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Resolving sky island speciation in populations of East African *Adolfus alleni* (Sauria, Lacertidae)

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Abstract. The genus *Adolfus* Sternfeld, 1912 currently contains three species from Equatorial Africa. Two of these occur in widespread, low- to mid-elevation habitats, but *Adolfus alleni* is only known from four montane peaks (Aberdares, Mt. Kenya, Cherangani Hills, Mt. Elgon) in Kenya and Uganda. An integrative approach using 58 morphological characters and genetic analyses of mitochondrial (16S and cyt *b*) and nuclear (c-mos and RAG1) DNA sequence data revealed differences between these populations, and indicated that *A. alleni* is a complex of at least two cryptic species. Herein, we describe the populations from the Aberdares and Mount Elgon as a new species, and restrict *A. alleni* to Mount Kenya. This action underscores the importance of conservation strategies to protect these montane peaks, which may harbour additional, unique evolutionary lineages.

Key words. Uganda, Kenya, montane grassland, Squamata, *Adolfus*, systematics.

Introduction

In Africa, the family Lacertidae is represented by 14 genera with about 80 species, which is not quite as diverse compared to the families Scincidae, Chamaeleonidae or Gekkonidae, each of which comprises more than 100 African species. However, recent research has shown that this number could be underestimated in at least one lacertid genus; new species of *Pedioplanis* Fitzinger, 1843 were recently described from Angola (Conradie et al. 2012), and additional cryptic taxa have been suggested from studies of *Pedioplanis* populations in Namibia, South Africa (Makokha et al. 2007, Tolley et al. 2009) and Angola (Conradie et al. 2012). Similar cryptic diversity is likely to occur in other African lacertids, particularly montane or forest species with disjunctive ranges.

The taxonomic history of the Central and East African genus *Adolfus* Sternfeld, 1912 has experienced considerable alterations over time. The currently recognized taxa *Adolfus jacksoni* (Boulenger, 1899) and *Congolacerta vauereselli* (Tornier, 1902) were historically placed in the genus *Lacerta* Linnaeus, 1758, whereas *A. africanus* (Boulenger, 1906) and *A. alleni* (Barbour, 1914) were formerly included in the genus *Algyroides* Bibron & Bory, 1833. In describing *Adolfus*, Sternfeld (1912) recognized differences between *A. africanus* and *A. alleni*, and included the former as well as his new species, *A. fridericianus* (today recognized as a synonym of *A. africanus fide* Bauer & Günther 1995) in the genus. Boulenger (1920) recognized *Lacerta* and *Algyroides*, but synonymised *Adolfus* with the latter genus. Arnold (1973) resurrected *Adolfus* for *A. africanus*, *A. alleni* and *A. vauereselli*, but continued to recognize *Lacerta jacksoni*. However, this remaining species was transferred to the genus *Adolfus* some years later by the same author (Arnold 1989a). In a review of the Equatorial African lacertids, Greenbaum et al. (2011) transferred *A. vauereselli* to their newly erected genus *Congolacerta*, and described the new species *C. asukului.*

Adolfus jacksoni has a widespread distribution in mid-elevation forests in East Africa, and is well known to be the *Adolfus* most tolerant of human disturbance (Spawls et al. 2002). *Adolfus africanus* has the largest distribution in East and Central Africa (e.g., Mertens 1968, Broadley 1991, Schmitz et al. 2000, Spawls et al. 2002, Köhler et al. 2003), but seems to be absent from the central Congo Basin (Köhler et al. 2003). Barbour (1914) described *Adolfus*

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alleni from a series of five specimens (name-bearing type MCZ R-9280) from the northeastern slopes of Mount Kenya, and subsequent authors reported additional populations from high altitudes between 2,700 and 4,500 m from the Aberdares, Cherangani Hills and Mt. Elgon in Kenya and adjoining Uganda (e.g., Loveridge 1957, Spawls & Rotich 1997, Spawls et al. 2002).

Genetic analyses of *A. alleni* (Greenbaum et al. 2011) revealed marked sequence divergence (10.9%, cyt *b* gene) between populations from Mt. Kenya and the Aberdares, which were consistent with morphological differences noted by Arnold (1989a). The purpose of this contribution is to provide morphological and genetic analyses from three of the four known populations of *A. alleni* to assess their taxonomic status.

Material and methods

Specimens

Twenty-nine specimens of *Adolfus alleni* (Mt. Kenya: seven; Mt. Elgon: 13; Aberdare Range: nine), seven specimens of *A. jacksoni,* and nine specimens of *A. africanus* were examined (Appendix 1). Specimens were studied from collections at the following institutions: Academy of Natural Sciences of Drexel University (ANSP), Philadelphia, PA, USA; California Academy of Sciences (CAS), San Francisco, CA, USA; Museum d'histoire naturelle (MHNG), Genève, Switzerland; Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, MA, USA; National Museums of Kenya (NMK), Nairobi, Kenya; The Natural History Museum (BMNH), London, United Kingdom; United States National Museum, Smithsonian National Museum of Natural History (USNM), Washington, DC, USA; Field Museum of Natural History (FMNH), Chicago, IL, USA; and Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany.

For each adult specimen, 58 biometric external character states were examined. Measurements were taken to the nearest 0.1 mm with dial callipers, corresponding to the methodology used by Greenbaum et al. (2011). Only adult specimens were included in the analysis of mensural characters, whereas subadult specimens were included for scale characters, because pholidosis does not change through ontogenetic stages (Carretero & Llorente 1993).

Mensural characters

Characters evaluated were snout–vent length (SVL) from tip of snout to cloaca; length of tail (TL) from tip of tail to cloaca, only for specimens with entire tails; maximum head width (HW); head length (HL) from tip of snout to ear opening; head height (HH) at angle of jaw; skull length (SKL) from tip of snout to posterior margin of occipital scale; snout–eye distance (SEL) from snout tip to anterior margin of eye; mouth length (ML); snout–arm distance (SAL) from tip of snout to anterior insertion point of forelimb; axilla–groin distance (AGD); humerus length (HML); radius–ulna length (RUL); femur length (FL); tibia–fibula length (TFL); and longest–toe length (LTL).

Meristic characters

Characters evaluated were the numbers of chin shields (CS); femoral pores (FP); supralabials (SL); infralabials (IL); supraoculars (SO); supraciliaries (SC); supraciliary granules (SG); supratemporals (ST) adjacent to parietal, from anterior to posterior edge; temporals (TE) behind postoculars below supratemporals and above supralabials; anterior dorsal scale rows (ADS), counted transversely behind forelimbs; posterior dorsal scale rows (PDS), counted transversely at the anterior insertion point of the hind limbs; dorsal scale rows at midbody (DSR), counted transversely at midpoint between fore and hind limbs; dorsal scales (DSN), counted longitudinally from posterior margin of occipital scale to posterior margin of hind limbs; ventral scale rows (VR), counted transversely at midbody; ventral scales (VN), counted longitudinally from posterior margin of collar plates to anterior margin of pre-cloacal scales; number of collar plates (CP); caudal scales (CDS), counted around the tail at the 11th and 15th scale rows to make provision for male–female differences; subdigital lamellae of fingers 1–5 (SDF); subdigital lamellae of toes 1–5 (SDT); gular scales (GS); and collar plates (COP).

Qualitative characters

Characters evaluated included nostril separated from the first supralabial or not; granular scales beneath the collar present or absent; dorsolateral bands present or absent; vertebral stripe extending onto occipital scale or not; vertebral scales smooth, feebly keeled or keeled; lateral scales smooth, feebly keeled or keeled; ventral scales smooth or keeled; number of supralabial scales in contact with the eye; scale shape lanceolate, diamond, or rhombic; dorsal scales imbricate or not; vertebral scales larger, smaller or same size as lateral scales; median row of ventral scales smaller or same size as other ventral scales; tail scales smooth or keeled.

Multivariate analyses

Principal component analyses (PCA) were performed with a correlation matrix using the program PAST, version 2.12 (Hammer et al. 2001) to assess overall morphological variation between the putative taxa without making *a priori* assumptions about groupings. Violations of non-independent data in the PCA were avoided by taking measurements only from the left side of the body (Manly 1994), and all data were log-transformed to ensure normality (Burbrink 2001). Size, being an important character, was included in multivariate analyses. Damage to several specimens pre-

cluded inclusion of tail measurements in our multivariate analyses. Preliminary analyses did not show any relevant differences between sexes (data not shown). Two Var-covar PCA analyses were performed. The first (Jolliffe cut-off: 12.7) included all species of the genus (*Adolfus africanus*, *A. alleni* and *A. jacksoni*) (Fig. 1); the second (Jolliffe cut-off: 4.49) included different populations of *A. alleni* (Fig. 2).

The data set was tested for significant differences regarding the four operational taxonomic units [OTU] (*A. africanus*, *A. alleni*, *A. jacksoni* and *A.* aff. *alleni* from the Aberdares and Mt. Elgon region, respectively). A non-parametric test, Mardia's test (NPMANOVA), was selected because it showed that the distribution of the dataset was significantly non-normal (Mardia 1970). Mardia's tests are multivariate measures of skewness and kurtosis. These measures are useful both as descriptive statistics for a multivariate sample and as the basis for two very useful hypothesis tests for the multivariate normality problem. Mardia's tests are probably the most commonly used formal procedure for goodness-of-fit to the multivariate normal distribution (Mecklin & Mundfrom 2004). If at least one of these tests shows a departure from normality (small *p* value), the distribution is significantly non-normal (Hammer et al. 2001, Tab. 1). In principle, morphological data sets are rarely normally distributed and thus violate assumptions of standard parametric statistics. Non-parametric techniques offer an alternative to parametric statistics, as they do not rely on standard parametric assumptions of random sampling, normality and homogeneity of variance (Anderson 2001). Mardia's test (Mardia 1970) was used with the following settings: 50,000 permutations, distance measure Gower, F = 31.35, p values = uncorrected pairwise significances, and a Type I error of 5% was chosen to reject the null hypothesis.

Table 1. Statistics for Mardia's test for multivariate skewness and kurtosis.

Multivariate	Coefficient	Statistic	df	*p* value (normal)
Skewness	833.6	6947	7770	1
Kurtosis	1198	-6.752		1.463

Molecular phylogenetic analyses

To be consistent with molecular data sets from previous studies (i.e., Greenbaum et al. 2011, Mayer & Pavlicev 2007) and identify the relationships of specimens from the three available disjunctive populations (samples from Cherangani Hills were not available) of *Adolfus alleni* to other lacertids in the Equatorial African group (*sensu* Arnold 1989a, b), we sequenced two mitochondrial (16S and cyt *b*) and two nuclear (c-mos and RAG1) genes from four samples of *A. alleni* from Mount Kenya (NMK H-86 and ZFMK 82078), Mount Elgon (ZFMK 75001), and the Aberdares (unvouchered "NM Nairobi" tissue sample from Greenbaum et al. 2011). Some of these samples did not amplify for all genes; all new sequences were deposited in GenBank (NM Nairobi, 16S: KC503126; NMK H-86, 16S: KC503127, cyt *b*: KC503124, c-mos: KC503122, RAG1: KC503120; ZFMK 75001 [tissue no. MB 408], 16S: KC503128, cyt *b*: KC503125, c-mos: KC503123, RAG1: KC503121). These data were combined with previously published sequences of the Equatorial African lacertids, including *A. africanus*, *A. jacksoni*, *A.* cf. *jacksoni*, *Congolacerta asukului*, *C. vauereselli*, *Holaspis laevis*, *Gastropholis prasina*, *G. vittatus* and *Acanthodactylus erythrurus*; two outgroups included *Atlantolacerta andreanskyi* and *Iberolacerta cyreni* (Greenbaum et al. 2011).

