both the ML and the Bayesian approaches produced identical topologies. Fig. 2 shows the ML tree (with lnL = -3437.70) and the strict consensus tree of the 18,000 trees sampled from both chains, with the ML bootstrap values above the nodes and the posterior probabilities (if not identical, for the first and the second run) below the nodes. Tab. 2 provides the estimates of the substitution parameters calculated by MRBAYES. The two independent MCMC runs converged on similar log-likelihood scores and reached stationarity no later than 100,000 generations (Fig. 3). The posterior probability (PP) values supporting congruent nodes between the

two runs were highly correlated (Fig. 2), further indicating that the analyses converged.

Our analyses revealed two separate, well supported monophyletic *Euprepis* "*affinis*"-clades, one comprising all *affinis* specimens (ML: 86; PP: 1.00) and one comprising the two cf. *affinis* specimens (ML: 95; PP: 1.00). The results indicate *perroteti* being the sister species of *affinis* (ML: 54; PP: 0.85). While the ML analysis supports with a low bootstrap value the clade comprising *Euprepis* cf. *affinis*, *albilabris*, *perroteti* and *affinis* (ML: 74), the posterior probability of the Bayesian analysis revealed significant support for this group being monophyletic (PP: 1.00).

Regarding the systematics of *Euprepis maculilabris*, the analyses revealed strong support for a monophyletic group, comprising all *maculilabris* specimens and *Euprepis comorensis* (ML: 83; PP: 1.00). Within this clade we found two significantly distinct clades, a *maculilabris* clade including the two specimens from West Africa and another *maculilabris* clade including the two specimens from East Africa (ML: 94; PP: 1.00). *Euprepis comorensis* is the sister species of the east African *maculilabris* (ML: 74; PP: 0.81, 0.79).

Finally, the clade containing all three *Euprepis perroteti* specimens (ML: 90; PP: 1.00) and the clade including the *Euprepis* cf. *irregularis* and *E.* sp. nov. (ML: 100; PP: 1.00) are very well supported in both ML and Bayesian analyes.

Genetic variation within the *affinis* clade varies from 0.4% between the Bagwor *affinis* and the Benakuma *affinis* (MNHN 2002.742) to 2.7% between *affinis* Guinea-Bissau and the Benakuma *affinis* (MNHN 2002.743) (Appendix 3). The two haplotypes of the cf. *affinis* clade vary in 0.9%. Genetic differentiation between the *affinis* and the cf. *affinis* clade ranges from 3.8% between *affinis* Guinea Bissau and the Benakuma cf. *affinis* (MNHN 2002.744) to 5.5% between the Benakuma *affinis* (MNHN 2002.742) and the Ngoule-makong cf. *affinis* (MNHN 2002.745).

The two southeastern *maculilabris* specimens differ in 0.8%, and 2.7% from *comorensis*. The two *maculilabris* from Cameroon differ in 0.9% from each other, but in 4.1% and 4.8% from the two southeastern *maculilabris*.

The genetic difference between the three *Euprepis perroteti* specimens ranges from 3.9% to 4.4%. Regarding the new *Euprepis* species included in our analysis, the present results show strong support for this new Cameroon species being the sister species to the Uganda cf. *irregularis* (ML: 100; PP: 1.00); they show a genetic differentiation of 4%.
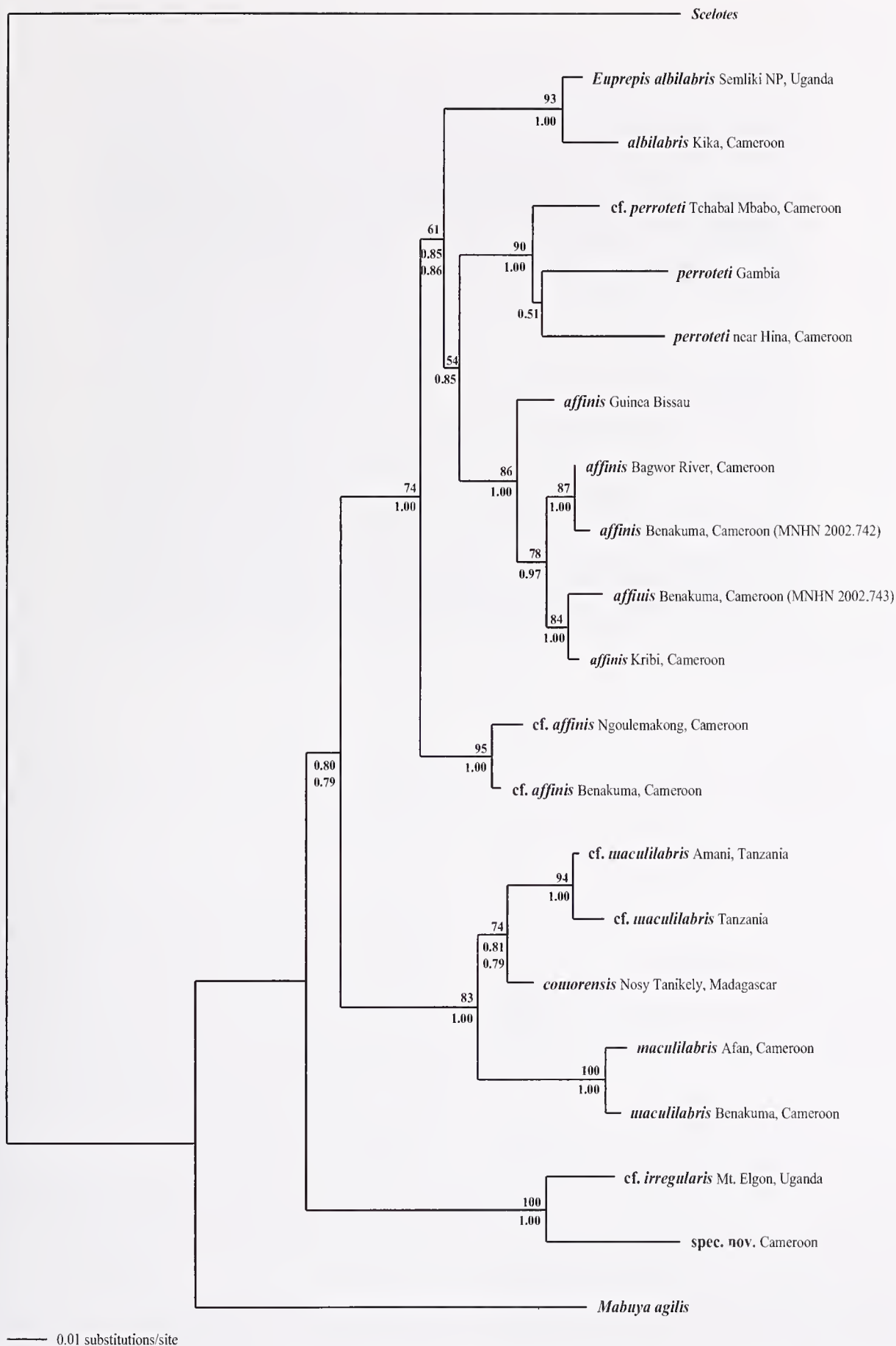
—— 0.01 substitutions/site

