A molecular phylogeny of Equatorial African Lacertidae, with the description of a new genus and species from eastern Democratic Republic of the Congo

ELI GREENBAUM[1]*, CESAR O. VILLANUEVA[1], CHIFUNDERA KUSAMBA[2], MWENEBATU M. ARISTOTE[3] and WILLIAM R. BRANCH[4,5]

[1]*Department of Biological Sciences, University of Texas at El Paso, 500 West University Avenue, El Paso, TX 79968, USA*

[2]*Laboratoire d'Herpétologie, Département de Biologie, Centre de Recherche en Sciences Naturelles, Lwiro, République Démocratique du Congo*

[3]*Institut Superieur d'Ecologie pour la Conservation de la Nature, Katana Campus, Sud Kivu, République Démocratique du Congo*

[4]*Bayworld, P.O. Box 13147, Humewood 6013, South Africa*

[5]*Research Associate, Department of Zoology, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa*

Currently, four species of the lacertid lizard genus *Adolfus* are known from Central and East Africa. We sequenced up to 2825 bp of two mitochondrial [16S and cytochrome *b* (cyt *b*)] and two nuclear [(c-mos (oocyte maturation factor) and RAG1 (recombination activating gene 1)] genes from 41 samples of *Adolfus* (representing every species), two species each of *Gastropholis* and *Holaspis*, and in separate analyses combined these data with GenBank sequences of all other Eremiadini genera and four Lacertini outgroups. Data from DNA sequences were analysed with maximum parsimony (PAUP), maximum-likelihood (RAxML) and Bayesian inference (MrBayes) criteria. Results demonstrated that *Adolfus* is not monophyletic: *Adolfus africanus* (type species), *Adolfus alleni*, and *Adolfus jacksoni* are sister taxa, whereas *Adolfus vauereselli* and a new species from the Itombwe Plateau of Democratic Republic of the Congo are in a separate lineage. *Holaspis* and *Gastropholis* were recovered in separate clades. Based on these molecular data, relatively substantial sequence divergence, and multiple morphological differences, we describe a new genus of lacertid for the lineage including *A. vauereselli* and the new Itombwe species. The recognition of this new, endemic genus underscores the conservation importance of the Albertine Rift, especially the Itombwe Plateau, a unique region that is severely threatened by unchecked deforestation, mining, and poaching.

INTRODUCTION

Meadow and forest lizards of the lacertid genus *Adolfus* are currently known from Central and East Africa, including *Adolfus africanus* (mid- to low-elevation forests from Cameroon to Kenya), *Adolfus alleni* (montane moorlands of Kenya and Uganda), and *Adolfus jacksoni* and *A. vauereselli*, which are both known from mid- to high-elevation forests in countries surrounding the Albertine Rift (Spawls *et al.*, 2002; Köhler *et al.*, 2003). *Adolfus* are medium-sized (total size to 25.6 cm), relatively slim

*Corresponding author. E-mail: egreenbaum2@utep.edu

lizards, and tend to be good climbers on standing and fallen timber, rocky walls, holes, and crevices (*A. africanus* is also known to climb twiggy and herbaceous plants), but tend to hunt on the ground (Arnold, 1989a, 1998; Spawls *et al*., 2002). Recent work on this genus has included aspects of reproduction (*A. jacksoni*, Goldberg, 2009), endoparasites (*A. jacksoni*, Goldberg & Bursey, 2009), geographical distribution (*A. africanus*, Köhler *et al*., 2003), and morphology and colour pattern (*A. jacksoni*, Poblete, 2002).

The taxonomic status and affinities of the currently recognized species of *Adolfus* have changed considerably over time. The genus *Adolfus* was first proposed by Sternfeld (1912) for the taxon *Adolfus fridericianus*, which was presumably in honour of Adolphus Frederick, Duke of Mecklenburg, who led the German Central Africa Expedition in 1907–08 when the specimens were collected (Frederick, 1910). In his opus on the family Lacertidae, Boulenger (1920) considered *A. fridericianus* to be a synonym of *Algiroides africanus* (= *Algyroides africanus*), a species he described in 1906, and recognized *Algiroides alleni*, *Lacerta jacksonii* (a species he described in 1899), and *Lacerta vauereselli*. Based on morphological characters, Arnold (1973) resurrected the genus *Adolfus* for *A. africanus*, *A. alleni*, and *A. vauereselli*, and noted a close relationship between this genus and *Bedriagaia*, *Gastropholis*, and *L. jacksoni*. In morphology-based parsimony and compatibility analyses, Arnold (1989a) transferred *L. jacksoni* to the genus *Adolfus*, synonymized *Bedriagaia* with *Gastropholis*, recognized a clade called the 'Equatorial African group' including *Adolfus*, *Gastropholis*, and *Holaspis* (a well-supported clade recovered in a later morphology-based phylogeny by Harris, Arnold & Thomas, 1998), and discussed the problematic relationship of *Holaspis* to the paraphyletic genus *Adolfus*; if the latter two genera were to be joined, *Holaspis* would have priority. Arnold (1989a, b) admitted that *Adolfus* was poorly defined, and considered *A. jacksoni* to be the most plesiomorphic member of the Equatorial African clade. In a more extensive morphological analysis of the entire family Lacertidae, Arnold (1989b) grouped the Equatorial African Clade with *Lacerta jayakari* (now *Omanosaura jayakari*), *Lacerta australis* (now *Australolacerta australis*) and several other genera (e.g. *Tropidosaura*, *Poromera*, *Nucras*) in an 'Ethiopian and advanced Saharo-Eurasian forms' (ESE) group, which was later included in an 'Armatured Clade' (Afrotropical species plus *Eremias*, *Acanthodactylus*, *Mesalina*, and *Ophisops*) in recognition of the members' unique supporting structure of the male hemipenis (Arnold, 1986a, 1998; Harris *et al*., 1998). Mayer & Benyr (1994) used an albumin-based analysis of most lacertid genera to imply paraphyly of the ESE group, with some of the Saharo-Eurasian genera grouping with European lacertids. Based on a combination of morphology and mtDNA data that contradicted several findings of Mayer & Benyr (1994), Harris *et al*. (1998) assigned the subfamily Eremiainae (Szczerbak, 1975) to the Armatured Clade.