Genomic DNA was isolated from alcohol-preserved liver or muscle tissue samples with the Qiagen DNeasy tissue kit (Qiagen Inc., Valencia, CA, USA). We used 25 µl PCR reactions with gene-specific primers (Greenbaum et al. 2011) with an initial denaturation step of 95°C for 2 min., followed by denaturation at 95°C for 35s, annealing at 50°C for 35 s, and extension at 72°C for 95 s, with 4 s added to the extension per cycle for 32 (mitochondrial genes) or 34 (nuclear genes) cycles. Amplicons were visualized on a 1.5% agarose gel stained with SYBR Safe DNA gel stain (Invitrogen Corporation, Carlsbad, CA, USA), and target products were purified with AMPure magnetic bead solution (Agencourt Bioscience, Beverly, MA, USA) and sequenced with BigDye® Terminator Cycle Sequencing Kits (Applied Biosystems, Foster City, CA, USA). Sequencing reactions were purified with CleanSeq magnetic bead solution (Agencourt Bioscience) and sequenced with an ABI 3130xl automated sequencer at the DNA Core Facility of the University of Texas at El Paso (UTEP). Forward and reverse sequence contigs for each sample were assembled and edited using SeqMan (DNAStar, Maison, WI, USA) to ensure accuracy. Although Pavlicev & Mayer (2006) and Greenbaum et al. (2011) reported c-mos pseudogenes in the genera *Adolfus*, *Congolacerta* and *Lacerta*, we did not amplify pseudogenes in this study.

An initial alignment of each gene was produced in MEGALIGN (DNA Star) with the Clustal W algorithm, and manual adjustments were made in MacClade 4.08 (Maddison & Maddison 2005). Protein-coding genes were translated into amino acids with MacClade to confirm conservation of the amino acid reading frame, ensure alignment and check for premature stop codons. No ambiguously aligned regions were observed, and as a result, no data were excluded from phylogenetic analyses. After preliminary analyses confirmed there was no conflict between mitochondrial and nuclear gene data sets (data not shown), we conducted phylogenetic analyses on the combined four-gene data set.

Phylogenetic relationships among the samples were assessed with maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI) optimality criteria in the programs PAUP* 4.0b10 (Swofford 2002), RAxML (Stamatakis 2006) and MrBayes 3.1 (Ronquist & Huelsenbeck 2003), respectively. For MP analyses, the heuristic search algorithm was used with 100 random-ad-

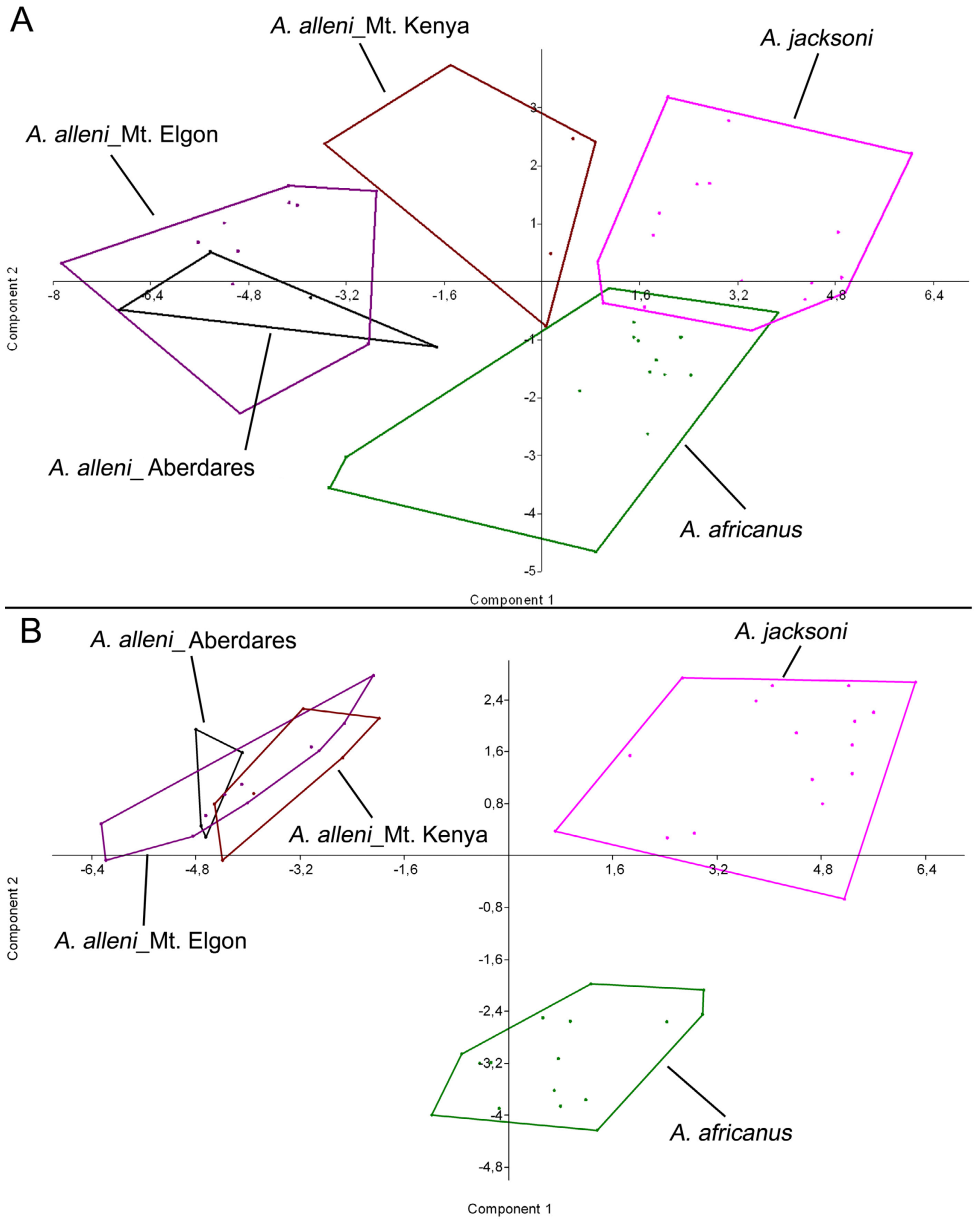

Figure 1. Plot of specimen scores on the first two axes of principal components analyses of *Adolfus africanus, A. jacksoni*, and three populations (Mt. Kenya, Mt. Elgon, Aberdare Range) of *A. alleni*. Male and female specimens were analysed together. A) log-transformed mensural data, B) meristic data.

dition replicates, accelerated character transformation and tree bisection-reconnection branch swapping, zero-length branches collapsed to polytomies, and gaps treated as missing data; we used non-parametric bootstraps (1,000 pseudoreplicates) to assess node support in resulting topologies from these parsimony searches (Felsenstein 1985). The Akaike Information Criterion (Posada & Buckley 2004) in jModelTest (Posada 2008) was used to find the model of evolution that would best fit the data for subsequent BI analyses. RAxML analyses were executed with partitioned data sets (one for 16S, and one for each codon position of all other protein-coding genes), and 100 replicate ML inferences were performed for each analysis. Each analysis was initiated with a random starting tree, included the GTRGAMMA option (-m), and employed the rapid hill-climbing algorithm (-x) (Stamatakis et al. 2007). Clade support was assessed with 1,000 bootstrap replicates, with the rapid-hill climbing algorithm (Stamatakis et al. 2008). Phylogenetic trees were visualized with FigTree (http://tree.bio.ed.ac.uk/software/figtree/).

Partitioned Bayesian analyses were conducted with default priors. Analyses were initiated with random starting

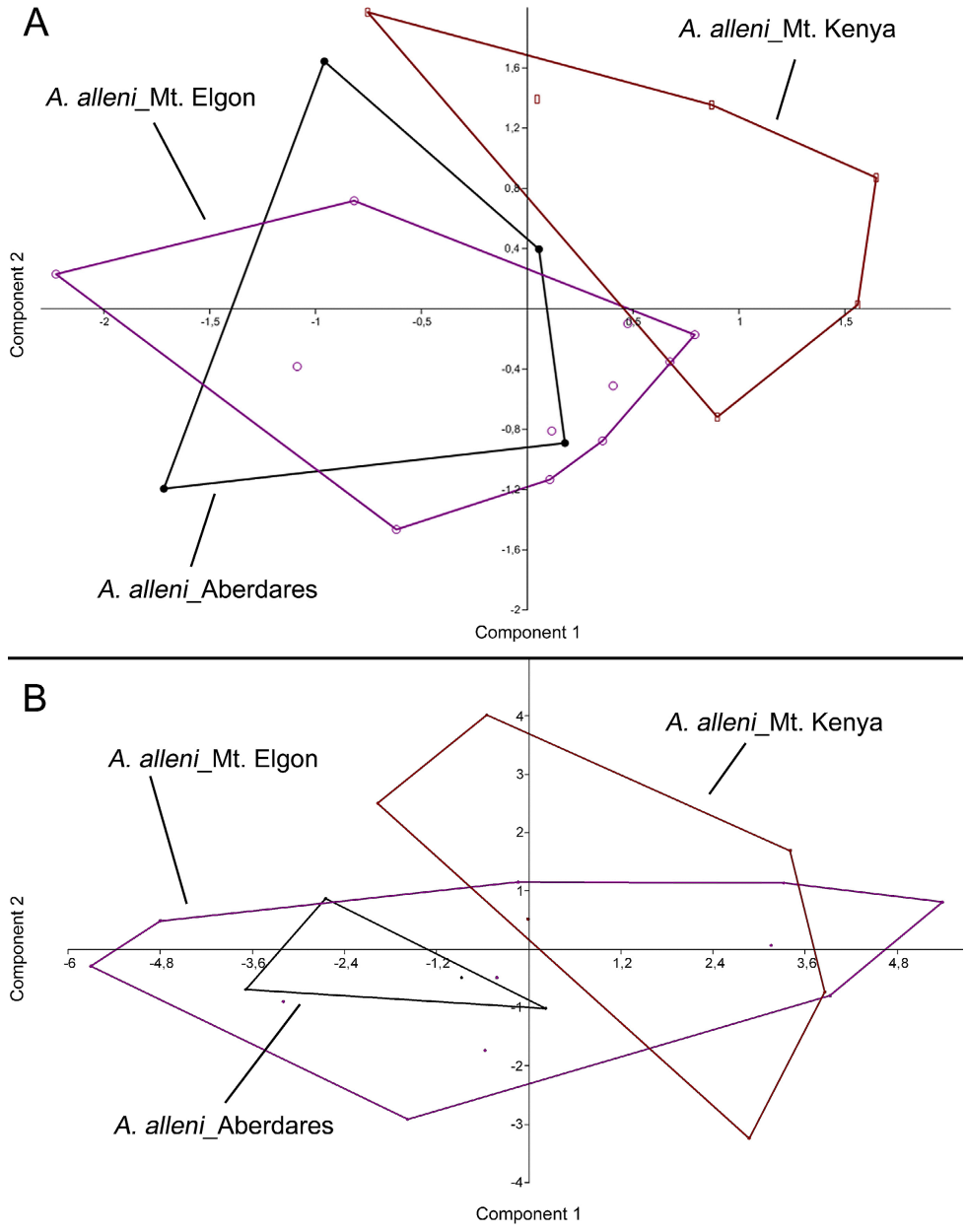

Figure 2. Plot of specimen scores on the first two axes of principal components analyses of three populations (Mt. Kenya, Mt. Elgon, Aberdare Range) of *A. alleni*. Male and female specimens were analysed together. A) log-transformed mensural data, B) meristic data.

trees and run for 20,000,000 generations; Markov chains were sampled every 1,000 generations. Convergence was checked by importing the trace files (p files) from the MrBayes output to the computer program Tracer v1.3 (http://tree.bio.ed.ac.uk/software/tracer/), which plots the likelihood values against generation numbers. Once the graphical plot levelled out, convergence had been met; we conservatively discarded 25% of the trees as "burn-in." Four separate analyses with two independent chains were executed to check for convergence of log-likelihoods in stationarity (Huelsenbeck & Ronquist 2001, Leaché & Reeder 2002).