Fig. 2. Phylogram of the maximum-likelihood and Bayesian analyses using *Mabuya agilis* and *Scelotes mirus* as outgroup. Numbers above nodes represent bootstrap proportions for 100 pseudoreplicates for maximum-likelihood analysis. Bootstrap proportions of less than 50% are not shown. Numbers below nodes represent posterior probabilities values (if not identical, for the first and the second run, respectively).
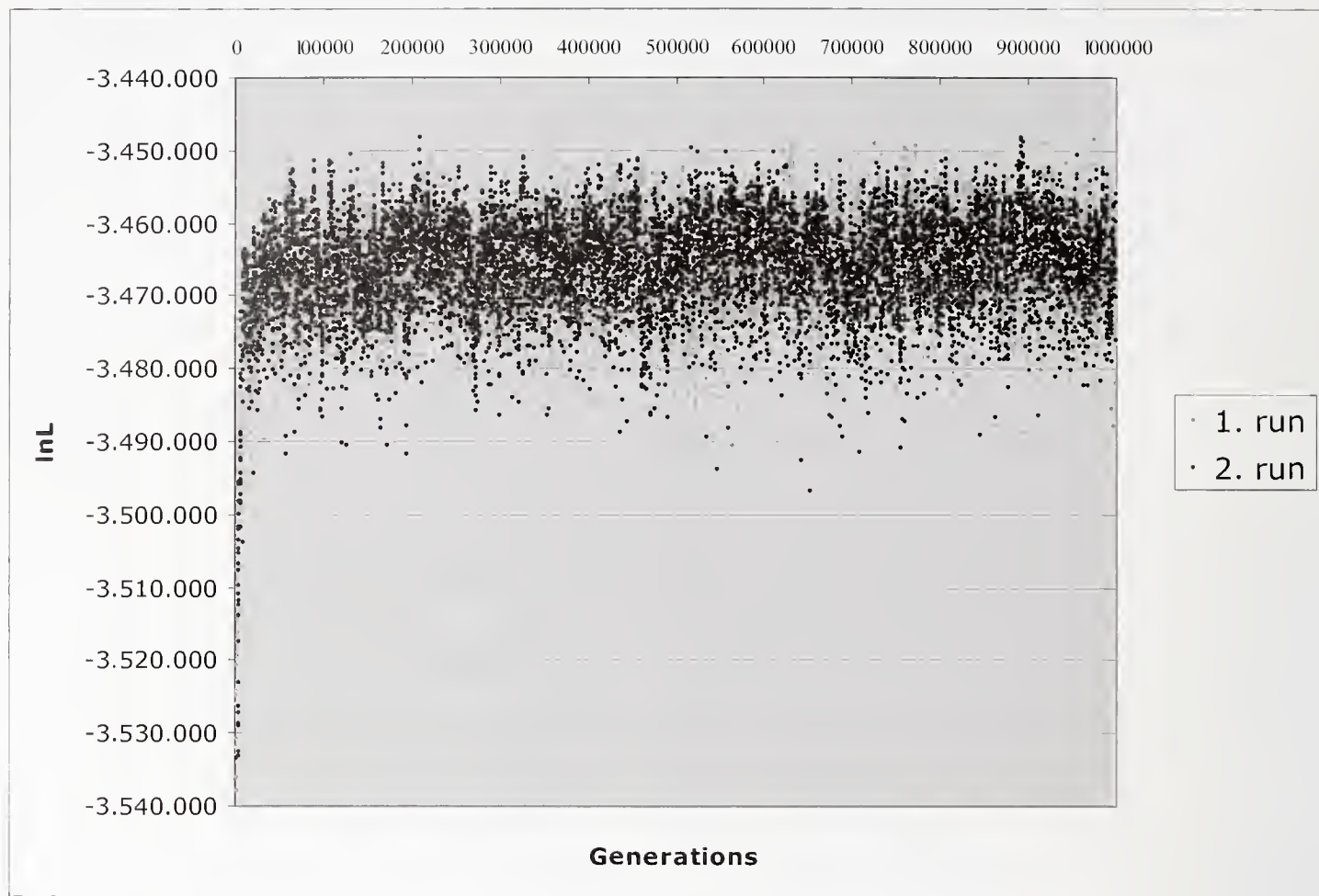
Fig. 3. The log probability of the observed DNA sequences through time for both of the chains run in this study. Each chain started from a different random tree. The samples taken from the first 100,000 generations were discarded as the burn-in for the chain, and inferences are based on samples from the remaining parts of the chain.

4. DISCUSSION

4.1. Systematics of *Euprepis affinis*

Our analyses of the genetic variation within *Euprepis affinis* revealed that *E. affinis* comprises two genetically separated species (Fig. 2). Since GRAY (1838) based his description of *Euprepis affinis* on only one specimen of unknown origin, here we cannot clarify which of the two distinct *affinis* clades represents the nominotypic *Euprepis affinis* (Gray). Considering that Grandison examined the type of *affinis* (BM 1946.8.18.21/XIV 929) (HOOGMOED 1974) and concluded that it was conspecific with the nominal species *blandingii*, a species described from Gabon, we only can state that *affinis* represents an *Euprepis* species, which occurs from Guinea-Bissau to Gabon. Because one clade, herein named *affinis*, comprises *affinis* specimens over a large distribution area (at least Guinea-Bissau to Cameroon; see Tab. 1), whereas the other clade, named cf. *affinis*, only includes two cf. *affinis* from mountainous regions in Cameroon, we consider the well-supported monophyletic group (ML: 86; PP: 1.00) of the specimens

named *affinis* provisionally as the nominotypic *Euprepis affinis* Gray, 1845, whereas the specimens named cf. *affinis* probably represent a cryptic, yet undescribed species. But only a direct comparison of *affinis* and cf. *affinis* with the type specimen will allow to assign one of these two species to true *affinis* (Gray) and to describe this new species properly. However, both ML and Bayesian analyses indicate that *affinis* and cf. *affinis* do not even represent direct sister species. We cannot be sure which taxa represents the direct sister species of *affinis*, but both trees show *perroteti* to be the most probable candidate. Genetic distances (Appendix 3) clearly support the distinct separation of *affinis* and cf. *affinis*. Whereas on one hand within true *affinis* we found a genetic variation from 0.4% to maximal 2.3% (between the Guinea-Bissau specimen and the one from Bena-kuma (MNHN 2002.743)) and on the other hand a genetic variation of only 1% could be found between the two included cf. *affinis*, we detected a genetic differentiation of at least 3.8% between *affinis* and cf. *affinis*. Considering genetic differences found within different scincid genera (DANIELS et al. 2002; MAUSFELD et al.

2002; MAUSFELD & SCHMITZ 2003; SCHMITZ unpubl.), the observed genetic differences between *affinis* and cf. *affinis* support their distinctness as species. Besides the molecular evidences for considering cf. *affinis* as a full species, zoogeographically, the sympatric occurrence of *affinis* and cf. *affinis* in Benakuma gives also supports the hypothesis of two distinct species being included under the name *affinis*.

Regarding the former consideration of *Euprepis albilabris* as a synonym of *Euprepis affinis* (e.g. BOULENGER 1887; BOETTGER 1888; SCHMIDT 1919) the results presented here, together with the observed genetic differentiation of at least 4.1% between *E. albilabris* and *E. affinis* confidently show that the present status of *E. albilabris* as full species is justified.