More recent analyses of lacertids with mitochondrial data have done little to clarify the position of *Adolfus* in relation to other members of the Equatorial African clade, or the ESE group as a whole. Although Fu (1998) recovered a monophyletic 'African clade' in a mitochondrial phylogeny of lacertids, no members of the Equatorial African clade were included. Harris (1999) combined the mitochondrial data of Fu (1998) and Harris *et al*. (1998) with some new data to produce a phylogeny of Lacertidae, but support for the ESE clade (still recognized as Eremiainae) was weak; two samples of *Adolfus* (*A. africanus* and *A. jacksoni*) were not supported as sister taxa. Fu (2000) published another phylogeny of Lacertidae with six mitochondrial genes (4.7 kb of DNA data), with most trees supporting the monophyly of the ESE clade, but with the exception of three closely related genera (*Nucras*, *Latastia*, and *Heliobolus*), relationships amongst ESE genera were unclear, and the monophyly of two samples of *Adolfus* (*A. jacksoni* and *A. vauereselli*) was again not supported. The latter two species of *Adolfus* were not recovered as monophyletic in a study focused on *Australolacerta australis* with mitochondrial data (Salvi, Bombi & Vignoli 2011).

Mayer & Pavlicev (2007) published the first lacertid phylogeny based on nuclear data [c-mos (oocyte maturation factor) and RAG1 (recombination activating gene 1)], and recovered two clades within a well-supported ESE (Eremiainae) group: clade B$_1$, mainly from sub-Saharan Africa, including *Poromera*, *Nucras*, *Latastia*, *Philochortus*, *Pseuderemias*, *Heliobolus*, *Tropidosaura*, *Pedioplanis*, *Ichnotropis*, and *Meroles*; and clade B$_2$, mainly from the Saharo-Eurasian region, including *Ophisops*, *Omanosaura*, *Acanthodactylus*, *Eremias*, *Mesalina*, *Adolfus*, and *Holaspis*, with the latter two Central African genera as well-supported sister taxa. Arnold, Arribas & Carranza (2007) re-analysed the data sets of Harris *et al*. (1998) and Fu (2000), and published yet another lacertid phylogeny based on two mitochondrial genes [12S and cytochrome *b* (cyt *b*)]. Although their main focus was not on the ESE group, they redefined the Eremiainae as the tribe Eremiadini, and placed the North African monotypic genus *Atlantolacerta* as the most basal member of the Eremiadini. Pavlicev & Mayer (2009) criticized the data set of the latter study as 'relatively short mitochondrial sequences when all taxa are considered', rejected the tribe Eremiadini (instead recognizing it as subfamily Eremiadinae), but confirmed the placement of *Atlantolacerta* as the most basal member of the group. Hipsley *et al*. (2009) used mitochondrial and

Table 1. Primer sequences used in this study

Name	Source	Sequence	Gene
16SA-L	Palumbi *et al.* (1991)	5′-CGCCTGTTTATCAAAAACAT-3′	16S
16SB-H	Palumbi *et al.* (1991)	5′-CCGGTCTGAACTCAGATCACGT-3′	16S
Cyt*b*F700	Bauer *et al.* (2007)	5′-CTTCCAACACCAYCAAACATCTCAGCATGATGAAA-3′	cyt *b*
Cyt*b*R700	Bauer *et al.* (2007)	5′-ACTGTAGCCCCTCAGAATGATATTTGTCCTCA-3′	cyt *b*
Hcmos3	Mayer & Pavlicev (2007)	5′-GGTGATGGCAAATGAGTAGAT-3′	c-mos
L-1zmos	Mayer & Pavlicev (2007)	5′-CTAGCTTGGTGTTCTATAGACTGG-3′	c-mos
Hcmos1	Mayer & Pavlicev (2007)	5′-GCAAATGAGTAGATGTCTGCC-3′	c-mos
R13	Groth & Barrowclough (1999)	5′-TCTGAATGGAAATTCAAGCTGTT-3′	RAG1
R18	Groth & Barrowclough (1999)	5′-GATGCTGCCTCGGTCGGCCACCTTT-3′	RAG1
RAG1f700	Bauer *et al.* (2007)	5′-GGAGACATGGACACAATCCATCCTAC-3′	RAG1
RAG1r700	Bauer *et al.* (2007)	5′-TTTGTACTGAGATGGATCTTTTTGCA-3′	RAG1
RAG-R1	Mayer & Pavlicev (2007)	5′-AAAATCTGCCTTCCTGTTATTG-3′	RAG1
RAG-fo	Mayer & Pavlicev (2007)	5′-GAAAAGGGCTACATCCTGG-3′	RAG1
RAG-re	Mayer & Pavlicev (2007)	5′-CCAGTTATTGCTTTTACAGTTC-3′	RAG1

cyt *b*, cytochrome *b*.

nuclear data from several previous studies to confirm the main findings of Mayer & Pavlicev (2007), but continued to recognize the tribe Eremiadini (*sensu* Arnold *et al.*, 2007) and revised the date of its origin to the mid to late Eocene, when the group could have invaded north-western Africa via small island chains.

Three of the four species of *Adolfus* can be found in eastern Democratic Republic of the Congo (DRC), which harbours a panoply of habitats ranging from lowland rainforest to alpine grassland (Vande weghe, 2004; Bastin *et al.*, 2004). Based on fieldwork in the poorly known Itombwe Plateau (eastern DRC) by E. G., C. K., and M. M. A., we collected several specimens of an *Adolfus* that does not fit the description of any currently recognized species. To clarify the position of the Itombwe population to other *Adolfus*, we sequenced multiple genes from several members of the Equatorial African group of lacertids (*Adolfus*, *Gastropholis*, and *Holaspis*), and discovered that the Itombwe population is a new species belonging to a lineage that deserves recognition as a distinct genus. We follow the general lineage species concept (de Queiroz, 1998, 1999), an extension of the evolutionary species concept (Wiley, 1981), which provides a consistent philosophical framework for taxonomic decisions, and rejects the premise of subspecies as natural groups. Our species recognition criteria (Wiens & Penkrot, 2002; de Queiroz, 2007) correspond in part to traditional morphological species, which are diagnosed by unique morphological characters, size, and colour pattern. We utilize a molecular estimate of phylogenetic relationships that is based on multiple, unlinked markers from multiple individuals within species to guide species delimitation and diagnosis, and identify relevant comparisons for species diagnoses (Barraclough & Davies, 2005; Brown *et al.*, 2009).