Results

Morphological analyses

The PCA analyses were conducted with data sets containing *Adolfus* species and included 41 characters (Tab. 2) for 45 specimens. The PCA analyses of mensural and meristic data indicated a separation of some populations within the *A. alleni* group, and that *A. alleni* was morphometrically distinct from the other two *Adolfus* species (Fig. 1). The analysis with mensural data (Fig. 1A) showed a minimal overlap between *A. africanus* and *A. jacksoni*, and that both were

distinct from the *A. alleni* complex. A PCA using residuals of mensural data was conducted (not shown), but did not show contradicting results. Within the latter complex, *A. alleni* from Mt. Kenya is distinct from the populations from Mt. Elgon and the Aberdares, with the latter two species showing a considerable overlap (eigenvalue PC1: 12.38, 53.8% variance; eigenvalue PC2: 2.8606, 12.4% variance). The major contributors to PC1 were head measurements (HW, HL, SKL, and SEL); and PC2 reflected limb measurements (ADG). The analysis of meristic data (Fig. 1B) showed a strong overlap between the populations of the *A. alleni* complex, but this complex is clearly distinct from both *A. africanus* and *A. jacksoni* (eigenvalue PC1: 12.93, 47.9% variance; eigenvalue PC2: 4.73, 17.5% variance; PC3: 2.61, 9.7% variance). The major contributors to PC1 were subdigital lamellae (SDF_3, SDF_4, SDT_3, and SDT_4), PC2 was a reflection of ventral scale rows (VR) and caudal scales (CDS_11, and CDS_15), and PC3 was a reflection of head (SL, IL) and ventral scales (VN).

Within the *A. alleni* complex, biometric characters revealed differences between specimens from Mount Kenya and those from populations in the Aberdare Range and Mount Elgon (Figs. 1A, 2A). The analysis using mensural data (Fig. 2A) showed an overlap of specimens from Mt. Elgon and the Aberdares, but only a slight overlap with the Mt. Kenya population (eigenvalue PC1: 11.84, 51.5% variance; eigenvalue PC2: 4.05, 17.6% variance). The major contributors to PC1 were body length (SVL), head measurements (HW, HH, HL, SKL, ML), and limb measurements (TFL); PC2 was a reflection of limb measurements (HUL/RUL, FL/TFL, and FL/TOL) (Tab. 2). Our analysis of meristic data (Fig. 2B) showed a strong overlap between the Mt. Elgon and Mt. Kenya populations, whereas the Aberdare population fell completely within that of Mt. Elgon (eigenvalue PC1: 9.73, 38.9% variance; eigenvalue PC2: 2.79, 11.2% variance). The major contributors to both principal components were body scale counts (PC1: ADS, DSN, VR; PC2: DSN, VR) (Table 2). Eigenvalues of PC3 were low (eigenvalue: 0.007, 6.6% variance) and therefore not examined in greater detail.

The data set and additional variables (see material and methods) were tested with Mardia's test for significant differences regarding four OTUs (*A. africanus*, *A. alleni*, *A. jacksoni* and specimens from the Aderdares and Mt. Elgon; see also Tab. 3). The test resulted in the following significantly different mensural variables and meristic characters: HL/SVL, HW/HL, HW/HH, SEL/SL, ML/SAL, SAL/ADG, HUL/RUL, FL/TFL, FL/TOL, CS, FP, SL, IL, SC, SO, SG, ST, ADS, PDS, DSR, DSN, VR, VN, CDS 1, CDS 2, SDF 1–5, and SDT 1–5. This test shows that there are significant differences in size (HL/SVL), as well as head shape (HW/HL, HW/HH) and several pholidotic characters.

Molecular phylogenetic analyses

Relationships of our four samples of *Adolfus alleni* to other members of the Equatorial African Group of lacertid lizards are shown in Figure 3; MP, ML and BI analyses produced nearly identical topologies for each data set, with only minor differences in bootstrap support for each analysis. The following models of nucleotide substitution were selected by jModelTest for BI analyses: 16S (GTR + I + G); cyt *b* 1st codon (TIM2ef + I); cyt *b* 2nd codon (TIM2 + I); cyt *b* 3rd codon (GTR + I + G); c-mos 1st codon (TPM1uf + I); c-mos 2nd codon (TIM3); c-mos 3rd codon (TPM2uf + G); RAG1 1st codon (TPM1uf + G); RAG1 2nd codon (TPM3uf + I); RAG1 3rd codon (K80 + G). The combined four-gene data set included 2,413 characters (16S: 551 bp; cyt *b*: 344 bp; c-mos: 571 bp; RAG1: 947 bp), with 1,887 bp constant and 401 parsimony-informative characters. The MP analysis produced five most-parsimonious trees (length = 1277, CI = 0.553, RI = 0.675); the ML analysis likelihood score was -8807.196192.

Our preferred tree (Fig. 3) showed weak support (MP: 51; ML: 78; BI: 1.0) for a monophyletic Equatorial African Group of lacertids with the following well-supported clades: *Gastropholis*, *Congolacerta*, *Holaspis laevis,* and *Adolfus*. Within the latter genus, well-supported clades included samples of *Adolfus jacksoni*, *A. africanus*, *A. alleni* (Mt. Kenya), and *A.* cf. *alleni* (Mt. Elgon and Aberdares). We uncovered weak support (MP: 0; ML: 64; BI: 0.85) for a clade including *A. alleni* + *A.* cf. *alleni*. Uncorrected *p* genetic divergences among the populations of *A. alleni* and *A.* cf. *alleni* (Supplemental Material 1–4) ranged from moderate to high (16S: 1.7–3.2%; cyt *b*: 9.1–13.5%; c-mos: 0.02–0.07%; RAG1: 0.01%).

Conclusion

Our morphological analyses of mensural characters, genetic analyses and sequence divergence data support a taxonomic separation between Mt. Kenya-*A. alleni* and Aberdare/Mt. Elgon populations of *A. alleni.* Although our analyses of meristic data do not separate the populations, the Mt. Kenya population is well differentiated by both mensural and genetic data, and also has a distinctive colour pattern. We therefore consider the latter population as specifically distinct, and as it is nominotypic, we refer it to *A. alleni*. The populations from the Aberdares and Mt. Elgon are not as well differentiated genetically, and even though they can be distinguished by certain mensural characters (e.g., type of lateral scale keeling, relationship between rostral and frontonasal scales, and number of temporal scales), we treat them conservatively as conspecific, and herein describe them together as a new species.

Species accounts

Adolfus alleni (Barbour, 1914)

Algiroides alleni Barbour, 1914, Proc. New Engl. Zool. Club, 4: 97 (Fig. 5, Tab. 4).

Table 2. Principal components analysis elements of the unit eigenvectors for log-transformed data of PC1 and PC2 for specimens of *A. alleni* populations from Mt. Kenya, Mt. Elgon and the Aberdare Range. Left: mensural values, right: meristic values. See text for explanation of variables. Variables above 0.2 are shown in boldface.

Variable	PC 1	PC 2	Variable	PC 1	PC 2
SVL	-0.4172	-0.8755	CS	0.01291	-0.3295
HW	-0.01877	**0.6759**	FP	-0.1042	0.01412
HH	0.0804	**0.7779**	SL	-0.2427	0.1394
HL	0.1219	**0.5992**	IL	-0.1902	0.1621
SKL	-0.2354	0.1725	SC	0.121	**0.3968**
SEL	**0.3019**	**0.5969**	SO	-0.1059	-0.1153
ML	-0.6478	**0.6319**	ST	0.1166	-0.03276
SAL	-0.403	-0.2377	TE	**0.2093**	-0.1801
ADG	-0.2537	-0.6168	ADS	0.06346	0.06505
HUL	**0.9508**	-0.1848	DSR	0.05651	**0.2793**
RUL	-0.2495	**0.6667**	PDS	**0.2663**	0.1349
FL	**0.89**	0.1544	DSN	**0.2923**	-0.1501
TFL	-0.1773	**0.5509**	VR	0.1269	**0.4485**
TOL	-0.1642	**0.3482**	VN	0.1859	**0.2965**
			CDS_11	**0.2501**	-0.07181
			CDS_15	**0.2649**	0.09279
			SDF_1	**0.276**	-0.0346
			SDF_2	**0.2819**	0.1481
			SDF_3	0.1928	**0.2119**
			SDF_4	0.1732	-0.2916
			SDF_5	0.1596	-0.02424
			SDT_1	**0.2375**	-0.1434
			SDT_2	**0.2282**	-0.1662
			SDT_3	**0.2234**	-0.1168
			SDT_4	**0.2385**	0.001633
			SDT_5	0.01291	-0.3295
			COP	-0.1042	0.01412
Eigenvalue	0.000806896	0.000469366		9.72713	2.79078
% variance	42.966	24.993		38.909	11.163

Table 3. Results of the Mardia's test (NP MANOVA, 50000 permutations, distance measure Gower, F = 31.35, p values = uncorrected pairwise significances).

OTU	*A. africanus*	Aberdares/Mt Elgon	*A. jacksoni*	*A. alleni*
A. africanus	0	0.000020	0.000020	0.000040
Aberdares/Mt Elgon	0.000020	0	0.000020	0.047160
A. jacksoni	0.000020	0.000020	0	0.000080
A. alleni	0.000040	0.047160	0.000080	0

Holotype: MCZ R-9280, from "near the tree limit, north-east slope of Mt. Kenia [= Mt. Kenya]", Kenya, collected on 9 September 1909 by G. M. Allen.

Diagnosis: This species is unique by the following combination of characters: medium size (SVL 54.3–62.8 mm), low number of temporal scales (5–10), low number of scales around midbody (18–23), and a vertebral stripe often including the occipital scale (for a detailed differencial diagnosis to the new species see there).