Another surprising and thus noteworthy result of the present analysis is the discovery that the widespread *Euprepis perroteti* may well be comprised of at least 3 distinct species. The three in the analysis included specimens form a well-supported monophyletic group (Fig. 2; ML: 90; PP: 1.00), but show a genetic differentiation of at least 3.4% between cf. *perroteti* from the Tchabal Mbabo, Cameroon, and the Gambian *perroteti*. Such high genetic differences emphasize the need of further studies of the *Euprepis perroteti* complex and of the speciation processes, which might have led to this genetic differentiation. Considering that *perroteti* is a predominantly savannah species, former climate changes (e.g. in the Pleistocene, a period of fluctuating wet periods – relatively short fluvials – and dry periods – relatively long interfluvials) could have played an important role for speciation events in *Euprepis perroteti*. CHABANAUD (1921) already described a subspecies of *perroteti* from Kerouane, Guinea, *perroteti keroanensis* [but sympatric with the typical form], which up to now has been considered valid (BRYGOO 1985). As Gambia is surrounded by Senegal, the type locality of true *perroteti* (DUMÉRIL & BIBRON 1839), it is likely that the Gambian specimen used in the present study represents the typical form. DE WITTE (1953) described *M. perroteti upembae* from the Upemba National Park in the southeast DR Congo, but LOVERIDGE (1956) considered this form a synonym of *M. planifrons* (Peters), which he had recorded from northern Zambia in 1933. This underlines the need for a comprehensive analysis of the *perroteti – planifrons* complex throughout its entire range.

Furthermore, it is interesting to note the strongly supported sister relationship between *Euprepis* cf. *irregularis* and *Euprepis* sp. nov. (Fig. 2; ML: 100; PP: 1.00).

Described from Soy (1935 m), Mt. Elgon (Kenya), BROADLEY (1977) stated that *Euprepis irregularis* (LÖNNBERG 1922) occurs in montane grassland (above 3000 m) areas of Kenya and adjacent Uganda. The series of 18 specimens of cf. *irregularis* in the collection of the ZFMK is exceptional in lacking the diagnostic character of the frontonasal "broken up in three fully separated pieces" and the supralabial separated from the eye by a subocular (LÖNNBERG 1922). Even though the collection locality "Mt. Elgon" remains, because of the two above-mentioned significant differences it seems likely that our cf. *irregularis* represents a distinct, yet undescribed species. Even though GREER (pers. com.) believes the presence or absence of a subocular scale (dividing eye and supralabial) could characterize different evolutionary sublineages, we still find so many similarities between these two sympatric species, that we tentatively continue to use the term cf. *irregularis*. Both cf. *irregularis* and sp. nov. represent montane species with both being restricted to quite small areas. Thus, the strongly supported sister relationship between the Cameroon montane *Euprepis* sp. nov. (Hossere Ngang-Ha, Adamaoua Plateau) and the montane *Euprepis* cf. *irregularis* from Uganda, is zoogeographically remarkable. And the observed genetic divergence of 4% between those two species further supports that these specimens represent two distinct species. Interestingly, a convergent example to the situation just described above has recently been discovered. CHIRIO & INEICH (2000) described *Euprepis mekuana* from Mount Mekua in Cameroon, at an altitude between 2550 and 2700 m. They considered this new species to be closely related to a widespread east African montane species, *Euprepis megalura* (Peters, 1878). Our, yet unpublished molecular data could confirm that *mekuana* is the direct sister species of *Euprepis megalura*, a species, described from the Taita Hills in Kenya and for which SPAWLS & ROTICH (1997) mention a typical altitude of 1600 m and above. Besides the molecular evidences, the fact that both *megalura* and *mekuana* have smooth dorsal scales, a character found in no other *Euprepis* species except *laevis* (for which even a new genus has been proposed (STEYN & MITCHELL 1965)), strongly support this finding.

4.2. Systematics of *Euprepis maculilabris*

Our analysis revealed that *Euprepis maculilabris* consists of at least two distinct species. Our results show a clear separation between the western *maculilabris* populations and the clade formed by the eastern *maculilabris* populations plus *Euprepis comorensis* (Fig. 2). Since *maculilabris* was originally described from West Africa, the West African form represents the nominotypic *maculilabris* whereas the East African forms are considered to represent a cryptic species (further the term cf. *maculilabris* will be used in regard to the East African populations).

To investigate speciation events that have led to the origin of a new species several biogeographic aspects should be considered. Physiogeographically, the African Massif can be divided into Low Africa (<900m) and High Africa (>900m) (O'BRIEN & PETERS 1999). Within Low Africa, the nominotypic *maculilabris* is likely to be restricted to the subcontinental section of Mid-Africa (see O'BRIEN & PETERS 1999) while cf. *maculilabris* seems to be restricted to the East Africa. Looking at the climatic conditions in these two different regions, one can find that the area of nominotypic *maculilabris* is mainly characterized by a humid-equatorial diurnal climate with rain more-or-less year-around (tropical lowland rainforest), whereas in the East Africa, the area of the new species, equatorial bimodal-rain climate with two marked dry seasons is particularly pronounced (O'BRIEN & PETERS 1999).

It seems likely that the actual speciation process has taken place in the Plio-Pleistocene, a period of important changes in climate and vegetation.

Existing evidence strongly suggests that northern and equatorial Africa's climate was generally wetter during the Middle and Late Pleistocene (e.g. WILLIAMSON 1985; YEMANE et al. 1985; DUPONT & LEROY 1995). Less mesic, and in some cases arid, conditions appear after 2 Myr. (e.g. LEROY & DUPONT 1994). According to AXELROD & RAVEN (1978), the modern flora of Africa was virtually fully established by the Late Miocene/Early Pliocene. Apparently, nearly all Africa was vegetated in the Pliocene. The extensive deserts we know today apparently did not exist. In the equatorial region, rainforest associated with the humid equatorial-diurnal climate and the Guinea-Congolian phytochorion is thought to have extended uninterrupted from West Africa (no Dahomey gap) to what is now the Eastern rift belt, plus farther north and south of its present-day position. This type of forest probably also extended south-eastward into parts of southern Tanzania and northern Mozambique, where it graded into coastal forest (relict forests from this period are still found in the Uluguru and Usambara Mountains) (O'BRIAN & PETERS 1999). Until the Late Pliocene, there were no major mountain ranges in what is now the Western Rift Belt. Thus, wet prevailing westerly windflow would have been uninterrupted in the equatorial region up to the volcanic highlands of the Eastern Rift Belt. These conditions support the hypothesis that the ancestor of *maculilabris* in West Africa and the cf. *maculilabris* in East Africa had a continuous distribution area from tropical East to West Africa. The evidences above suggest that there were no major geographical barriers at that time. An example for the changing climatic conditions in the Pliocene of Africa and its effects on the faunal community is the appearance of large grazers among bovid taxa around 2.5 Myr. This suggests that open savanna or grassland conditions had become more prevalent (VRBA 1985, 1992). *Equus* species entered and spread rapidly through Africa at about this time (BERNOR & ARMOUR-CHELU 1999). Among geladas, a specialized grazer replaced a leaf-browsing form (BENEFIT 1999).

In the Pleistocene and the previous transitional period climatic changes and subsequent vegetation changes occurred (MAYR & O'HARA 1986). These changes are of fundamental importance, and might have led to allopatric speciation within *maculilabris*. Together with the later uplift of the Eastern Rift belt, these changes definitely led to the fragmentation of the originally continuous distribution area and habitat changes. VRBA (1999) could show that strong habitat changes are causally associated with significant evolutionary changes, and more nearly constant habitats are associated with stable evolutionary lineage. Disruption of habitats and species by geographical fragmentation and by qualitative changes within habitats is needed for speciation (VRBA 1999). The situation we now found in *maculilabris* underlines such findings. The biogeographic scenario described above would result in a distribution area of the nominotypic *maculilabris* along the tropical belt from Guinea-Bissau in the North and Angola in the South to the East African Rift Belt. Other yet unpublished data shows that the *maculilabris* populations from the Republic of Congo (Congo-Brazzaville) clearly belong to the West African *maculilabris* clade shown in Fig. 2. Nevertheless, the publications of STERNFELD (1912, 1917), with the descriptions of a subspecies and several variations, indicate that the Central African *maculilabris* populations (DR Congo) might need further investigations.