MATERIAL AND METHODS
DNA EXTRACTION, PCR AMPLIFICATION, AND SEQUENCING

Two mitochondrial (16S and cyt *b*) and two nuclear (c-mos and RAG1) genes were sequenced from all genera in the Equatorial African Group, including 41 samples of all species of *Adolfus*, *Holaspis guentheri*, *Holaspis laevis*, *Gastropholis prasina*, *Gastropholis vittatus*, and five outgroup taxa, including: *Acanthodactylus erythrurus* (clade B$_2$ of Mayer & Pavlicev, 2007), the basal-most member of Eremiadini (*Atlantolacerta andreanskyi*, Arnold *et al.*, 2007), and three Lacertini genera (*Iberolacerta cyreni*, *Podarcis muralis*, *Timon tangitanus*). Some samples (e.g. *A. alleni*) did not amplify for all genes; all sequences were deposited in GenBank (Appendix 1). 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 (Table 1) with an initial denaturation step of 95 °C for 2 min, followed by denaturation at 95 °C for 35 s, 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 puri-

fied 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 at 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. Four samples of *Adolfus* showed evidence of pseudogenes (i.e. six codon insertion relative to all other lacertids with a reading frame shift) for c-mos, including *A. jacksoni* (CAS 201598), *A. vauereselli* (UTEP 20294, 20296), and the new species (UTEP 20263); Pavlicev & Mayer (2006) also reported c-mos pseudogenes in three species of *Lacerta*. Our pseudogene sequences were excluded from the data set of this study.

SEQUENCE ALIGNMENT AND PHYLOGENETIC ANALYSES

An initial alignment of each gene was produced in MEGALIGN (DNA Star) with the ClustalW algorithm, and manual adjustments were made in MacClade 4.08 (Maddison & Maddison, 2005). Protein-coding genes were translated to 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. Phylogenetic relationships amongst 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-addition replicates, accelerated character transformation and tree bisection-reconnection branch swapping, zero-length branches collapsed to polytomies, and gaps treated as missing data; we used nonparametric bootstraps (1000 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 best fitted 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 1000 bootstrap replicates, with the rapid-hill climbing algorithm (Stamatakis, Hoover & Rougemont, 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 trees and run for 10 000 000 generations; Markov chains were sampled every 1000 generations. Convergence was checked by importing the trace files (p files) from the MrBayes output to the computer program TRACER v.1.3 (http://tree.bio.ed.ac.uk/software/tracer/), which plots the likelihood values against generation number. Once the graphical plot levelled off, convergence had been met; we conservatively discarded 25% of 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). To test the monophyly of polyphyletic lineages recovered in our phylogenetic analyses of the four-gene data set, we used the Shimodaira–Hasegawa (SH) and approximately unbiased (AU) tests as implemented in CONSEL v0.1i (Shimodaira & Hasegawa, 2001; Shimodaira, 2002). We tested the hypothesis of zero-length branches for polyphyletic lineages of the Equatorial African lacertids by comparing the likelihood of the optimal ML tree from the four-gene data set (16S, cyt *b*, c-mos and RAG1) to the likelihood of the optimal tree with one branch collapsed with the 'describe trees' function in PAUP* (*sensu* Poe & Chubb, 2004), and a Bonferroni-corrected *P*-value of 0.025.

Combining data from multiple mitochondrial genes is appropriate because the entire animal mitochondrial genome is inherited as a single unit, and different mitochondrial genes are not independent estimates of organismal phylogeny (Moore, 1995; Page, 2000). We combined mitochondrial and nuclear gene data sets if there was no strong bootstrap support for conflicting nodes [exceeding 70% for MP analyses (Hillis & Bull, 1993) and 95% for ML and BI analyses (Leaché & Reeder, 2002; Wilcox *et al.*, 2002)] when these data sets were analysed independently. After preliminary analyses confirmed that there was no conflict between mitochondrial and nuclear gene data sets (data not shown), we conducted two analyses: (1) c-mos and a 1012-bp fragment of RAG1 (primers from Mayer & Pavlicev, 2007) for samples from this study and previously sequenced lacertids from GenBank (Appendix 1) with *Gallotia* as the outgroup; and (2) both mitochondrial (16S and cyt *b*) genes, c-mos, and a 1394-bp fragment of RAG1

[primers from Groth & Barrowclough (1999) and Bauer *et al*. (2007)] for every sample from this study with three Lacertini outgroups.

MORPHOLOGY

Specimens examined for this study (Appendix 2) were preserved in 10% buffered formalin in the field, and transferred to 70% ethanol at the conclusion of each expedition. Tissues were harvested before formalin fixation from the liver or hind limb muscle of lizards, and preserved in 95% ethanol. Institutional abbreviations are listed at http://www.asih.org/codons.pdf. The first author recorded morphometric data from these preserved specimens with vernier callipers to the nearest 0.1 mm under a stereomicroscope. Colour descriptions were based on preserved specimens, field notes, and colour digital images in life. Sex was determined by direct examination of gonads, or from the presence of everted hemipenes as noted in field notes. X-rays for descriptions of the postcranial skeleton were taken with a Kodak Image Station In-Vivo FX (Carestream Health, Inc., Rochester, NY, USA) under the following conditions: f-stop: 8.0; field of view: 198 mm; focal plane: 0; exposure time: 288 s; kilovolt potential energy: 35; filter: 600 WB.