Description: A medium-sized lizard of its genus (max. SVL 63 mm), having a short head and pointed snout. Limbs and tail comparably stout, tail about two thirds of total length. Rostral scale not in contact with frontonasal scale, nostril in contact with first upper labial scale. Granules between

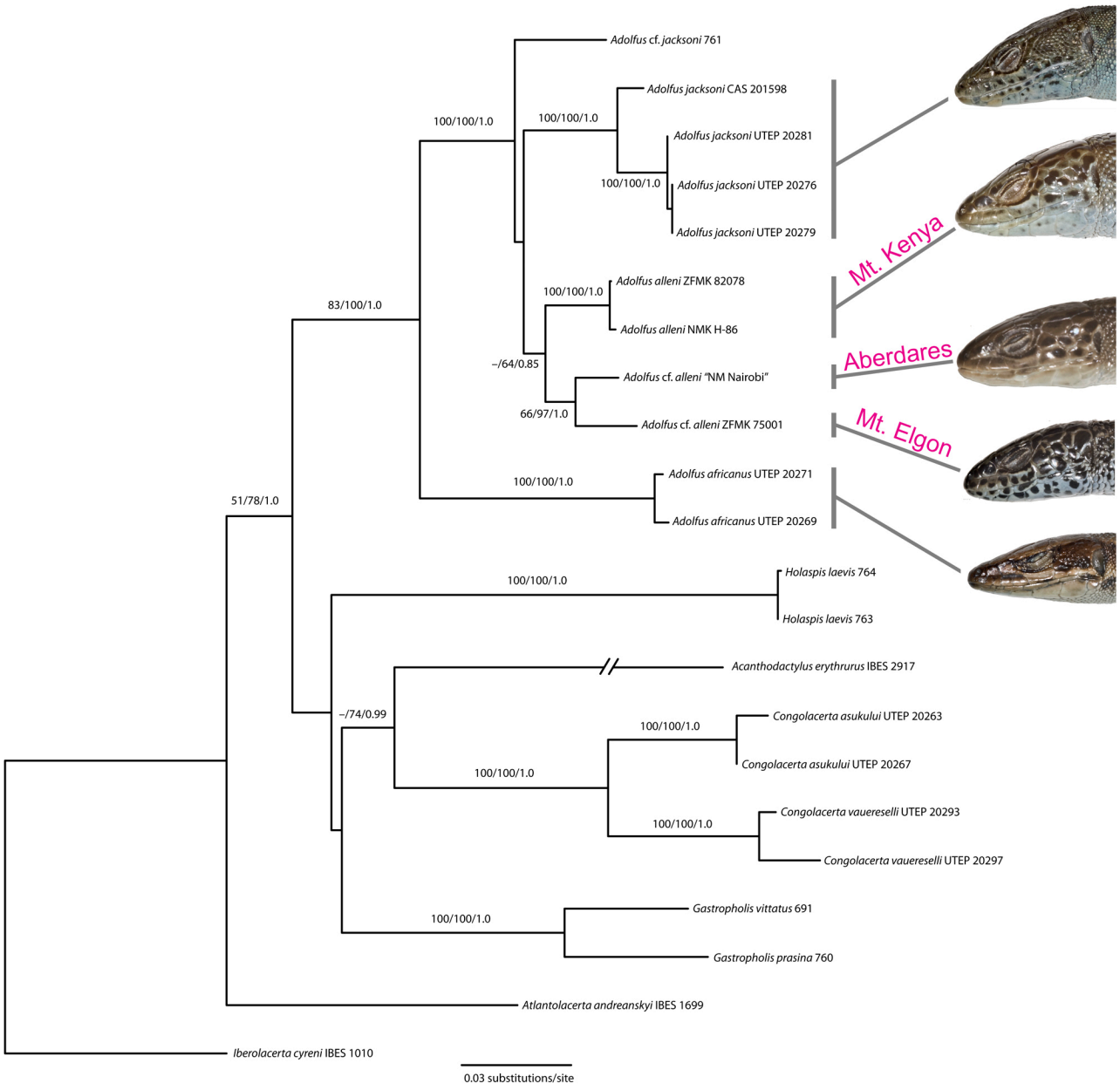

Figure 3. Maximum likelihood phylogeny (RAxML tree) of three populations of *Adolfus alleni* and other lacertid lizards in the Equatorial African Group, based on the combined 16S, cyt *b*, c-mos and RAG1 data set. Bootstrap and posterior probability values for each well-supported node are listed in the order maximum parsimony – maximum likelihood – Bayesian inference.

supraoculars and supraciliaries absent. Occipital scale of medium size, about same size as interparietal scale. Temple without granular scales, but with 5–10 (X = 7) larger scales. Gular scales (15–16) on a line between third pair of chin shields and collar. Granular scales beneath collar absent; collar consists of 5–6 scales. Vertebral scales lanceolate, imbricate, weakly keeled; lateral scales rhomboidal, smooth. Vertebral scales not distinctly larger than those on flanks. Dorsal scales in 18–19 rows around midbody, and in 51–52 longitudinal rows. Ventral scales large, in six transverse and 24 longitudinal rows, outermost rows usually incomplete. Two or three lateral scales correspond in length with one ventral scale. Precloacal scale large, distinctly larger than the large plate in front of it; one enlarged scale (larger than surrounding scales) on both sides. Femoral pores in males 12–14 on either side, in females 10–13. Hind limb reaches to midsection of body between limbs when adpressed, 17–18 lamellae on the underside of fourth toe. Scales on upper tail strongly keeled; keels forming longitudinal rows.

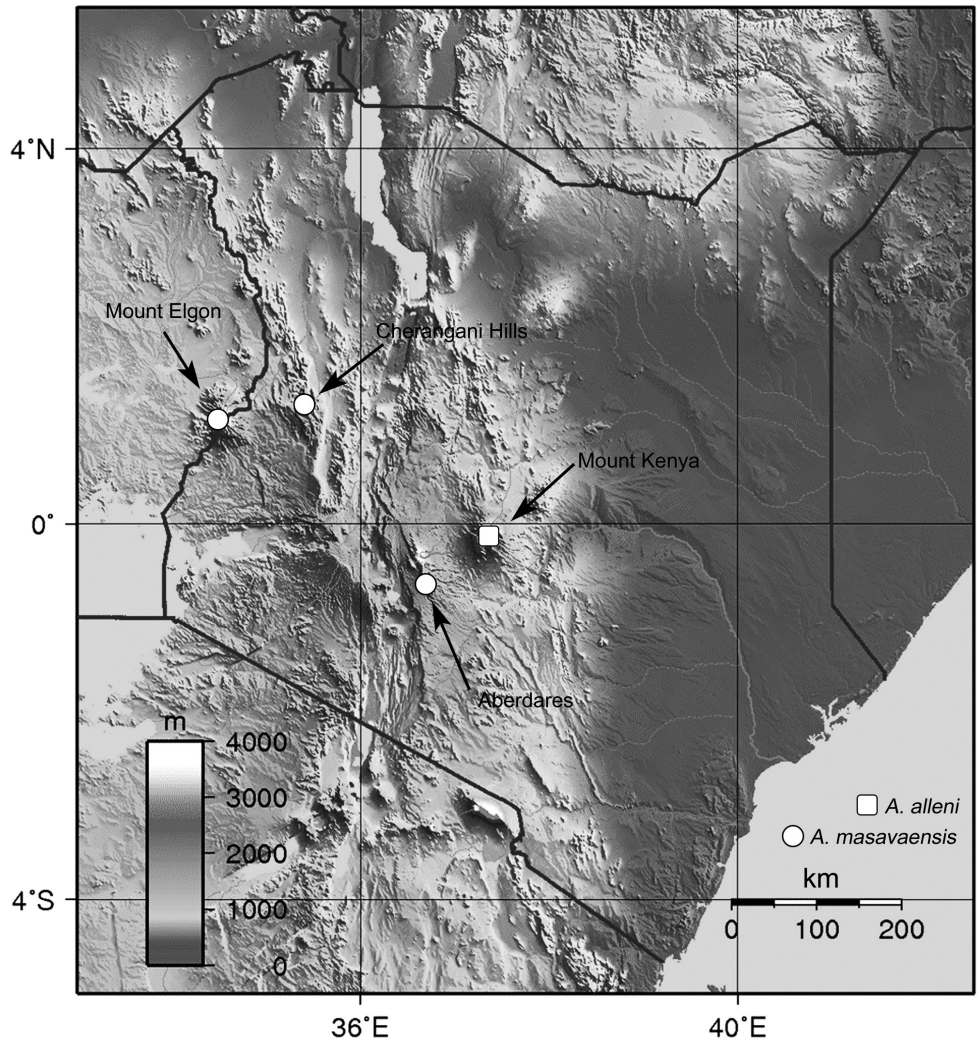

Figure 4. Topographic map of Kenya, showing the four areas of occurrence of the *Adolfus alleni* group.

Dorsal surface brownish, with a strong black vertebral stripe, often (90%) excluding the occipital scale. Two red-brown and black-edged dorsolateral stripes. Flanks rufous, belly orange.

Distribution and habitat: *A. alleni* is a montane species and known only from higher altitudes (2700–4500 m) on Mount Kenya, usually in moorland above the tree line in the Alpine *Calluna* and *Hagenia-Hypericum* zones.

***Adolfus masavaensis* sp. n.**
Wagner, Greenbaum & Branch
(Figs 6–7, Tab. 4).

Holotype: ZFMK 75001 (field no. SL85, Fig. 6), adult female from Mount Elgon, Kenya, near Koitobos Guest House [coordinates approximately: 1.040983, 34.783645], 3372 m a.s.l., collected on 5 November 2001 by Stefan Lötters.

Paratypes: CAS 162680–81 from Mount Elgon (Uganda), Arugot, "9500 ft. [= 2895.6 m a.s.l.]"; FMNH 35290–91 from Mount Elgon; MCZ R-41178–79, MCZ R-41185–88 from Mount Elgon, Kapchorwa, Tingey Kaburoni, 10,500 ft [= 3200 m a.s.l.]; ANSP 24237 from Mt. Elgon, Kaburomi, 3200 m a.s.l., Uganda.

Diagnosis: This species is unique by the following combination of characters: small size (SVL 38.9–55.5 mm), low number of temporal scales (3–12; Mt. Elgon: 8–12, Aberdares: 3–5), low number of scales around midbody (19–23), and a vertebral stripe often including the occipital scale.

Differential diagnosis: From *A. jacksoni*, the new species differs in having fewer scale rows around midbody (19–23 *versus* more than 35), fewer temporal scales (3–12 large scales *versus* < 40 small scales), no granular scales beneath the collar (present in *A. jacksoni*), and a lower number of lamellae under the 4th toe (15–21 *versus* 22–26).

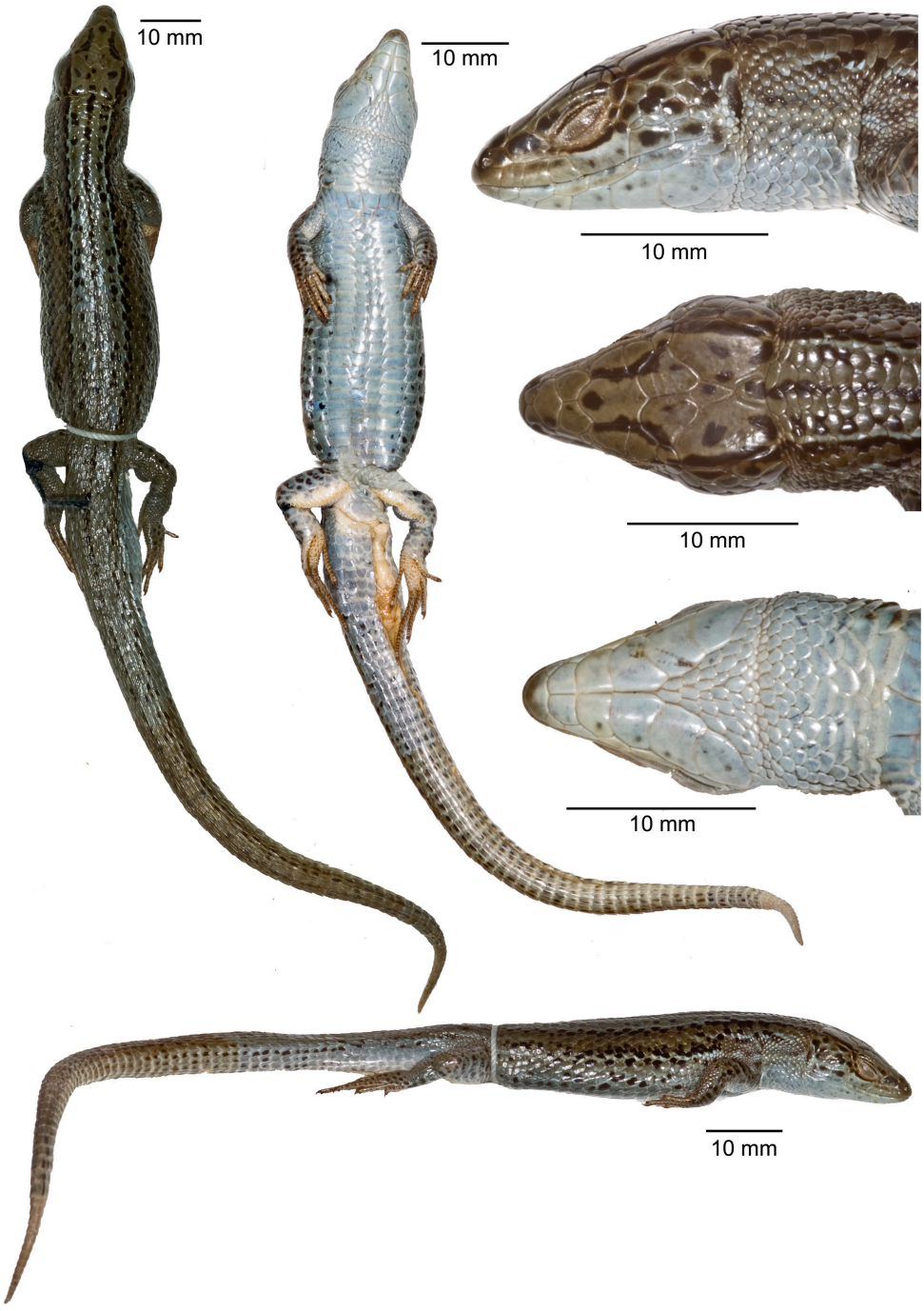

Figure 5. Male specimen (ZFMK 82078, topotype) of *A. alleni* from Mt. Kenya.