Another relevant biogeographic aspect, which probably led to speciation processes as herein revealed, is the so called "drought corridor" (BALINSKY 1962), an area extending across the continent from north east to south west Africa where monthly rainfall is <10 mm in at least 3 consecutive months. BALINSKY (1962) suggested that "during cold and wet periods the rainforests must have expanded and closed the drought corridor completely, or at least narrowed it, enabling the animals of the wet tropics to migrate from west to east (and from east to west)". BIGALKE (1972) points out that a number of mammal and bird species have a discontinuous distribution in south western and north eastern Africa which tends to support Balinsky's concept. Our finding that the *maculilabris* in West and Central Africa represents species differing from cf. *maculilabris*, occurring in East Africa, would further support this concept. HORTON (1973) already based his argumentation on Balinsky's theory, when he hypothesized that the radiation of the *Euprepis perroteti-brevicollis* group (which Horton considers to have given rise to *maculilabris*) started in north-east/middle-east Africa at a time when

the entire area was considerably wetter and more heavily forested than it is now. When conditions became hotter and drier in northern, eastern and southern Africa, the nominotypic *maculilabris* became restricted to the wet areas of West Africa. Following HORTON (1973) the East African cf. *maculilabris* populations still represent the basic stock of which the western *maculilabris* got separated by allopatric speciation processes.

Regarding the taxonomy of *Euprepis comorensis*, a former subspecies of *Euprepis maculilabris* (e.g. LOVERIDGE 1942; BROADLEY 1974), our molecular results raise some doubt about the species status of *comorensis*. Our findings indicate the close affinity between *comorensis* and *maculilabris* (Fig. 2). However, considering *comorensis* represents a species with an exceptionally insular distribution (allopatric populations), a genetic differentiation of maximal 2.6% from cf. *maculilabris* indicates that a reevaluation of the taxonomic status of *comorensis* should be subject to further studies. In the framework of our study we also wanted to scrutinize the taxonomic status of *Euprepis casuarinae*, another former subspecies of *Euprepis maculilabris* (BROADLEY 1974, 2000). In order to do so, we used the only available 12S mtDNA sequence of *Euprepis casuarinae* from Fogo Is., Mozambique, deposited in Genbank by CARRANZA et al. (2001). The direct comparison of the 12S sequences revealed that *casuarinae* is 100% identical to our *comorensis* from Nosy Tanikely, Madagascar. Consequently, the populations from Fogo Is. represent *Euprepis comorensis*. This on the other hand raises reasonable doubt about the taxonomic status of the *Euprepis* populations on Casuarina Is., which is situated only less than 50 km northeast of Fogo Island. In his description of *Euprepis maculilabris casuarinae* BROADLEY (1974) found the number of midbody scales the only character that differentiate *comorensis* and *E. m. casuarinae*: *E. m. casuarinae* "is distinguished from *comorensis* by its lower count of midbody scale rows (31-32 compared with 34-38)". Later, BROADLEY (2000) erected *casuarinae* to species level, but without additional explanation. He hypothesized that "it seems likely that all the islands were colonized independently by ancestral specimens rafting from the mainland on floating trunks".

Together with the fact that BRYGOO (1981) already listed several *comorensis* specimens with 32 midbody scale rows from Grand Comore and Mohéli, Comoros, our findings indicate that the species rank of *casuarinae* might not be justified. However, a detailed morphological as well as molecular comparison of the *Euprepis* populations from Casuarina Is. and all the islands in the Comoro archipelago should help to clarify the systematic affinities of these populations. On the basis of these results a further analysis of the insular taxa *Euprepis infralineata* from Europa Is., Mozambique Channel, an-

other former subspecies of *E. maculilabris* (BRYGOO 1981), and *Euprepis maculilabris albotaeniata* from Pemba Is., Mozambique, seems necessary. In this framework of investigating the taxonomic status of *Euprepis casuarinae*, we also used another 12S sequence of CARRANZA et al. (2001), referred to as *Euprepis maculilabris maculilabris*, from Mozambique. A direct comparison of this sequence with our cf. *maculilabris* from Amani, Tanzania, revealed a 27 bp-difference between these two specimens, which is equivalent to a genetic divergence of 7.2%, indicating that another cryptic species of the cf. *maculilabris* group can be found in Mozambique.

REFERENCES

AGUINALDO, A. M., TURBEVILLE J. M., LINFORD L. S., RIVERA M. C., GAREY J. R., RAFF R. A. & LAKE J.A. (1997): Evidence for a clade of nematodes, arthropods and other moulting animals. Nature **387**: 489-493.

AKANI, G. C. & LUISELLI, L. (2001): Some observations on diurnal activity patterns, habitat, and natural history of *Mabuya affinis* (Scincidae) in the Niger Delta, Nigeria. Herpetological Bulletin **73**: 2-7.

AXELROD, D. I. & RAVEN, P. H. (1978): Cretaceous and tertiary vegetation history of Africa. Pp. 77-131 in: WERGER, M. J. A. (ed.) Biogeography and Ecology of Southern Africa. W. Junk, The Hague.

BALINSKY, B. I. (1962): Patterns of animal distribution on the African continent. Annals of the Cape Province Museum **2**: 299-310.

BARBAULT, R. (1974): Ecologie comparée des lézards *Mabuya blandingi* (Hallowell) et *Panaspis kitsoni* (Boulenger) dans les forêts de Lamto (Côte-d'Ivoire). La Terre et la Vie **28**: 272-295.

BARBOUR, T. & LOVERIDGE, A. (1928): A comparative study of the herpetological faunae of the Uluguru and Usambara Mountains, Tanganyika Territory with descriptions of new species. Memoirs of the Museum of Comparative Zoology **50**: 87-265.

BARNETT, L. K., EMMS, C. & SANTONI, C. (2001): The herpetofauna of Abuko Nature Reserve, The Gambia. Herpetological Bulletin **77**: 5-14.

BENEFIT, B. R. (1999): *Victoriapithecus*, the key to Old World monkey and catarrhine evolution. Evolutionary Anthropology **7**: 155-174.

BERNOR, R. L. & ARMOUR-CHELU, M. (1999): Toward an evolutionary history of African hipparionine horses. Pp. 189-215 in: BROMAGE, T. G. & SCHRENK, F. (eds.) African biogeography, climate change & human evolution. Oxford University Press, Oxford.

BIGALKE, R. C. (1972): The contemporary mammal fauna of Africa. Pp. 141-194 in: KEAST, A., ERK, F. C. & GLASS, B. (eds.) Evolution, mammals, and southern continents. University of New York Press Albany.

BOETTGER, O. (1888): Materialien zur Fauna des unteren Congo II. Reptilien und Batrachier. I. **1887/1888**: 1-108.

BOETTGER, O. (1913): Reptilien und Amphibien von Madagaskar, den Inseln und dem Festland Ostafrikas (Sammlung Voeltzkow 1889-1895 und 1903-1905). In VOELTZKOW, A. (ed.) Reise in Ostafrika in den Jahren 1903-1905 mit Mitteln der Hermann und Elise geb. Heckmann Wentzel-Stiftung ausgeführt von Professor Dr. Alfred Voeltzkow. Wissenschaftliche Ergebnisse, Stuttgart. Band III. Systematische Arbeiten **Heft IV**: 269-375.

BÖHME, W. & SCHMITZ A. (1996): A new lygosomine skink (Lacertilia: Scincidae: *Panaspis*) from Cameroon. Revue suisse de Zoologie **103**: 767-774.