Meristic and mensural characters were chosen from lacertid studies by Arnold (1989b) and Lue & Lin (2008). Measurements were taken on the right side of the lizard and included: snout–vent length (SVL, from tip of snout to anterior margin of vent); tail length (TL, from posterior margin of vent to tail tip, measured only from specimens with complete and original tails); head length (HL, from tip of snout to anterior margin of ear opening); maximum head width (HW, measured at the broadest point); head height (HH, measured at the jaw rictus); skull length (SKL, from tip of snout to posterior margin of occipital); snout–eye length (SEL, from tip of snout to anterior margin of eye); mouth length (ML); snout–arm length (SAL, from tip of snout to anterior margin of forelimb); axilla–groin distance (AGD, from posterior edge of forelimb insertion to anterior edge of hind limb insertion); humerus length (HML); radius–ulna length (RUL); femur length (FL); tibia–fibula length (TFL); and longest toe length (LTL, length of fourth toe on hind limb).

Meristic data were taken from the right side of each lizard, except for femoral pore counts if field/museum tags were tied to the right leg. Definition of scales follow those of Arnold (1989b) and Arnold *et al*. (2007), and included: chin shields (CS); femoral pores (FP); supralabials (SL); infralabials (IL); supraoculars (SO); supraciliaries (SC); supraciliary granules (SG); supratemporals (ST); anterior dorsal scale rows (ADS, counted transversely at posterior insertion of forelimbs); posterior dorsal scale rows (PDS, counted transversely at anterior insertion of hind limbs); dorsal scale rows at midbody (DSR, counted transversely at midpoint between fore and hind limbs); dorsal scale numbers (DSN, counted longitudinally from posterior margin of occipital to posterior margin of hind limbs); ventral rows (VR, counted transversely at midbody); ventral scale numbers (VN, counted longitudinally from posterior margin of collars to anterior margin of preanal scales, average taken from the middle two rows); caudal scales (CDS, counted around the tail at the position of the 11th and 15th scale to avoid the difference between males and females); and subdigital lamellae on fingers (SDF1 to SDF5) and toes (SDT1 to SDT5).

RESULTS

MOLECULAR PHYLOGENETICS

Relationships amongst members of the Equatorial African Group of lacertid lizards are shown in Figures 1 and 2; MP, ML, and BI analyses produced nearly identical topologies for each data set, with only minor differences in bootstrap support for each analysis. For the four-gene data set (Fig. 2), we noted a six-codon deletion in the RAG1 gene (between positions 134–151) in multiple samples of *A. africanus* and *A. jacksoni*.

The following models of nucleotide substitution were selected by jModeltest for BI analyses: 16S [general time reversible (GTR) + invariable sites (I) + gamma distribution (G)]; cyt *b* first codon (TIM (transitional) 2ef + I); cyt *b* second codon (GTR + I); cyt *b* third codon (GTR + I + G); c-mos first codon (HKY (Hasegawa, Kishino and Yano) + G); c-mos second codon (TIM3 + G); c-mos third codon (TrN (Tamura-Nei) + G); RAG1 first codon (TrN + I); RAG1 second codon (TPM1uf + G); RAG1 third codon (TPM (Kimura three parameter) 3uf + I + G). The MP analysis of the c-mos/RAG1 data set (Fig. 1) included 1605 bp (933 constant, 429 parsimony-informative, 243 parsimony uninformative) and resulted in 28 908 most parsimonious trees [length = 1511, consistency index (CI) = 0.574, retention index (RI) = 0.768]; the ML analysis likelihood score was –11 052.633819. The MP analysis of the four-gene data set (Fig. 2) included 2825 bp (2185 constant, 444 parsimony-informative, 196 parsimony uninformative) and resulted in 5368 most parsimonious trees (length = 1588, CI = 0.520, RI = 0.777); the ML analysis likelihood score was –11 185.625563.