From *A. africanus*, the new species differs in having no granular scales beneath the collar or between the supraciliaries and supraocular (*versus* granular scales present in both cases), vertebral scales not distinctly larger than those on the flanks (*versus* vertebral scales distinctly larger), few (3–12) and smooth temporal scales (*versus* many [< 40] keeled ones), and fewer collar scales (4–5 *versus* 7–9).

From *A. alleni*, the new species differs mainly in its smaller snout–vent length (38.9–55.5 mm *versus* 54.3–62.8 mm), the lower number of temporal scales (3–9 *versus* 8–12), and a lower number of longitudinal dorsal scales (below 50 *versus* more than 50), whereas other characters are overlapping (Tab. 4).

Table 4. Comparison of mensural and meristic variables of *Adolfus africanus*, *A. jacksoni*, *A. alleni* and *A. masavaensis*. Data are averages (ranges in parentheses). SVL/TL in percent data. [1*]*n*=3; [2*]*n*=2; [3*]*n*=2; [4*]*n*=2.

Character	*A. africanus* (*n* = 16)	*A. jacksoni* (*n* = 17)	*A. alleni* Mt Kenya (*n* = 6)	*A. masavaensis* Aberdares (*n* = 4)	*A. masavaensis* Mt. Elgon (*n* = 11)
SVL	58.9 (55.7–61.8)	70.4 (62.3–84.3)	60.2 (54.3–62.8)	48.3 (45.7–55.5)	47.7 (38.9–52.8)
TL	107.1 (103.0–113.6) [1*]	107.0 (101.3–112.6) [2*]	–/–	87.8 (76.9–98.7)[3*]	86.6 (81.8–91.4)[4*]
SVL/TL	54.9 (49.0–60.0)	60.1 (56.8–63.3)	–/–	58.0 (56.2–59.8)	54.8 (54.1–55.5)
HL	14.4 (13.4–15.1)	16.3 (12.4–20.2)	13.1 (10.2–14.5)	10.1 (8.8–11.7)	9.8 (8.0–11.3)
HW	8.7 (8.2–9.5)	10.6 (7.8–14.2)	8.4 (6.9–9.5)	6.7 (6.0–8.1)	6.5 (5.4–7.7)
HH	6.2 (6.0–6.6)	7.2 (5.6–9.4)	6.6 (5.0–7.6)	5.4 (4.5–6.1)	5.0 (4.1–5.9)
SKL	14.1 (13.1–14.7)	16.8 (12.5–20.5)	13.0 (10.0–14.4)	10.4 (9.4–11.4)	10.2 (8.2–11.9)
SEL	6.3 (6.0–6.6)	6.5 (5.3–7.7)	4.7 (3.9–5.5)	4.0 (3.0–4.6)	3.9 (3.3–4.5)
ML	11.1 (10.7–11.8)	12.1 (9.3–14.1)	10.9 (8.6–12.3)	8.9 (7.9–11.1)	8.4 (6.6–10.4)
SAL	20.8 (19.0–23.7)	25.7 (19.5–32.0)	20.7 (15.3–22.6)	16.8 (14.6–19.2)	17.1 (16.5–19.8)
AGD	26.4 (23.0–30.4)	32.1 (25.9–40.2)	31.6 (28.7–34.0)	23.9 (21.9–28.4)	23.5 (18.0–27.3)
HML	7.5 (6.6–8.9)	7.5 (5.5–9.2)	6.2 (4.7–7.7)	4.2 (3.5–4.7)	4.6 (3.0–6.3)
RUL	7.8 (7.5–8.1)	7.7 (6.0–9.1)	6.2 (5.8–7.6)	4.9 (3.9–6.9)	4.6 (3.7–5.7)
FL	10.1 (9.3–11.0)	10.1 (8.6–11.9)	8.4 (6.8–10.2)	5.7 (4.1–6.7)	5.7 (4.5–6.7)
TFL	10.2 (9.3–10.9)	10.0 (7.6–11.7)	7.4 (6.4–8.1)	6.1 (5.3–7.5)	6.0 (4.8–6.9)
LTL	10.4 (9.3–11.7)	10.5 (8.6–12.3)	8.0 (6.9–9.2)	6.6 (6.0–7.9)	6.2 (4.8–7.4)
CS	5.4 (5–6)	5.6 (5–6)	4.8 (4–5)	5.0	5.0
FP	15.3 (14–17)	17.3 (15–19)	12.0 (11–13)	13.5 (11–18)	10.6 (10–12)
SL	7.1 (7–8)	6.1 (6–7)	6.3 (5–8)	6.5 (5–8)	6.8 (7–9)
IL	7.2 (6–10)	6.9 (6–9)	6.0 (5–7)	5.8 (5–7)	5.7 (5–7)
SO	4	4.1 (4–5)	4.0	4.0	4.0 (3–5)
SC	5.9 (5–6)	5.0 (4–6)	4.3 (3–5)	3.8 (3–4)	3.7 (3–5)
SG	6.4 (6–8)	3.5 (2–5)	–/–	–/–	–/–
ST	4.9 (4–6)	4.8 (3–6)	2.3 (2–3)	2.3 (2–3)	2.2 (2–3)
ADS	49.3 (36–60)	61.1 (51–74)	36.5 (25–55)	32.8 (23–49)	29.8 (23–36)
PDS	25.4 (20–28)	40.1 (37–44)	21.0 (17–23)	21.8 (20–23)	21.8 (19–24)
DSR	24.1 (23–26)	40.3 (35–44)	19.3 (18–23)	20.8 (19–22)	20.7 (19–23)
DSN	48.0 (42–53)	95.4 (90–105)	50.2 (45–55)	46.0 (44–49)	49.2 (42–57)
VR	6.0	6.0	6.0	6.0	6.0
VN	23.1 (22–24)	27.3 (24.5–31.5)	27.7 (24–33)	25.8 (25–28)	27.0 (22–32)
CDS 11th	15.4 (14–16)	24.3 (22–27)	22.0 (20–24)	20.3 (19–21)	20.4 (17–23)
CDS 15th	15.1 (14–16)	24.0 (21–26)	20.8 (20–22)	20.0 (19–21)	21.1 (18–25)
SDF1	8.1 (7–10)	8.3 (7–9)	5.3 (6–8)	6.0	6.5 (5–8)
SDF2	13.2 (12–14)	13.3 (12–15)	10.3 (10–11)	9.5 (9–10)	9.7 (8–12)
SDF3	16.7 (15–18)	18.0 (16–20)	13.2 (12–15)	12.0 (11–13)	12.8 (11–14)
SDF4	16.7 (16–18)	19.4 (17–22)	14.8 (14–16)	12.8 (12–14)	13.3 (11–16)
SDF5	11.6 (11–12)	12.4 (11–14)	9.7 (9–10)	9.0 (8–10)	8.9 (8–10)
SDT1	8.3 (7–9)	8.7 (6–10)	7.3 (6–9)	6.3 (6–7)	7.3 (7–9)
SDT2	12.7 (11–14)	13.4 (11–15)	10.5 (9–11)	10.0 (9–11)	10.8 (10–12)
SDT3	16.0 (15–17)	18.8 (17–21)	14.0 (13–16)	12.8 (12–13)	14.0 (12–16)
SDT4	19.0 (18–20)	23.6 (21–27)	18.3 (17–20)	18.5 (18–19)	17.7 (15–21)
SDT5	13.7 (13–15)	16.1 (15–17)	11.5 (10–13)	11.5 (11–12)	12.0 (10–15)

Description: A small lizard of its genus (max. SVL 53 mm in Mt. Elgon populations; max. SVL 56 mm in Aberdares populations; *versus* max. SVL 63 mm in *A. alleni*, 62 mm in *A. africanus*, and 84 mm in *A. jacksoni*), with a short head and pointed snout. Limbs and tail comparatively stout, tail about two thirds of total length. Rostral scale not in contact with frontonasal scale, nostril in contact with first upper labial scale. Granules between supraoculars and supracili-

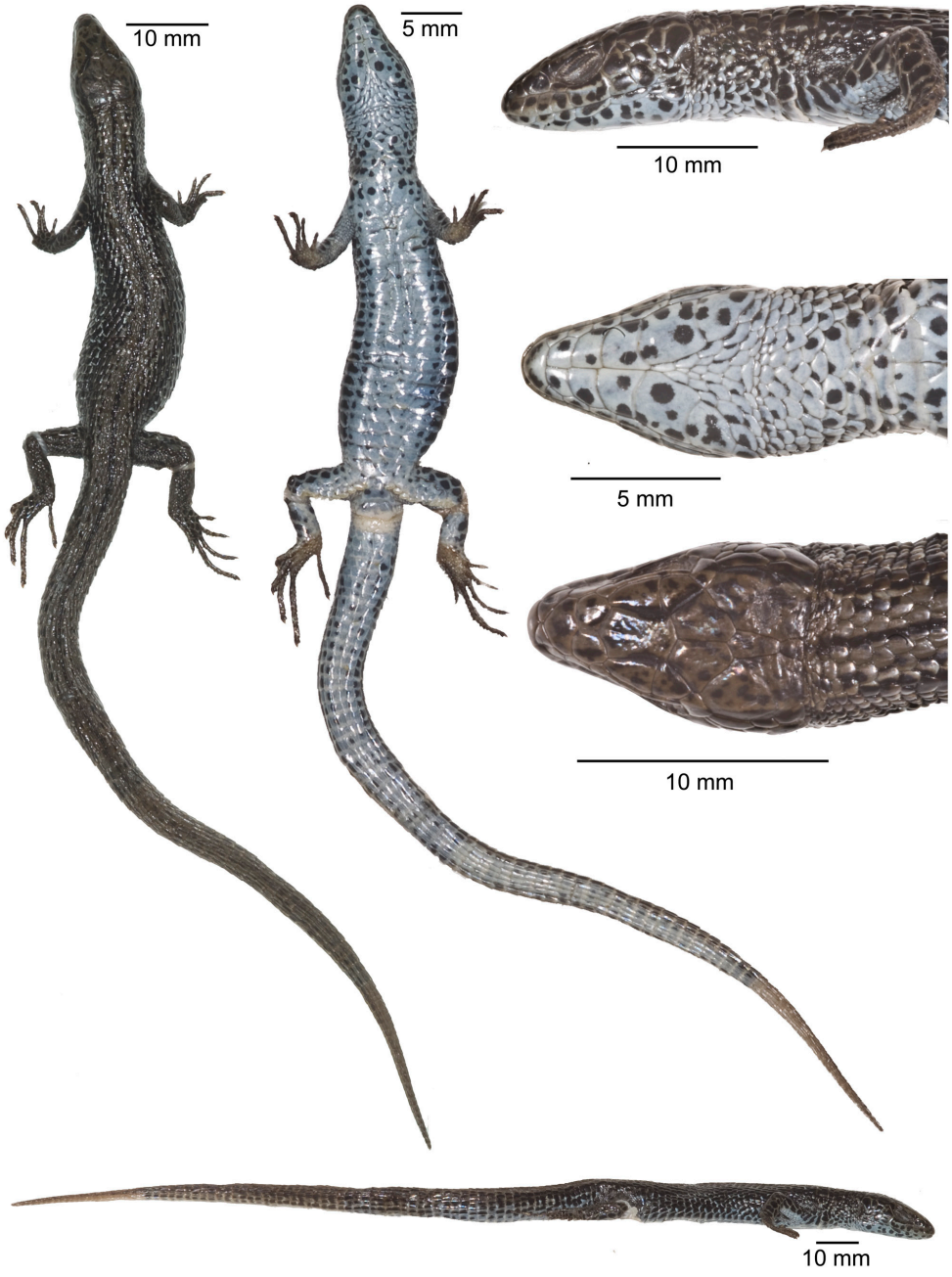

Figure 6. Female specimen (ZFMK 75001, holotype) of *Adolfus masavaensis* from Mt. Elgon.