BÖHME, W., MEINIG, H. & RÖDEL, M.-O. (1996): New records of amphibians and reptiles from Burkina Faso and Mali. British Herpetological Society Bulletin **56**: 7-26.

BÖHME, W. & SCHNEIDER, B. (1987): Zur Herpetofaunistik Kameruns (III) mit Beschreibung einer neuen *Cardioglossa* (Anura: Arthroleptidae). Bonner zoologische Beiträge. **38**: 241-263.

BOULENGER, G. A. (1887): Catalogue of the lizards in the British Museum (Natural History). Vol. III. 575 pp., The Trustees of the British Museum, London

BROADLEY, D. G. (1974): A review of the *Mabuya maculilabris* group in South-Eastern Africa (Sauria: Scincidae). Arnoldia Rhodesia **6**, No. 23: 1-10.

BROADLEY, D. G. (1977): A review of the *Mabuya striata* complex in South-Eastern Africa (Sauria: Scincidae). Occasional Papers of the National Museums and Monuments of Rhodesia **B6**: 45-79.

BROADLEY, D. G. (2000): A review of the genus *Mabuya* in southeastern Africa (Sauria: Scincidae). African Journal of Herpetology **49**: 87-110.

BROADLEY, D. G. & HOWELL, K. M. (1991): A check list of the reptiles of Tanzania, with synoptic keys. Syntarsus **1**: 1-70

BRYGOO, É. R. (1981): Systématique des Lézards Scincidés de la région malgache. VIII. Les *Mabuya* des îles de l'Océan Indien occidental: Comores, Europa, Séchelles. Bulletin du Muséum National d'Histoire naturelle (sér. 4) **3**: 911-930.

BRYGOO, É. R. (1985): Les types de Scincidés (Reptiles, Sauriens) du Muséum national d'Histoire naturelle. Catalogue critique. Bulletin du Muséum National d'Histoire naturelle (scr. 4) **7**: 1-126.

CARRANZA, S., ARNOLD, E. N., MATEO, J. A. & LÓPEZ-JURADO, L. F. (2001): Parallel gigantism and complex colonization patterns in the Cape Verde scincid lizards *Mabuya* and *Macroscincus* (Reptilia: Scincidae) revealed by mitochondrial DNA sequences. Proceedings of the Royal Society of London, Series B **268**: 1595-1603.

CHABANAUD, P. (1921): Contribution à l'étude de la faune herpétologique de l'Afrique Occidentale. Bulletin du Comité d'Etudes Historiques et Scientifiques de l'Afrique Occidentale Française **3**: 445-472.

CHIRIO, L. & INEICH, I. (2000): Description d'un nouveau scincidé endémique des montagnes du Cameroun (Lacertilia: *Mabuya mekuana*). Bulletin de la Société zoologique de France **123**: 185-196.

DE WITTE, G. F. (1953): Reptiles. Exploration du Parc National de l'Upemba, Mission G.-F. de Witte **6**: 1-322.

DE WITTE, G. F. (1966): Reptiles. Exploration du Parc National de la Garamba, Mission H. de Saeger **48**: 5-108.

DU BOCAGE, J. V. B. (1866): Reptiles nouveaux ou peu connus recueillis dans les possessions portugaises de l'Afrique occidentale, qui se trouvent au Muséum de Lisbonne. Jornal de Sciencias Mathematicas, Physicas e Naturales (Lisboa) (1) **1**: 58-78.

DU BOCAGE, J. V. B. (1872): Diagnoses de quelques espèces nouvelles de reptiles d'Afrique occidentale. Jornal de Sciencias Mathematicas, Physicas e Naturales (Lisboa) (1) **4**: 72-82.

DU BOCAGE, J. V. B. (1895): Herpétologie d'Angola et du Congo. 203 pp., Imprimerie Nationale, Lisbonne.

DUNGER, G. T. (1972): The lizards and snakes of Nigeria. Part 6: The Skinks of Nigeria. The Nigerian Field **37**: 99-120.

DUPONT, L. M. & LEROY, S. A. G. (1995): Steps towards drier climatic conditions in northwestern Africa during the upper Pliocene. Pp. 289-298 in: VRBA, E. S., DENTON, G. H., PARTRIDGE, T. C. & BURCKLE, L. H. (eds.) Palaeoclimate and Evolution. University of Chicago Press, Chicago.

FELSENSTEIN, J. (1981): Evolutionary trees from DNA sequences: A maximum likelihood approach. Journal of Molecular Evolution **17**: 368-376.

FISCHER, J. G. (1885): Ichtyologische und herpetologische Bemerkungen. Jahrbücher der hamburgischen Wissenschaftlichen Anstalt **2**: 47-121.

GATESY, J., DESALLE, R. & WHEELER, W. (1993): Alignment-ambiguous nucleotide sites and the exclusion of systematic data. Molecular Phylogenetics and Evolution **2**: 145-158.

GEYER, C. J. (1991): Markov chain Monte Carlo maximum likelihood. Pp. 156-163 in: KERAMIDAS, E. M. (ed.) Computing Science and Statistics: Proceedings of the 23rd Symposium on the Interface. Interface Foundation, Fairfax Station.

GRANDISON, A. G. C. (1956): On a collection of lizards from West Africa. Bulletin de l'Institut Fondamental d'Afrique Noire, Série A, Sciences Naturelles **18**: 224-245.

GRAY, J. E. (1838): Catalogue of the Slender-tongued Saurians with Descriptions of many new Genera and species. Annals and Magazine of Natural History **2**: 287-293.

GRAY, J. E. (1845): Catalogue of the specimens of lizards in the collection of the British Museum. 289 pp., The Trustees of the British Museum, London.

GREEN, P. J. (1995): Reversible jump Markov chain Monte Carlo computation and Bayesian model determination. Biometrika **82**: 711-732.

HALLERMANN, J. (2001): Bemerkenswerter Mageninhalt von *Mehelya stenophthalmus* (Mocquard, 1887) (Serpentes: Colubridae). Salamandra **37**: 105-106.

HALLOWELL, E. (1844): Description of new species of reptiles from Africa. Proceedings of the Academy of Natural Sciences of Philadelphia **2**: 118-120.

HALLOWELL, E. (1857): Notice of a collection of reptiles from the Gaboon country, West Africa, recently presented to the Academy of Natural Sciences of Philadelphia, by Dr. Henry A. Ford. Proceedings of the Academy of Natural Sciences of Philadelphia **1857**: 48-72.

HASTINGS, W. K. (1970): Monte Carlo sampling methods using Markov chains and their applications. Biometrika **57**: 97-109.

HELLMICH, W. (1957): Die Reptilienausbeute der Hamburgischen Angola-Expedition. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut **55**: 39-80.

HILLIS, D. M. & HUELSENBECK, J. P. (1992): Signal, noise, and reliability in molecular phylogenetic analyses. Journal of Heredity **83**: 189-195.

HOOGMOED, M. S. (1974): Ghanese lizards of the genus *Mabuya* (Scincidae, Sauria, Reptilia). Zoologische Verhandelingen **138**: 1-61.

HORTON, D. R. (1973): Evolution in the genus *Mabuya* (Lacertilia, Scincidae). Unpublished Ph.D. Thesis, University of New England, Australia.

HUELSENBECK, J. P. & RONQUIST, F. (2001): MRBAYES: Bayesian inference of phylogeny. Bioinformatics **17**: 754-755.

HUELSENBECK, J. P., RONQUIST, F., NIELSEN, R. & BOLLBACK, J. P. (2001): Bayesian inference of phylogeny and its impact on evolutionary biology. Science **294**: 2310-2314.