The c-mos/RAG1 tree (Fig. 1) showed strong support for a monophyletic Eremiadini, and a well-supported clade of Ethiopian lacertids (corresponding to clade B_1 of Mayer & Pavlicev, 2007). The remaining Eremiadini lineages were recovered with the following well-supported clades: *Eremias* (two species),
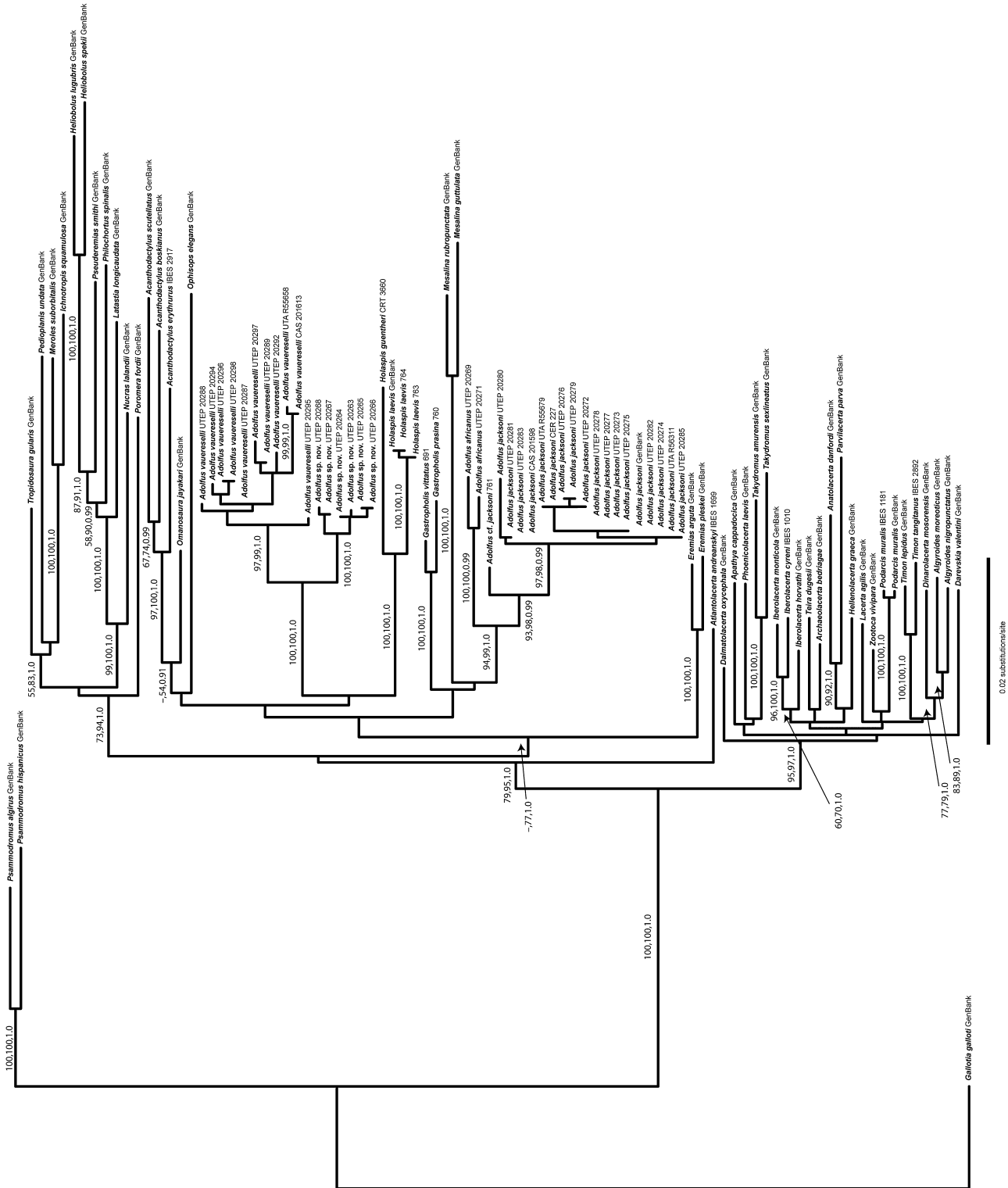
Figure 1. Maximum likelihood phylogeny (RAxML tree) of lacertid lizards in the Equatorial African Group, based on the combined nuclear c-mos (oocyte maturation factor)/RAG1 (recombination activating gene 1) data set from this study and GenBank samples from Mayer & Pavlicev (2007). Bootstrap and posterior probability values for each well-supported node are listed in the order: maximum parsimony/maximum likelihood/Bayesian inference.
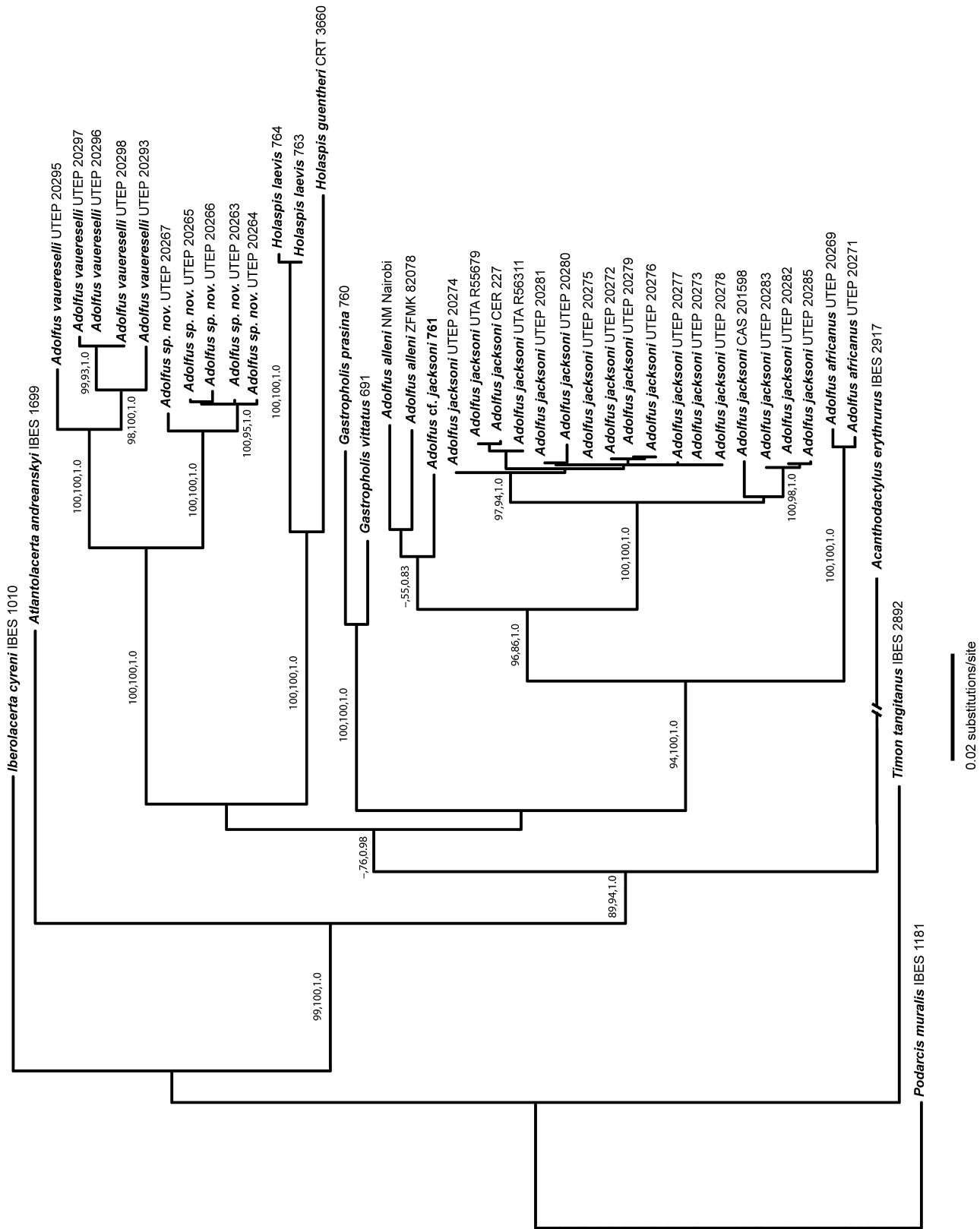
Figure 2. Maximum likelihood phylogeny (RAxML tree) of the Equatorial African clade of lizards based on the combined 16S, cytochrome *b* (cyt *b*), *c-mos*, and RAG1 genes. Bootstrap and posterior probability values for each well-supported node are listed in the order: maximum parsimony/maximum likelihood/Bayesian inference.