aries absent. Occipital scale small, only half the size of the interparietal scale. Temples without granular scales, but with 6–12 (X = 8) in Mt. Elgon populations, and 3–6 (X = 4.6) larger scales in Aberdare populations. Gular scales (14–15) in a line between third pair of chin shields and collar. Granular scales beneath collar absent; collar consists of four scales. Vertebral scales lanceolate, imbricate, keeled; lateral scales rhomboidal, smooth. Vertebral scales not distinctly larger than those on flanks. Dorsal scales in 19–23 rows around midbody, and in 42–57 longitudinal rows. Ventral scales large, in six transverse and 22–31 longitudinal rows, outermost rows usually incomplete. Three lateral scales correspond in length with one ventral scale. Precloacal scale small, large plate in front of it about the same size as the precloacal scale, one enlarged scale (larger than surrounding scales) on each side. Femoral pores in males 10–18 on either side, in females 10–14. Hind limb reaches upper third of body between limbs when adpressed, 15–21 lamellae under fourth toe. Scales on upper tail strongly keeled, keels forming longitudinal rows.

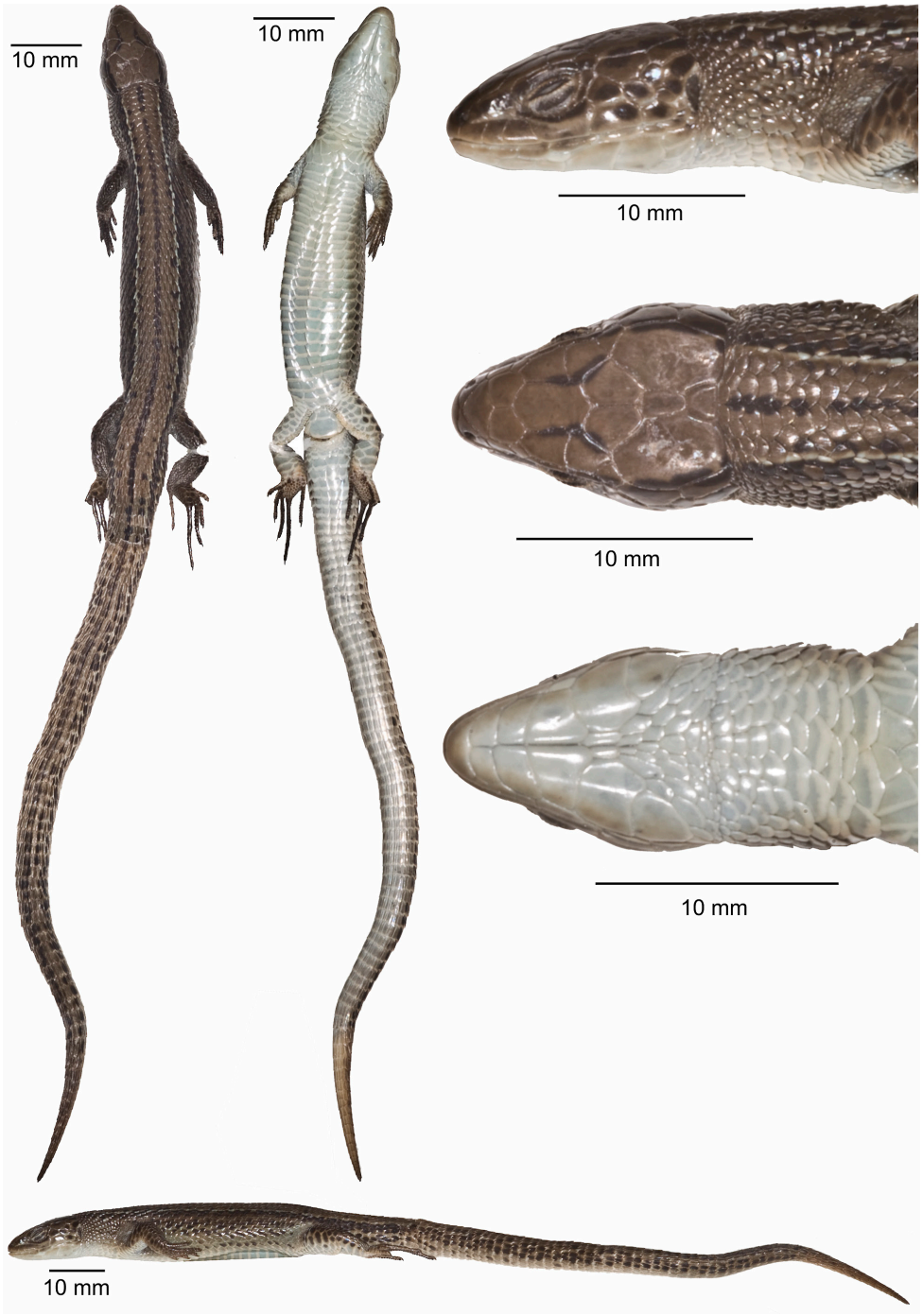

Figure 7. Male specimen (ZFMK 68875) of *Adolfus masavaensis* from the Aberdare Range.

Colouration of specimens from Mt. Elgon: dorsal surface dark brown, with a narrow black vertebral stripe, often extending onto the occipital scale. Flanks black, not separated by dorsolateral stripes from the brown dorsal colouration. Venter whitish with black spots (highest density on the chest).

Colouration of specimens from the Aberdares: dorsal surface light brownish, with a narrow black vertebral stripe. Flanks dark brown, separated from the dorsal colouration by a narrow, whitish, black-framed stripe. Often with a green-edged lateral stripe. Venter dirty white, without black spots or flecks.

Variation: The Mt. Elgon population of *A. masavaensis* differs from specimens of the Aberdare population (Fig. 7, Tab. 4) in having smooth scales on the flanks (*versus* keeled), the moderately keeled *versus* strongly keeled vertebral scales, a rostral scale that is not usually in con-

tact with the frontonasal scale (*versus* usually in contact), a higher number of temporal scales (6–12 *versus* 3–6), and a small precloacal scale, about the same size of the scale in front of it, *versus* a large precloacal plate, larger than the scale in front of it. In specimens from Mt. Elgon, the vertebral stripe often includes the occipital scale whereas it is excluded in those from the Aberdares.

Description of the holotype: An adult female with a long, but regenerated tail. Upper head scales smooth, large and clearly distinct from body scales. Nostril in contact with first upper labial scale, 5th upper labial on both sides in contact with eye; 8–7 (left, right) supralabial scales, 6–5 (left, right) infralabial scales, 4–4 (left, right) supraocular scales. 4–3 (left, right) supraciliary scales. Temporal region with large scales: 2–3 (left, right) supratemporal scales and 6–7 (left, right) temporal scales. Dorsal scales uniform in size (mid-dorsal scales not larger than those on flanks), lanceolate, keeled and imbricate, in 20 transverse scale rows behind forelimbs, 21 at midpoint between fore and hind limbs, 21 just anterior to hind limbs, and in 46 longitudinal scale rows along vertebral column. Ten femoral pores on either side. Four collar scales present, granular scales beneath collar absent. Ventral scales smooth and overlapping, in 22–22 longitudinal and six transverse rows, median and outer scales narrower than others. Tail scales strongly keeled, keels aligned in longitudinal rows, 19 caudal scales around 11th segment, 21 scales around 15th segment (counted from tail base). Subdigital lamellae of fingers 1–5: 5–7–11–12–7; subdigital lamellae of toes 1–5: 6–10–11–15–11.

Measurements (in mm) of the holotype are as follows: snout–vent length 51.8; head length 10.8; head width 6.9; head height 5.5; skull length 11.6; snout–eye distance 3.6; mouth length 10.8; tail length 89.7 (reduced); snout–arm distance 18.1; axilla–groin distance 25.2; humerus length 4.2; radius–ulna length 5.4; femur length 5.6; tibia–fibula length 7.5; 4th toe length 6.7.

Colouration of holotype in preservative: ground colouration of upper head, mid-dorsal parts of the body and upper parts of the tail brownish, with a fine black vertebral stripe extending from the nape to the first half of the tail. Sides of the head, flanks and sides of the tail black, each single scale black or black with a fine white margin or tip, with some intermixed white granular scales on the sides of the nape. Ventral parts dirty white with black dots mainly on nape and chin.

Etymology: The English name of 'Mount Elgon' refers to the indigenous tribe of the Elgonyi who live on the southern slopes of the mountain. 'Masava' is the local name for Mount Elgon used by the tribes on the Ugandan side of the mountain, and is used to form the species name for the taxon described herein.

Distribution and habitat: *Adolfus masavaensis* sp. n. is known from the Mt. Elgon area and the Aberdare Range. Within the Mt. Elgon area, there is a single record from the Cherangani Hills (BMNH 1969.2584, Sondang, 3,150 m; Arnold 1989a) that probably represents a third distinct population of the new species, but still requires additional study.

Like *A. alleni*, specimens of the new species were only found at high altitudes from 2,895.5 m (CAS 162680–81) to 3,372 m (ZFMK 75011), and are presumed to have similar habitat preferences, i.e., the Páramo-like [alpine] zone, a form of open grassland with *Dendrosenecio battiscombei* (Asteraceae). However, Angel (1925) mentioned a specimen from the bamboo forests on the Aberdares, at the lower altitudinal limit of the species, a zone that is ecologically distinct from the other species' known habitats.

Relationships: As shown in Figure 3, the new species is the sister taxon to *A. alleni*, and both species are closely related to the *A. jacksoni* complex from the Albertine Rift and Mt. Elgon region (including Kakamega Forest), and more distantly related to *A. africanus*. Within the new species, the two populations from Mt. Elgon and the Aberdares are genetically distinct, but show low *p*-distances (Fig. 3; Supplemental Material 1–4). Arnold (1989a) mentioned specimens from the southern parts of the Aberdares with less developed keels on the vertebral scales. Therefore, there could be a small differentiation between northern and southern populations in this range. This may be correlated with the habitat differences noted by Angel (1925) and would be a good example for habitat-induced evolution.