KOCHER, T. D., THOMAS, W. K., MEYER, A., EDWARDS, S. V., PÄÄBO, S., VILLABLANCA, F. X. & WILSON A.C. (1989): Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences USA **86**: 6196-6200.

LAWSON, D. P. (1993): The reptiles and amphibians of the Korup National Park Project, Cameroon. Herpetological Natural History **1**: 27-90.

LARGET, B. & SIMON, D. (1999): Markov chain Monte Carlo for the Bayesian analysis of phylogenetic trees. Molecular Biology and Evolution **16**: 750-759.

LEBRETON, M. (1999): A working checklist of the herpetofauna of Cameroon, with localities for species occurring in southern Cameroon and a list of herpetofauna for the Dja Faunal Reserve. Netherlands Commitee for IUCN, Amsterdam.

LEROY, S. A. G. & DUPONT, L. M. (1994): Development of vegetation and continental aridity in northwestern Africa during the Late Pliocene: the pollen record of ODP Site 658. Palaeogeography, Palaeoclimatology, Palaeoecology **109**: 295-316.

LI, S., PEARL, D. K. & DOSS, H. (2000): Phylogenetic tree reconstruction using Markov chain Monte Carlo. Journal of the American Statistic Association **95**: 493-508.

LÖNNBERG, E. (1922): Sammlungen der Schwedischen Elgon-Expedition im Jahre 1920. Arkiv för Zoologi **14**: 1-8.

LOVERIDGE, A. (1929): East African reptiles and amphibians in the United States National Museum. Bulletin of the United States National Museum **151**: 1-129.

LOVERIDGE, A. (1933): Scientific results of an expedition to the southwestern highlands of Tanganyika Territory.

VII Herpetology. Bulletin of the Museum of Comparative Zoology Harvard **74**: 197-416.

LOVERIDGE, A. (1936): African reptiles and amphibians in Field Museum of Natural History. Publications of Field Museum of Natural History, Zoological Series **22**: 1-111.

LOVERIDGE, A. (1941): Report on the Smithsonian-Firestone expedition's collection of reptiles and amphibians from Liberia. Proceedings of the United States National Museum **91**: 113-140.

LOVERIDGE, A. (1942): Scientific results of a fourth expedition to forested areas in east and central Africa. IV. Reptiles. Bulletin of the Museum of Comparative Zoology Harvard **91**: 237-373.

LOVERIDGE, A. (1953): Zoological results of a fifth expedition to East Africa. III Reptiles from Nyasaland and Tete. Bulletin of the Museum of Comparative Zoology Harvard **110**: 143-322.

LOVERIDGE, A. (1956): On a third collection of reptiles taken in Tanganyika by C.J.P. Ionides, Esq. Tanganyika Notes and Records **43**: 1-19.

LOVERIDGE, A. (1957): Check list of the reptiles and amphibians of East Africa (Uganda; Kenya; Tanganyika; Zanzibar). Bulletin of the Museum of Comparative Zoology Harvard **117**: 153-362.

MANAÇAS, S. (1951): Sáurios de Guine Portuguesa. Anais Junta Investigações Colonias **6**: 55-67.

MAU, B., NEWTON, M. & LARGET, B. (1999): Bayesian phylogenetic inference via Markov chain Monte carlo methods. Biometrics **55**: 1-12.

MAUSFELD, P. & SCHMITZ, A., (2003): Molecular phylogeography, intraspecific variation and speciation of the Asian scincid lizard genus *Eutropis* Fitzinger, 1843 (Squamata: Reptilia: Scincidae): taxonomic and biogeographic implications. Organisms, Diversity and Evolution **3**: 161-171.

MAUSFELD-LAFDHIYA, P., SCHMITZ, A., MISOF, B., VRCIBRADIC, D. & ROCHA, C. F. D. (2002): On the phylogenetic affinity of *Mabuya atlantica* Schmidt, 1945, endemic to the Atlantic Ocean archipelago of Fernando de Noronha (Brazil): necessity of partitioning the genus *Mabuya* (Scincidae: Lygosominae). Zoologischer Anzeiger **241**: 281-293.

MAYR, E. & O'HARA, R. J. (1986): The biogeographic evidence supporting the Pleistocene forest refuge hypothesis. Evolution **40**: 55-67.

MERTENS, R. (1941): Zur Kenntnis der Herpetofauna von Fernando-Poo. Zoologischer Anzeiger **135**: 275-281.

MERTENS, R. (1955): Amphibien und Reptilien aus Ostafrika. Jahresheft des Vereins für Vaterländische Naturkunde in Württemberg **110**: 47-61.

MERTENS, R. (1964): Die Reptilien von Fernando Poo. Bonner Zoologische Beiträge **15**: 211-238.

METROPOLIS, N., ROSENBLUTH, A. W., ROSENBLUTH, M. N., TELLER, A. H. & TELLER, E. (1953): Equations of state calculations by fast computing machines. Journal of Chemistry and Physics **21**: 1087-1091.

MILINKOVITCH, M. C & LYONS-WEILER, J. (1998): Finding optimal ingroup topologies and convexities when the choice of outgroups is not obvious. Molecular Phylogenetics and Evolution **9**: 348-357.

MISOF, B., RICKERT, A. M., BUCKLEY, T. R., FLECK, G. & SAUER, K. P. (2001): Phylogenetic signal and its decay in mitochondrial SSU and LSU rRNA gene fragments

of Anisoptera. Molecular Biology and Evolution **18**: 27-37.

MONARD, A. (1951): Résultats de la Mission zoologique Suisse au Cameroun. Mémoires de l'Institut Francais d'Afrique Noire (Sciences Naturelles) **1**: 1-244.

NYLANDER, J. A. A. (2002): MrModeltest 1.1b. Uppsala, Sweden.

O'BRIAN, E. M. & PETERS, C. R. (1999): Landforms, climate, ecogeographic mosaics, and the potential for Hominid diversity in Pliocene Africa. Pp. 115-137 in: BROMAGE, T. G. & SCHRENK, F. (eds.) African biogeography, climate change, & human evolution. Oxford University Press, Oxford.

PAKENHAM, R. H. W. (1947): Modifications to the Reptilian and Amphibian list of the Zanzibar Protectorate. Annals and Magazine of Natural History Ser 11, **14**: 134-140.

PAKENHAM, R. H. W. (1983): The reptiles and amphibians of Zanzibar and Pemba Island. Journal of the East Africa Natural History Society and Natural Museum **177**: 1-40

PALUMBI, S. R., MARTIN, A., ROMANO, S., McMILLAN, W. O., STICE, L & GRABOWSKI, G. (1991): The Simple Fool's Guide to PCR, Version 2.0. Privately published document compiled by S Palumbi, Department of Zoology, University of Hawaii, Honolulu, HI, 96822.

PETERS, W. C. H. (1854): Diagnosen neuer Batrachier, welche zusammen mit der früher (24. Juli und 17. August) gegebenen Übersicht der Schlangen und Eidechsen mitgetheilt werden. Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlichen-Preussischen Akademie der Wissenschaften zu Berlin **1854**: 614-628.

PETERS, W. C. H. (1864): Über die Eidechsenfamilie der Scincoiden, insbesondere über die Schneider'schen und Wiegmann'schen und neue Arten des zoologischen Museums. Monatsberichte der königlichen Akademie der Wissenschaften zu Berlin **1864**: 44-58.

PETERS, W. C. H. (1879): Neue oder weniger bekannte Eidechsenarten aus der Familie der Scinci (*Eumeces guentheri*, *Euprepes notabilis*, *Ablepharus rutilus*). Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin **1879**: 35-37.