Acanthodactylus (three species), *A. vauereselli* + *A.* sp. nov. (Itombwe Plateau), and *A. africanus* + *A. jacksoni*. The four-gene data set (Fig. 2) also shows well-supported clades for *A. vauereselli* + *A.* sp. nov. (Itombwe Plateau), and *A. africanus* + *A. alleni* + *A. jacksoni*, with both of these lineages included in a clade with *Acanthodactylus*, *Gastropholis*, and *Holaspis*, and a well-supported sister relationship of all of these taxa to *Atlantolacerta*, again confirmed as the most basal member of Eremiadini.

Amongst genera of previously recognized lacertids, uncorrected *p* sequence divergence for the c-mos/RAG1 data set (Table 2) ranged from 2.4% (*Ichnotropis* vs. *Meroles*) to 8.5% (*Heliobolus* vs. *Ophisops*). Amongst previously recognized genera of the Equatorial African Group, uncorrected *p* sequence divergence for the c-mos/RAG1 data set ranged from 2.2–3.7% (*Adolfus sensu stricto* vs. *Gastropholis*) to 3.5–4.1% (*Adolfus sensu stricto* vs. *Holaspis*); divergences between the two well-supported lineages of *Adolfus* [*A. africanus* + *A. alleni* + *A. jacksoni* vs. *A. vauereselli* + *A.* sp. nov. (Itombwe Plateau)] ranged from 2.7–3.4% (Table 2). Uncorrected *p* sequence divergence for the c-mos/RAG1 data set ranged from 0.0–0.1% within populations of *A. vauereselli* and *A.* sp. nov. (Itombwe Plateau), but ranged from 1.3–2.2% between these well-supported taxa; equivalent 16S mitochondrial data ranged from 0.0–1.5% within populations of each taxon to 5.9–6.3% between these taxa (data not shown). Between the two disjunct, montane populations of *A. alleni*, cyt *b* divergence (the only gene that amplified for both samples) was 10.9% (data not shown). Hypothesis tests that constrained the monophyly of *Adolfus* were not significantly different from our preferred tree (AU: *P* = 0.381; SH: *P* = 0.382). Tests for zero-length branches for the lineage containing *Holaspis* + *A. vauereselli* + *A.* sp. nov. (*P* = 0.263) and the lineage containing *Gastropholis* + *A. africanus* + *A. alleni* + *A. jacksoni* (*P* = 0.139) were not significantly different from zero.

TAXONOMIC IMPLICATIONS

Our molecular data sets indicate that *Adolfus* is polyphyletic (with weak support) with regard to *Acanthodactylus*, *Gastropholis*, and *Holaspis* (Figs 1, 2); there is a six-codon deletion in the RAG1 gene for the lineage including *A. alleni*, *A. africanus*, and *A. jacksoni*, and c-mos/RAG1 uncorrected *p* sequence divergence between the two well-supported *Adolfus* lineages is equal to or exceeds divergences noted for previously recognized lacertid genera (Table 2; Mayer & Pavlicev, 2007). Although our hypothesis tests that constrained the monophyly of *Adolfus* were not significant, these results are not surprising given the zero-length branches separating the lineages of Equatorial

African lacertids. As there are numerous mensural, meristic, and qualitative differences between the well-established genera of Equatorial African lacertids (Table 3; Arnold, 1989a), and considerable taxonomic instability would be created by grouping this diverse assemblage of lizards into one genus, we recognize each well-supported lineage of *Adolfus* as a distinct genus. Accounts for both genera are provided below, and follow the format of Arnold *et al.* (2007).

Our data also suggest that species diversity within *Adolfus sensu stricto* is currently underestimated. The sequence divergence (cyt *b*) between the samples of *A. alleni* from the Aberdares and Mt Kenya suggest that these populations are not conspecific, and Arnold (1989a: table 2) provided mensural and meristic data that showed marked differences amongst populations from Mt Kenya, Mt Elgon, and the Aberdares. Loveridge (1957) did not recognize any of these populations as taxonomically distinct, but additional sampling is needed before taxonomic recognition of these populations would be warranted. Further study is also needed on the Arusha, Tanzania population of *A. jacksoni*, which has a colour pattern that is noticeably different from populations in the Albertine Rift (see also Poblete, 2002; Spawls *et al.*, 2002).

ADOLFUS STERNFELD, 1912

Type species: Adolfus africanus (Sternfeld, 1912 '1913') [= *Adolfus fridericianus* Sternfeld 1912 '1913'; Adolphs (2006) noted Sternfeld's chapter was published in 1912 before the complete work in 1913.].

Synonymy

1. *Algiroides* Duméril & Bibron, 1839 (part); Boulenger, 1906. Proceedings of the Zoological Society of London 1906:570 [*Algiroides africanus*]; Barbour, 1914. Proceedings of the New England Zoological Club, Boston 4:97 [*Algiroides alleni*].
2. *Lacerta* Linnaeus, 1758 (part); Boulenger, 1899. Proceedings of the Zoological Society of London 1899:96 [*Lacerta jacksoni*]; Lönnberg in Sjöstedt, 1907 '1910'. Wissenschaftliche Ergebnisse der Swedischen Zoologischen Expedition nach dem Kilimandjaro, dem Meru und den umgebenden Massaisteppen Deutsch-Ostafrikas 4:5 [*Lacerta jacksoni kibonotensis*]; Boulenger 1920. Monograph of the Lacertidae. Vol. 1:295 [*Lacerta jacksonii*].