Conservation: Because of our division of *A. alleni* into two taxa, the conservation status of both species need to be reassessed. *Adolfus alleni* was categorised by the IUCN (Spawls 2010) as 'Vulnerable' due to its small area of occupancy of about 5,226 km², and because individuals were known from only four localities, even though they mainly occurred within National Parks (Mt. Kenya, Mt. Elgon, Aberdares).

However, because of our taxonomic partition, both species have more reduced areas of occupancy and are only known from one population (*A. alleni*, Mt. Kenya) and two clearly isolated populations (*A. masavaensis* sp. n., Aberdares/Mt. Elgon + Cherangani Hills), respectively, which may render their conservation status more critical. Habitat degradation was considered the major threat (Spawls 2010), because despite the protected status of the parks, moorlands were still being burned and the human population in proximity to the parks was dense. These observations now also apply to the new species *Adolfus masavaensis* sp. n.

Discussion

The principal motivation of this work was to clarify the status of the high-altitude populations of *Adolfus alleni*. In Africa, species that are adapted to montane grasslands and forests at high altitudes are often endemic to small high-altitude mountain ranges. This phenomenon is well known from East African high-altitude chameleons

(e.g., *Kinyongia gyrolepis* Greenbaum, Tolley, Joma & Kusamba, 2012: Lendu Plateau 2,150 m; *Trioceros kinetensis* [Schmidt, 1943]: Imatong Mts., 3,000 m; *T. ntunte* Necas, Modrý & Slapeta, 2005: Mt. Nyiru, 2,500 m; *T. schubotzi* [Sternfeld, 1912]: Mt. Kenya, 3,000 m; *T. hanangensis* Krause & Böhme, 2010: Mt Hanang, 2,800 m), but is still poorly documented in other East African reptile groups. It is not surprising that a lack of gene flow among populations adapted to montane grasslands will lead to genetic distinctness (Fig. 3, Supplemental Material 1–4). As mentioned by Arnold (1989a), the overall similarity between populations of *A. alleni* could be due to the conservation of shared ancestral characters, whereas the features (e.g., low temporal counts, low number of femoral pores, strong keeling of dorsal scales) of the Aberdare population seem to be derived, and suggest at least some level of genetic drift.

Both Mt. Kenya and the Aberdares are separated from Mt. Elgon by about 300 km, whereas Mt. Kenya and the Aberdares are only 50 km apart. All of these mountains are extinct volcanoes and isolated ecosystems (Petursson et al. 2006) associated with the Rift Valley. Mount Elgon (formed ca. 20 million years ago [mya]) is much older than Mt. Kenya (ca. 3 mya) (Hamilton 1981, 1982) or the Aberdares (ca. 4 mya) (Baker et al. 1988). This is reflected in the zoogeography of the Aberdare Range and Mt. Kenya, which are geographically closely linked, but rarely share high-altitude species – an exception is the small adder *Montatheris hindii* (Boulenger 1910), which is known from both localities above 2,700 m. Conversely, both mountains have their endemic vertebrate species (e.g., Mt. Kenya: Chamaeleonidae, *T. schubotzi*; Aberdares: Soricidae, *Surdisorex norae* Thomas, 1906*;* Spalacidae*, Tachyoryctes audax* Thomas, 1910), but neither are known to share an endemic species, or have an endemic sister species distribution. Among high-altitude species, only the skink *Trachylepis irregularis* (Lönnberg, 1922) occurs at all three localities, as well as the Mau Escarpment, a steep natural cliff approximately 3,000 m high, running along the western edge of this part of the Gregory Rift Valley and connecting the Aberdares with the Cherangani Hills and Mt. Elgon. However, only a single sample of *T. irregularis* has as yet been examined as to its molecular data (Mausfeld et al. 2000), and this taxon might represent a complex of cryptic species. Mount Elgon's biota is poorly known, but was recently the focus of a biodiversity survey (Davenport et al. 1996), which led to it being provisionally ranked among the top ten most species-rich forests in Uganda (Davenport et al. 1996, Howard et al. 2000).

Previously, *A. alleni* was considered to occur in three isolated mountain systems, but our results demonstrate that relationships between the *A. alleni*-isolates are in fact more complex. The sole specimen of *A. alleni* recorded from the Cherangani Hills was not examined by us (given its locality, we tentatively assign it to *A. masavaensis*), but it may indicate that a zoogeographic corridor exists between Mt. Elgon and the Aberdares. Given the somewhat paradoxical distribution of the three *A. alleni*-isolates, with the Aberdare population being more closely related to that of Mt Elgon (300 km away) rather than Mt Kenya (50 km), we hypothesize that the Mt. Elgon-populations are ancestral populations, whereas those on the Aberdares and Mt. Kenya represent more recent migrations. This is supported by the structure of the landscape in this area (Fig. 4): Mount Elgon has a connection with the Cherangani Hills, followed by a mountainous corridor (Mau Escarpment) to the Aberdares and the mountain systems of northern Tanzania, whereas Mt. Kenya is clearly isolated.

Future research will be focused on *A. jacksoni* (shown to be paraphyletic in our phylogeny) and the skink *T. irregularis*, both of which could show the same zoogeographic pattern as *A. alleni* and *A. masavaensis*. Additional field surveys could reveal the presence of *A. masavaensis* in the Mau Escarpment. Moreover, future studies can serve to test our zoogeographic hypothesis by incorporating the phylogeographies of *A. alleni* and *A. masavaensis* and more extensive sampling of their populations.

Revised key to the species of *Adolfus*

1a Vertebral scales distinctly larger than those on the flanks; outermost ventral scale rows incomplete and faintly keeled ..... *Adolfus africanus*

1b Vertebral scales about the same size as the scales on the flanks; outermost ventral scale rows incomplete and smooth 2

2a Temporal scales small and numerous; granular scales beneath the collar present; dorsal scales in 37–48 rows around midbody ..... *Adolfus jacksoni*

2b Temporal scales large and few in number; granular scales beneath the collar absent; dorsal scales in 18–24 rows around midbody 3

3a Vertebral and lateral scales keeled; vertebral scales strongly keeled; rostral and frontonasal scale usually in contact; number of temporal scales low, 3–6; number of femoral pores on either thigh 8–12 ..... *Adolfus masavaensis*, Aberdare population

3b Vertebral scale row weakly to moderately keeled; rostral and frontonasal scale usually not in contact; maximum number of temporal scales high, 5–12; number of femoral pores on either thigh 10–14 4

4a More than 50 dorsal scales in a longitudinal row; number of temporal scales 8–12; 5–6 collar scales; 17–20 lamellae under 4th toe; side of the head and flanks rufous or brown; two black-edged dorsolateral stripes ..... *Adolfus alleni*

4b Less than 50 dorsal scales in a longitudinal row; number of temporal scales 6–9; 4 collar scales; 15 lamellae under 4th toe; side of the head and flanks black, each scale with a fine white edge or tip; two black-edged dorsolateral stripes absent ..... *Adolfus masavaensis*, Mt. Elgon population

Acknowledgements

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Appendix 1

Material examined and unvouchered tissue samples [according to the new taxonomic concept]

Adolfus africanus: Cameroon: ZFMK 5804: Dikume, Rumpi Hills, 04°55' N, 09°15' E; ZFMK 67573, 68274: Edib, Bakossi Mountains, 1,250 m, 05°03' N, 09°35' E; ZFMK 59513: Mt. Kupe, 04°49' N, 09°42' E, 950 m. Democratic Republic of the Congo: ZFMK 47575–76, 53435, 55656–58: Irangi Forest, South Kivu Province; ZFMK 55655: Itebero, South Kivu Province, 01°43' S, 28°06' E; ZFMK 57598: Kahuzi-Biega National Park, South Kivu Province, 2,200 m. Rwanda. ZFMK 55767, Cyamudongo, Nyungwe Forest, 02°30' S, 29°14' E.

Adolfus alleni: Kenya: MCZ R-9281: Mount Kenya, tree line NE slope, 00.7058° 37.335082° (WGS84, Error: 26.625 miles); NMK H-35: Mount Kenya, Hombe route, 0°16.776' S, 37°13.450' E, 2,843 m; NMK H-123, NMK H-120, NMK L/3199/1: Mount Kenya, Sirimon route, near Old Moses Camp, 0°04'08.6" S, 37°18'06.5" E, 3,778 m; ZFMK 14086, 82078: Mount Kenya; NMK H-86: Mount Kenya National Park, Chogoria route, 0°08'46.85" S, 37°25'13.17" E, 3,171 m (no voucher).

Adolfus masavaensis: Kenya: ANSP 24237: Kaburomi, Mt. Elgon; FMNH 35290–91: Mount Elgon; MHNG 1578.44–46: Aberdare Mountains, Kinangop, Njabini (2500m a.s.l.); "NM Nairobi": Aberdare Mountains, seepage areas next to river a few kilometres west of the fishing lodge (00°29'02" S, 36°43'24"E, 2980 m) (no voucher); USNM 49410–11: Aberdare Range, Aberdare Range, Summit, 0°19'00" S, 36°37'00" E; ZFMK 68875: Aberdare Mountains, north of Kinangop (south of the Fishing Lodge and the Kiandongoro Gate), Páramo zone, 3,500 m; ZFMK 75001 (holotype): Mount Elgon, Koitobos, "01.05 N 34.37 E", 3372 m. Uganda: CAS 162680–81: Mount Elgon, Arugot, 9500 ft.; MCZ R-41178–79, MCZ R-41185–88: Mount Elgon, Kapchorwa, Tingey Kaburoni, 10,500 feet.

Supplemental material

Additional information is available in the online version of this article at http://www.salamandra-journal.com.

S1–4. Uncorrected *p* sequence divergences for genetic samples included in this study.

Supplemental material 1. Uncorrected *p* sequence divergence (16S data set) for genetic samples included in this study. Names arranged after the new taxonomic concept.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1 *Adolfus alleni* ZFMK 82078	—																					
2 *Adolfus alleni* NMK H86	0.000	—																				
3 *Adolfus masavaensis* Nairobi	0.021	0.021	—																			
4 *Adolfus massavaensis* ZFMK 75001	0.032	0.032	0.017	—																		
5 *Adolfus* cf. *jacksoni* 761	0.046	0.046	0.038	0.046	—																	
6 *Adolfus jacksoni* CAS 201598	0.044	0.044	0.032	0.044	0.044	—																
7 *Adolfus jacksoni* UTEP 20276	0.038	0.038	0.036	0.040	0.040	0.021	—															
8 *Adolfus jacksoni* UTEP 20279	0.038	0.038	0.036	0.040	0.040	0.021	0.000	—														
9 *Adolfus jacksoni* UTEP 20281	0.038	0.038	0.036	0.040	0.040	0.021	0.000	0.000	—													
10 *Adolfus africanus* UTEP 20269	0.109	0.109	0.092	0.095	0.090	0.107	0.097	0.097	0.097	—												
11 *Adolfus africanus* UTEP 20271	0.109	0.109	0.092	0.095	0.090	0.107	0.097	0.097	0.097	0.000	—											
12 *Congolacerta vauereselli* UTEP 20293	0.103	0.103	0.109	0.107	0.120	0.124	0.120	0.120	0.120	0.134	0.134	—										
13 *Congolacerta vauereselli* UTEP 20297	0.101	0.101	0.113	0.116	0.116	0.122	0.118	0.118	0.118	0.141	0.141	0.019	—									
14 *Congolacerta vauereselli* UTEP 20267	0.101	0.101	0.105	0.107	0.109	0.113	0.113	0.113	0.113	0.141	0.141	0.061	0.061	—								
15 *Congolacerta vauereselli* UTEP 20263	0.099	0.099	0.103	0.105	0.103	0.107	0.107	0.107	0.107	0.134	0.134	0.065	0.061	0.008	—							
16 *Gastropholis vittatus*	0.105	0.105	0.109	0.107	0.099	0.101	0.092	0.092	0.092	0.118	0.118	0.120	0.118	0.120	0.116	—						
17 *Gastropholis prasina*	0.107	0.107	0.105	0.099	0.099	0.101	0.097	0.097	0.097	0.113	0.113	0.107	0.109	0.107	0.107	0.046	—					
18 *Holaspis laevis* 764	0.107	0.107	0.101	0.097	0.101	0.113	0.111	0.111	0.111	0.113	0.113	0.111	0.111	0.113	0.113	0.105	0.097	—				
19 *Holaspis laevis* 763	0.105	0.105	0.099	0.095	0.099	0.111	0.109	0.109	0.109	0.111	0.111	0.109	0.109	0.116	0.111	0.103	0.095	0.002	—			
20 *Acanthodactylus erythrurus*	0.132	0.132	0.139	0.141	0.128	0.141	0.134	0.134	0.134	0.128	0.128	0.147	0.141	0.134	0.134	0.141	0.134	0.130	0.130	—		
21 *Atlantolacerta andreanskyi*	0.092	0.092	0.090	0.095	0.097	0.097	0.095	0.095	0.095	0.113	0.113	0.122	0.126	0.118	0.113	0.113	0.109	0.118	0.116	0.137	—	
22 *Iberolacerta cyreni*	0.124	0.124	0.122	0.122	0.124	0.126	0.126	0.126	0.126	0.141	0.141	0.139	0.139	0.128	0.128	0.132	0.128	0.134	0.132	0.162	0.130	—