PETERS, W. C. H. (1882): Zoologie III. Amphibien. Naturwissenschaftliche Reise nach Mossambique auf Befehl seiner Majestät des Königs Friedrich Wilhelm IV. In den Jahren 1842 bis 1848 ausgeführt von Wilhelm C.H. Peters. G. Reimer, Berlin.

POSADA, D. & CRANDALL, K. A. (1998): MODELTEST: testing the model of DNA substitution. Bioinformatics **14**: 817-818.

POSADA, D. & CRANDALL, K. A. (2001): Selecting the best-fit model of nucleotide substitution. Systematic Biology **50**: 580-601.

RAMBAUT, A. (1996): Se-Al. Sequence Alignment Editor. Oxford.

RANNALA, B. & YANG, Z. (1996): Probability distribution of evolutionary trees: a new method of phylogenetic inference. Journal of Molecular Evolution **43**: 304-311.

SCHMIDT, K. P. (1919): Contributions to the herpetology of the Belgian Congo based on the collection of the American Congo Expedition, 1909-1915. Bulletin of the American Museum of Natural History **39**: 385-624.

SPAWLS, S. & ROTICH, D. (1997): An annotated checklist of the lizards of Kenya. Journal of East African Natural History **86**: 61-83.

STERNFELD, R. (1911): Zur Reptilienfauna Deutsch-Ostafrikas. Sitzungsbericht der Gesellschaft naturforschende Freunde zur Berlin **1**: 245-251.

STERNFELD, R. (1912): Reptilia. In *Ergebnisse der Deutschen Zentral-Afrika-Expedition 1907-1908*. Leipzig: Klinkhardt & Biermann.

STERNFELD, R. (1917): Reptilia und Amphibia. In: Ergebnisse der zweiten Deutschen Zentral-Afrika-Expedition 1910-1911. Klinkhardt & Biermann, Leipzig.

STEYN, W. & MITCHELL, A. J. L. (1965): A new scincid genus and a new record from South West Africa. Cimbebasia **12**: 2-12.

SWOFFORD, D. L. (2002): PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Ver. 4. Sinauer Associates, Sunderland, Massachusetts.

THOMPSON, J. D., GIBSON, T. J., PLEWNIAK, F., JEANMOUGIN, F. & HIGGINS, D. G. (1997): The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Research **24**: 4876-4882.

VRBA, E. S. (1985): African Bovidae: evolutionary events since the Miocene. South African Journal of Science **81**: 263-266.

VRBA, E. S. (1992): Mammals as the key to evolutionary theory. Journal of Mammalogy **73**: 1-28.

VRBA, E. S. (1999): Habitat theory in relation to the evolution in African neogene biota and Hominids. Pp. 19-34 in: BROMAGE, T. G. & SCHRENK, F. (eds.) African biogeography, climate change, & human evolution. Oxford University Press, Oxford.

WILLIAMSON, P. G. (1985): Evidence for an early Plio-Pleistocene rainforest expansion in east Africa. Nature **315**: 487-489.

YANG, Z. (1994): Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: Approximate methods. Journal of Molecular Evolution **39**: 306-314.

YEMANE, K., BONNEFILLE, R. & FAURE, H. (1985): Palaeoclimatic and tectonic implications of neogene microflora from northwestern Ethiopian Highlands. Nature **318**: 653-656.

Authors addresses: Patrick MAUSFELD-LAFDHIYA (corresponding author: pmausfeld@t-online.de), Andreas SCHMITZ, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Section Herpetology, Adenauerallee 160, 53113 Bonn, Germany; Ivan INEICH, Laurent CHIRIO, Muséum national d'Histoire naturelle, Institut d'Ecologie et de Gestion de la Biodiversité, Laboratoire de Zoologie (Reptiles & Amphibiens), 25, rue Cuvier, F-75005 Paris, France

Appendix 1. Overview of the taxonomic history of the *Euprepis affinis* complex

Author	Year	Full species	Considered Synonym(s)	Locality	n
GRAY	1838	*Tiliqua affinis**		not given	1
HALLOWELL	1844	*Euprepes blandingii**		Liberia & Gabon	1 & 5
GRAY	1845	*Euprepis raddoni**		West Africa	1
HALLOWELL	1857	*Euprepes blandingii*		Gabon	1
				Liberia	1
		*Euprepes frenatus**		Gabon	1
		*Euprepes albilabris**			
PETERS	1864	*Euprepes (Euprepis) aeneofuscus**		Elima (Ghana)	1
BOCAGE	1872	*Euprepes gracilis**		Bissau	2
FISCHER	1885	*Euprepes (Euprepis) pantaenii**		Sierra Leone	1
BOULENGER	1887	*Mabuia raddonii*	blandingii, albilabris, aeneofuscus, gracilis, pantaenii	West Africa	11
		M. affinis		not given	1
BOETTGER	1888	*M. raddoni*	blandingii, albilabris	DR Congo	3
BOCAGE	1895	*M. raddonii*	blandingii, gracilis	Angola	2
STERNFELD	1917	*M. raddoni*	blandingii	Cameroon	1
SCHMIDT	1919	*Mabuya raddoni*	blandingii, albilabris, frenatus, aeneofuscus, gracilis, pantaenii	DR Congo	19
LOVERIDGE	1941	*M. blandingii*	frenatus	Liberia	12
MONARD	1951	*M. raddoni*	blandingii	Cameroon	9
GRANDISON	1956	*M. blandingii*		Senegal	8
				French Guinea	4
				Ivory Coast	8
DE WITTE	1966	*M. affinis*		DR Congo	4
		M. blandingii	raddonii	DR Congo	94
HORTON	1973	*M. maculilabris*	blandingii, raddoni	uncertain	uncertain
HOOGMOED	1974	*M. affinis*	blandingii, raddonii, aeneofuscus	West Africa	119
		M. albilabris	frenatus ?	West Africa	48
BÖHME & SCHNEIDER	1987	*M. affinis*		Cameroon	10

* Original descriptions; n: number of listed specimens

Appendix 2. Overview of the taxonomic history of the *Euprepis maculilabris* complex

Author	Year	Full species	Considered Synonym	Subspecies	Locality	n
GRAY	1845	*Euprepis maculilabris**	/	/	West Africa	1
PETERS	1854	*Euprepes comorensis**	/	/	Nzawi, Como-ros	6
BOCAGE	1866	*Euprepes anchietae**	/	/	Cabinda, An-gola	1
PETERS	1879	*Euprepes notabilis**	/	/	Angola	2
PETERS	1882	*Euprepes angasijanus**	/	/	Grand Comoro	1
BOULENGER	1887	*Mabuia maculilabris**	anchietae, notabilis, angasijanus	/	West Africa, Comoros	5
BOCAGE	1895	*Mabuia maculilabris* (Gray)	anchietae, notabilis, angasijanus	/	R Congo Angola	2
STERNFELD	1911	*Mabuia boulengeri**	/		Tanzania	1
STERNFELD	1912	*maculilabris* (Gray)	/	m. maculilabris maculilabris major*,[1]	DR Congo	9 24
BOETTGER	1913	*Mabuia comorensis*	/	comorensis var. in-fralineata*	Europa Island, Mozambique Channel	10
		Mabuia comorensis	/		Mafia Islands, Zanzibar	3
			/	/		
		*Mabuia albotaeniata**		/	Pemba Island, Tanzania	12
STERNFELD	1917	*Mabuia maculilabris*	/	m. maculilabris		1
				m. major	DR Congo	15
SCHMIDT	1919	*Mabuya maculilabris*	m. major, m. ber-geri, anchietae, no-tabilis	/	DR Congo	143
BARBOUR & LOVERIDGE	1928	*Mabuya maculilabris*	boulengeri, m. ma-jor, m. kwidjwiensis, m. wauensis, m. schubotzi, m. grau-eri, m. rohrbecki & albotaeniata comorensis var. in-fralineata	/	Tanzania Africa	1 42
		Mabuya comorensis			Tanzania	32
LOVERIDGE	1942	*Mabuya maculilabris*	m. kwidjwiensis	m. maculilabris	Uganda, Ke-nya, Tanzania, DR Congo	82
				m. comorensis	Tanganyika	7
				m. boulengeri	Tanzania	5
PAKENHAM	1947	*Mabuya albotaeniata*	/	/	Pemba	17
		Mabuya maculilabris	/	m. maculilabris	Zanzibar, east, central and	60
		Mabuya comorensis			West Africa	
				m. comorensis	Comoros,	18
		Mabuya maculilabris			Zanzibar, Mo-zambique?	
LOVERIDGE	1953	*Mabuya maculilabris*	/	m. comorensis	Malawi	1
				m. boulengeri	Malawi	1
LOVERIDGE	1957	*Mabuya maculilabris*	anchietae, notabilis, m. major, m. kwid-jwiensis, m. wauen-sis, m. schubotzi, m. graueri, m. rohr-becki, m. bergeri,	m. maculilabris m. albotaeniata m. comorensis	East Africa Pemba Is., Tanzania East Africa, Comoros	not specified not specified not specified
				m. boulengeri	Tanzania, Ma-lawi	not specified