Content: Adolfus africanus (Boulenger, 1906); *A. alleni* (Barbour, 1914); *A. jacksoni* (Boulenger, 1899).

Distribution: Western Cameroon east to southern Sudan, Uganda, Kenya, and Tanzania, and south to north-western Zambia (Köhler *et al.*, 2003), with

Table 2. Uncorrected *p* sequence divergence (c-mos/RAG1 data set) for selected samples of *Adolfus* and other Eremiadini genera included in this study

	1	2	3	4	5	6	7	8	9	10	11	12
1 *Acanthodactylus erythrurus*	–											
2 *Adolfus africanus* (Hombo, DRC)	0.04219	–										
3 *Adolfus jacksoni* (Rukiva, Rwanda)	0.04085	0.02244	–									
4 *Adolfus jacksoni* (Arusha, Tanzania)	0.03840	0.01926	0.00835	–								
5 *Adolfus vauereselli* (Kahuzi-Biega NP, DRC)	0.04440	0.02735	0.03468	0.03390	–							
6 **Adolfus sp. nov.** (holotype)	0.03952	0.03264	0.03085	0.03144	0.01610	–						
7 *Atlantolacerta andreanskyi*	0.03963	0.03011	0.02969	0.02696	0.03358	0.03337	–					
8 *Eremias arguta*	0.04087	0.03452	0.03015	0.02817	0.03466	0.03271	0.03095	–				
9 *Gastropholis vittatus*	0.04130	0.03077	0.02514	0.02183	0.03854	0.03323	0.03082	0.03206	–			
10 *Heliobolus lugubris*	0.07169	0.06906	0.06469	0.06277	0.07254	0.06668	0.06189	0.06529	0.06534	–		
11 *Holaspis laevis* (Usambaras, Tanzania)	0.05157	0.04085	0.03455	0.03519	0.04305	0.03964	0.03788	0.03955	0.03833	0.07220	–	
12 *Ichnotropis squamulosa*	0.05354	0.05375	0.05100	0.04813	0.05742	0.05487	0.04363	0.05160	0.05039	0.07489	0.05350	–
13 *Latastia longicaudata*	0.06032	0.06008	0.05526	0.05187	0.06104	0.05789	0.05115	0.05587	0.05340	0.05022	0.06403	0.06421
14 *Meroles suborbitalis*	0.05024	0.04919	0.04710	0.04420	0.05211	0.04968	0.04229	0.04771	0.04838	0.07282	0.05148	0.02392
15 *Mesalina guttulata*	0.05473	0.05182	0.05150	0.04872	0.05979	0.05602	0.05244	0.05336	0.05216	0.08035	0.05964	0.06860
16 *Nucras lalandii*	0.05089	0.05177	0.04775	0.04485	0.05343	0.04974	0.04357	0.04648	0.04776	0.05967	0.05465	0.05478
17 *Omanosaura jayakari*	0.03586	0.03258	0.03078	0.03008	0.03209	0.03021	0.03158	0.03076	0.03205	0.06842	0.03829	0.04784
18 *Ophisops elegans*	0.05285	0.05491	0.05214	0.05054	0.05140	0.04847	0.05303	0.04896	0.05342	0.08475	0.05712	0.06608
19 *Pedioplanis undata*	0.05859	0.05364	0.04838	0.04734	0.05393	0.05226	0.04677	0.04677	0.04896	0.07156	0.05650	0.05478
20 *Philochortus spinalis*	0.06041	0.05757	0.05785	0.05515	0.06237	0.05757	0.05246	0.05246	0.05781	0.05089	0.06660	0.06234
21 *Poromera fordii*	0.04717	0.04981	0.04900	0.04734	0.04941	0.04908	0.04292	0.04583	0.04836	0.06340	0.05399	0.05602
22 *Pseuderemias smithi*	0.06599	0.06073	0.05402	0.05318	0.06040	0.05600	0.05304	0.05278	0.05713	0.04772	0.06530	0.06734
23 *Tropidosaura gularis*	0.04273	0.04338	0.04083	0.03838	0.04438	0.04153	0.03532	0.03955	0.03959	0.06215	0.04457	0.03966

Table 2. *Continued*

	13	14	15	16	17	18	19	20	21	22	23
1 *Acanthodactylus erythrurus*											
2 *Adolfus africanus* (Hombo, DRC)											
3 *Adolfus jacksoni* (Rukiva, Rwanda)											
4 *Adolfus jacksoni* (Arusha, Tanzania)											
5 *Adolfus vauereselli*											
6 **Adolfus sp. nov.** (holotype) (Kahuzi-Biega NP, DRC)											
7 *Atlantolacerta andreanskyi*											
8 *Eremias arguta*											
9 *Gastropholis vittatus*											
10 *Heliobolus lugubris*											
11 *Holaspis laevis* (Usambaras, Tanzania)											
12 *Ichnotropis squamulosa*											
13 *Latastia longicaudata*	–										
14 *Meroles suborbitalis*	0.05964	–									
15 *Mesalina guttulata*	0.07282	0.06591	–								
16 *Nucras lalandii*	0.04396	0.05276	0.06721	–							
17 *Omanosaura jayakari*	0.05399	0.04457	0.05524	0.04648	–						
18 *Ophisops elegans*	0.07156	0.06089	0.06905	0.06281	0.04708	–					
19 *Pedioplanis undata*	0.05964	0.05210	0.07282	0.05340	0.04457	0.06717	–				
20 *Philochortus spinalis*	0.03958	0.05906	0.07164	0.05153	0.05654	0.07664	0.05904	–			
21 *Poromera fordii*	0.05399	0.05461	0.06591	0.04646	0.04143	0.06152	0.05461	0.05529	–		
22 *Pseuderemias smithi*	0.03893	0.06404	0.07534	0.04837	0.05462	0.07785	0.05713	0.04147	0.05839	–	
23 *Tropidosaura gularis*	0.04959	0.03766	0.05838	0.04020	0.03515	0.05524	0.03766	0.05090	0.03892	0.05086	–

DRC, Democratic Republic of the Congo; NP, National Park.
When more than one sample was sequenced for a given species, specific locality information is provided for the sample included in this table.