Supplemental material 2. Uncorrected *p* sequence divergence (cyt *b* data set) for genetic samples included in this study. Names arranged after the new taxonomic concept.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1 *Adolfus alleni* FMK 82078	—																					
2 *Adolfus alleni* NMK H86	0.014	—																				
3 *Adolfus alleni* Nairobi	0.122	0.135	—																			
4 *Adolfus masavaensis* ZFMK 75001	0.135	0.135	0.091	—																		
5 *Adolfus* cf. *jacksoni* 761	0.132	0.132	0.139	0.125	—																	
6 *Adolfus jacksoni* CAS 201598	0.155	0.155	0.166	0.159	0.139	—																
7 *Adolfus jacksoni* UTEP 20276	0.149	0.162	0.169	0.166	0.145	0.064	—															
8 *Adolfus jacksoni* UTEP 20279	0.149	0.162	0.169	0.166	0.145	0.064	0.000	—														
9 *Adolfus jacksoni* UTEP 20281	0.149	0.162	0.169	0.166	0.145	0.064	0.000	0.000	—													
10 *Adolfus africanus* UTEP 20269	0.162	0.169	0.142	0.186	0.162	0.206	0.186	0.186	0.186	—												
11 *Adolfus africanus* UTEP 20271	0.166	0.172	0.139	0.182	0.159	0.203	0.182	0.182	0.182	0.003	—											
12 *Congolacerta vauereselli* UTEP 20293	0.226	0.230	0.236	0.203	0.216	0.230	0.216	0.216	0.216	0.209	0.206	—										
13 *Congolacerta vauereselli* UTEP 20297	0.233	0.236	0.233	0.206	0.230	0.233	0.226	0.226	0.226	0.213	0.209	0.068	—									
14 *Congolacerta vauereselli* UTEP 20267	0.209	0.216	0.206	0.203	0.199	0.230	0.226	0.226	0.226	0.199	0.196	0.145	0.155	—								
15 *Congolacerta vauereselli* UTEP 20263	0.223	0.230	0.220	0.216	0.209	0.236	0.233	0.233	0.233	0.226	0.223	0.166	0.176	0.034	—							
16 *Gastropholis vittatus*	0.199	0.206	0.203	0.196	0.216	0.216	0.209	0.209	0.209	0.186	0.182	0.172	0.166	0.206	0.213	—						
17 *Gastropholis prasina*	0.230	0.236	0.209	0.216	0.247	0.233	0.240	0.240	0.240	0.223	0.220	0.216	0.216	0.250	0.236	0.182	—					
18 *Holaspis laevis* 764	0.236	0.247	0.213	0.230	0.240	0.257	0.213	0.213	0.213	0.220	0.216	0.209	0.220	0.230	0.243	0.243	0.209	—				
19 *Holaspis laevis* 763	0.236	0.247	0.213	0.230	0.240	0.257	0.213	0.213	0.213	0.220	0.216	0.209	0.220	0.230	0.243	0.243	0.209	0.000	—			
20 *Acanthodactylus erythrurus*	0.240	0.250	0.243	0.260	0.253	0.280	0.267	0.267	0.267	0.230	0.226	0.253	0.260	0.264	0.284	0.226	0.233	0.260	0.260	—		
21 *Atlantolacerta andreanskyi*	0.206	0.216	0.193	0.209	0.203	0.226	0.213	0.213	0.213	0.220	0.216	0.220	0.216	0.236	0.236	0.186	0.199	0.209	0.209	0.243	—	
22 *Iberolacerta cyreni*	0.220	0.223	0.206	0.199	0.182	0.236	0.203	0.203	0.203	0.236	0.233	0.203	0.196	0.220	0.220	0.216	0.226	0.236	0.236	0.240	0.203	—

Supplemental material 3. Uncorrected *p* sequence divergence (c-mos data set) for genetic samples included in this study. Names arranged after the new taxonomic concept.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1 *Adolfus alleni* NMK H86	—																				
2 *Adolfus alleni* Nairobi	0.005	—																			
3 *Adolfus masavaensis* ZFMK 75001	0.007	0.002	—																		
4 *Adolfus* cf. *jacksoni* 761	0.009	0.004	0.005	—																	
5 *Adolfus jacksoni* CAS 201598	0.009	0.004	0.005	0.004	—																
6 *Adolfus jacksoni* UTEP 20276	0.004	0.009	0.011	0.009	0.005	—															
7 *Adolfus jacksoni* UTEP 20279	0.004	0.009	0.011	0.009	0.005	0.000	—														
8 *Adolfus jacksoni* UTEP 20281	0.009	0.004	0.005	0.004	0.000	0.005	0.005	—													
9 *Adolfus africanus* UTEP 20269	0.007	0.013	0.014	0.013	0.013	0.007	0.007	0.013	—												
10 *Adolfus africanus* UTEP 20271	0.007	0.013	0.014	0.013	0.013	0.007	0.007	0.013	0.000	—											
11 *Congolacerta vauereselli* UTEP 20293	0.022	0.027	0.027	0.027	0.027	0.022	0.022	0.027	0.018	0.018	—										
12 *Congolacerta vauereselli* UTEP 20297	0.024	0.029	0.029	0.029	0.029	0.024	0.024	0.029	0.020	0.020	0.002	—									
13 *Congolacerta vauereselli* UTEP 20267	0.025	0.020	0.018	0.020	0.020	0.025	0.025	0.020	0.022	0.022	0.016	0.018	—								
14 *Congolacerta vauereselli* UTEP 20263	0.027	0.022	0.020	0.022	0.022	0.027	0.027	0.022	0.024	0.024	0.018	0.020	0.002	—							
15 *Gastropholis vittatus*	0.031	0.025	0.027	0.022	0.025	0.031	0.031	0.025	0.031	0.031	0.038	0.040	0.031	0.033	—						
16 *Gastropholis prasina*	0.029	0.024	0.025	0.020	0.024	0.029	0.029	0.024	0.029	0.029	0.036	0.038	0.029	0.031	0.009	—					
17 *Holaspis laevis* 764	0.045	0.040	0.042	0.040	0.040	0.045	0.045	0.040	0.042	0.042	0.051	0.053	0.043	0.045	0.051	0.049	—				
18 *Holaspis laevis* 763	0.043	0.038	0.040	0.038	0.038	0.043	0.043	0.038	0.040	0.040	0.049	0.051	0.042	0.043	0.049	0.047	0.002	—			
19 *Acanthodactylus erythrurus*	0.040	0.036	0.038	0.036	0.036	0.040	0.040	0.036	0.036	0.036	0.038	0.040	0.033	0.034	0.047	0.043	0.060	0.058	—		
20 *Atlantolacerta andreanskyi*	0.020	0.025	0.027	0.027	0.027	0.022	0.022	0.027	0.018	0.018	0.025	0.027	0.029	0.031	0.038	0.036	0.047	0.045	0.043	—	
21 *Iberolacerta cyreni*	0.027	0.033	0.034	0.033	0.033	0.027	0.027	0.033	0.024	0.024	0.027	0.029	0.031	0.033	0.043	0.042	0.054	0.053	0.047	0.027	—

Supplemental material 4. Uncorrected *p* sequence divergence (RAG1 data set) for genetic samples included in this study. Names arranged after the new taxonomic concept.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1 *Adolfus alleni* NMK H86	—																				
2 *Adolfus masavaensis* ZFMK 75001	0.001	—																			
3 *Adolfus* cf. *jacksoni* 761	0.003	0.004	—																		
4 *Adolfus jacksoni* CAS 201598	0.009	0.007	0.012	—																	
5 *Adolfus jacksoni* UTEP 20276	0.009	0.007	0.012	0.000	—																
6 *Adolfus jacksoni* UTEP 20279	0.009	0.007	0.012	0.000	0.000	—															
7 *Adolfus jacksoni* UTEP 20281	0.009	0.007	0.012	0.000	0.000	0.000	—														
8 *Adolfus africanus* UTEP 20269	0.015	0.013	0.018	0.021	0.021	0.021	0.021	—													
9 *Adolfus africanus* UTEP 20271	0.016	0.015	0.019	0.022	0.022	0.022	0.022	0.001	—												
10 *Congolacerta vauereselli* TEP 20293	0.034	0.033	0.037	0.037	0.037	0.037	0.037	0.040	0.041	—											
11 *Congolacerta vauereselli* UTEP 20297	0.037	0.036	0.040	0.040	0.040	0.040	0.040	0.043	0.044	0.044	—										
12 *Congolacerta vauereselli* UTEP 20267	0.034	0.033	0.037	0.037	0.037	0.037	0.037	0.043	0.043	0.015	0.019	—									
13 *Congolacerta vauereselli* UTEP 20263	0.036	0.034	0.039	0.039	0.039	0.039	0.039	0.044	0.044	0.016	0.021	0.001	—								
14 *Gastropholis vittatus*	0.022	0.021	0.025	0.028	0.028	0.028	0.028	0.031	0.033	0.039	0.041	0.037	0.039	—							
15 *Gastropholis prasina*	0.030	0.028	0.033	0.033	0.033	0.033	0.033	0.039	0.040	0.043	0.046	0.041	0.043	0.010	—						
16 *Holaspis laevis* 764	0.027	0.025	0.030	0.030	0.030	0.030	0.030	0.036	0.037	0.040	0.043	0.040	0.041	0.034	0.039	—					
17 *Holaspis laevis* 763	0.027	0.025	0.030	0.030	0.030	0.030	0.030	0.036	0.037	0.040	0.043	0.040	0.041	0.034	0.039	0.000	—				
18 *Acanthodactylus erythrurus*	0.034	0.036	0.037	0.043	0.043	0.043	0.043	0.043	0.044	0.039	0.041	0.041	0.043	0.040	0.047	0.046	0.046	—			
19 *Atlantolacerta andreanskyi*	0.016	0.018	0.019	0.025	0.025	0.025	0.025	0.028	0.030	0.036	0.039	0.034	0.036	0.024	0.031	0.031	0.031	0.036	—		
20 *Iberolacerta cyreni*	0.024	0.025	0.027	0.033	0.033	0.033	0.033	0.036	0.037	0.043	0.046	0.043	0.044	0.036	0.043	0.037	0.037	0.040	0.025	—	