Author	Year	Full species	Considered Synonym	Subspecies	Locality	n
Broadley	1974	*Mabuya boulengeri*	/		Tanzania	54
		Mabuya maculilabris		m. *maculilabris*	East Africa	78
				m. *casuarinae**	Casuarina Is.	7
				m. *comorensis*	Comoros	6
				m. *albotaeniata*	Pemba Is.	1
				m. *infralineata*	Europa Is.	9
Brygoo	1981	*Mabuya maculilabris*	/	/	West Africa	77
		Mabuya comorensis			Comoros,	87
		Mabuya infralineata			Europa Is.	9
Pakenham	1983	*Mabuya maculilabris*	/	m. *albotaeniata*	Pemba Is.	26
				subsp.	Zanzibar	10
Broadley &	1991	*Mabuya maculilabris*	/	m. *maculilabris*	Tanzania	not specified
Howell			/	m. *albotaeniata*	Pemba Is.	not specified
		Mabuya comorensis	/		Comoro Is-	not specified
		Mabuya boulengeri			lands	not specified
					Tanzania	
Broadley	2000	*Mabuya maculilabris*	/	/	SE Africa	158
		Mabuya casuarinae			Casuarina Is.	7
		Mabuya boulengeri			SE Africa	63

* Original description
[1] with its variations: *kwidjwiensis* (DR Congo: Idjiwi Is., Lake Kivu), *wauensis* (DR Congo: Wau Is., Lake Kivu), *schubotzi* (DR Congo: Kisenyi, Lake Kivu, and Fort Beni), *graueri* (DR Congo: Aruwimi-Ituri region and between the Lualaba River and Lake Tanganyika), *rohrbecki* (Tanzania: Nguru Mountains and Manda, Lake Nyasa) and *bergi* (DR Congo: Fort Feni, Mawambi and Awakubi; Uganda: Dufile)

n number of listed specimens

Appendix 3. Summary of uncorrected p- distances of the *Euprepis affinis* and the *Euprepis maculilabris* complexes

	Species	1	2	3	4	5	6	7	8	9	10	11
1	*Scelotes mirus*	-										
2	*Mabuya agilis*	0.134	-									
3	*Euprepis affinis* Guinea Bissau	0.136	0.101	-								
4	*affinis* Bagwor River	0.135	0.109	0.023	-							
5	*affinis* Benakuma (MNHN 2002.742)	0.138	0.112	0.027	0.004	-						
6	*affinis* Benakuma	0.131	0.111	0.027	0.019	0.020	-					
7	*affinis* Kribi	0.135	0.110	0.023	0.014	0.015	0.011	-				
8	cf. *affinis* Ngoulema-kong	0.132	0.094	0.040	0.051	0.055	0.053	0.050	-			
9	cf. *affinis* Benakuma	0.136	0.098	0.038	0.045	0.049	0.051	0.047	0.010	-		
10	*albilabris* Uganda	0.127	0.109	0.049	0.041	0.042	0.043	0.041	0.051	0.050	-	
11	*albilabris* Kika	0.125	0.113	0.057	0.050	0.051	0.050	0.050	0.055	0.055	0.016	-
12	*perroteti* Gambia	0.137	0.106	0.054	0.063	0.067	0.068	0.062	0.062	0.063	0.063	0.065
13	cf. *perroteti* Tchabal Mbabo	0.132	0.097	0.049	0.054	0.057	0.058	0.054	0.053	0.053	0.055	0.062
14	*perroteti* Hina-Moufou	0.132	0.108	0.056	0.056	0.060	0.058	0.051	0.060	0.056	0.056	0.061
15	cf. *maculilabris* Amani, Tanzania	0.125	0.102	0.073	0.075	0.078	0.082	0.075	0.069	0.068	0.080	0.083
16	cf. *maculilabris* Tanzania	0.122	0.100	0.070	0.073	0.076	0.080	0.073	0.071	0.070	0.080	0.085
17	*maculilabris* Afan	0.126	0.106	0.080	0.089	0.092	0.091	0.085	0.076	0.078	0.087	0.092
18	*maculilabris* Benakuma	0.129	0.102	0.074	0.083	0.087	0.085	0.080	0.073	0.075	0.085	0.089
19	*comorensis* Nosy Tanikely	0.122	0.093	0.069	0.071	0.075	0.080	0.071	0.064	0.067	0.074	0.075
20	cf. *irregularis* Mt. Elgon	0.146	0.105	0.089	0.090	0.094	0.091	0.087	0.080	0.076	0.084	0.089
21	spec. nov. Hossere Ngang-Ha	0.152	0.116	0.096	0.099	0.103	0.099	0.095	0.088	0.084	0.096	0.098

Species	12	13	14	15	16	17	18	19	20	21
12 *perroteti* Gambia	-									
13 *perroteti* Tchabal Mbabo	0.039	-								
14 *perroteti* Hina-Moufou	0.045	0.042	-							
15 cf. *maculilabris* Tanzania	0.080	0.071	0.077	-						
16 cf. *maculilabris* Amani, Tanzania	0.080	0.071	0.077	0.008	-					
17 *maculilabris* Afan	0.090	0.083	0.087	0.047	0.041	-				
18 *maculilabris* Benakuma	0.091	0.082	0.089	0.048	0.042	0.009	-			
19 *comorensis* Nosy Ta-nikely	0.076	0.070	0.072	0.026	0.021	0.040	0.039	-		
20 cf. *irregularis* Mt. El-gon	0.087	0.087	0.090	0.093	0.091	0.095	0.094	0.087	-	
21 spec. nov Hossere Ngang-Ha	0.087	0.090	0.094	0.091	0.093	0.104	0.103	0.088	0.040	-

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: Bonn zoological Bulletin - früher Bonner Zoologische Beiträge.

Jahr/Year: 2004

Band/Volume: 52

Autor(en)/Author(s): Mausfeld-Lafdhiya Patrick, Schmitz Andreas, Ineich Ivan, Chirio Laurent

Artikel/Article: Genetic Variation in Two African Euprepis Species (Reptilia, Scincidae), Based on Maximum-Likelihood and Bayesian Analyses: Taxonomic and Biogeographic Conclusions 159-177