Table 3. Comparison of selected mensural, meristic, and qualitative diagnostic characters for genera in the Equatorial African group of lacertid lizards

Character	Adolfus	Congolacerta gen. nov.	Gastropholis	Holaspis
Adult SVL (mm)	55–84	50–58	80–110	38–52
SVL/TL	49–60	44–52	42–45	71–93
Ventral scale count (transversely)	6	6	10–14	6
Femoral pores	11–19	11–16	13–15	18–24
Frontoparietal scales	+	+	+	−
Vertebral series of enlarged scales	−	−	−	+
Tail strongly depressed and fringed laterally	−	−	−	+
Tail prehensile	−	−	+	+
Ventrals keeled	−	−	+	−
Dorsoanterior border of quadrate bone	Rounded	Rounded	Angular	Rounded
Size of long free ribs immediately posterior to thoracic ribs	Moderately elongated	Very elongated	Moderately elongated	Very elongated
Posterior border of medial loop of clavicle	Present and slender	Present and thickened	Present and slender	Absent
Intramuscular portion of hemipenial armature	Not deeply cleft	Deeply cleft anteriorly	Not deeply cleft	Deeply cleft anteriorly
Shape of hemipenial clavulae	Simple	Complexly lobed	Simple	Simple
Female genital sinus	Unlobed	Bilobed	Unlobed	Unlobed
Habitat	Forest clearings, grassland	Forest clearings, grassland	Forest canopy	Forest
Clutch size	3–5	—	5	2
Ventral coloration	Yellow, orange, green, or blue	Yellow or unpigmented	Yellow-green	Orange to orange-grey

Snout–vent length (SVL)/tail length (TL) given as percentage data. Data are from this study, Arnold (1989b), Kroniger & in den Bosch (2001), Schmidt (1919), and Spawls *et al.* (2002). + = present, − = absent. — = data not available.

isolated montane populations in the Aberdare Mountains, Mt Kenya, and Mt Elgon (Spawls *et al.*, 2002).

Diagnosis: Several mensural, meristic, and qualitative characters that diagnose *Adolfus* are shown in Tables 3–5, including: relatively large SVL (55–84 mm); dorsoanterior border of quadrate bone rounded; size of long free ribs immediately posterior to thoracic ribs moderately enlarged; posterior border of medial loop of clavicle present and slender; small postfemoral mite pockets absent (except in *A. jacksoni*); intramuscular portion of hemipenial armature not deeply cleft; shape of hemipenial clavulae simple; female genital sinus unlobed; habitat in forest, forest clearings and grasslands; clutch size three to five; and ventral coloration yellow, blue, orange, or green.

Description
Size and proportions: Relatively large member of the Equatorial African group of lizards (55–84 mm SVL), with no sexual dimorphism and a long tail (SVL/TL = 49–60%; Tables 4, 5) that is cylindrical without lateral fringes.

Skull: Premaxilla without anterior boss; postfrontal and postorbital bones fused; shape of squamosal bone slender; squamosal and parietal not in contact; dorsoanterior border of quadrate bone rounded; temporal osteoderms absent (except in *A. alleni*, which is variable); maxilla not extending to coronoid notch; and 14 scleral ossicles in each eye (Arnold, 1989).

Postcranial skeleton: Average number of presacral vertebrae in males 26–27 (except *A. africanus*, which has 25 or fewer); seven to nine long free dorsal ribs immediately posterior to thoracic ribs (except *A. africanus*, which has six to seven); moderately elongated long free dorsal ribs immediately posterior to thoracic ribs; posterior border of medial loop of clavicle present and slender; and transverse process of anterior autotomic caudal vertebrae directed roughly laterally (Arnold, 1989a).

Scaling: Contact between postnasal and supranasal scales below level of nostril absent; two loreal scales on each side (except *A. alleni*, which has one); supraciliary granules present (except *A. alleni*); lower eyelid opaque and covered with relatively small scales; parietal scales without lateral corner erosion; temporal scaling relatively fine (except *A. alleni*, which is very coarse, with 13 or fewer scales on each side, excluding the supratemporals and tympanic); keeling on temporal scales absent (*A. alleni*), present (*A. africanus*) or variable (*A. jacksoni*); keeling on collar scales absent (except *A. africanus*, which is variable); granules beneath collar scattered or absent (except *A. jacksoni*, which has many); dorsal scales more or less uniform in size (except *A. africanus*, which has flank scales that are distinctly smaller than the mid-dorsals); micro-ornamentation of dorsal scales smooth (except for *A. africanus*, which has pustullate scales with minute tubercles); flank scales in close contact; six or eight longitudinal rows of ventral body scales (except *A. africanus*, which has four complete rows and an outer row on each side that is strongly reduced anteriorly); keeling on ventrals absent (except *A. africanus*, which has keeling on the outer longitudinal row); preanal scale entire and without keeling; no keeling on scales beneath limbs; row of femoral pores long, extending almost to knee (except *A. africanus*, which has a shortened row of femoral pores, well separated from the knee); scales bearing femoral pores not or only slightly projecting, close together in males; hind toes without fringes; no pad of spinous scales on dorsum of tail base (Arnold, 1989a). In contrast to Arnold, we observed gular folds (as indicated by a heavy crease between the ear openings on the throat of adult animals) in *A. jacksoni*; the character was noted as absent in *A. alleni* and *A. jacksoni*, and variable in *A. africanus* by Arnold (1989a).

Colouring: Adolfus africanus: the entire head is metallic copper bronze with a continuous mid-dorsal band of the same colour and width of the head continuing to the end of the tail. Within the mid-dorsal band are numerous randomly distributed black spots, usually beginning near the origin of the fore limbs and extending slightly beyond the base of the tail. A longitudinal series of white round spots border the mid-dorsal metallic band laterally; these coalesce into thin narrow stripes on the tail. The lateral sides of the body have dark brown bands originating on the side of the head and extending posteriorly onto the tail; some specimens have additional, diffuse rounded white spots aligned along the lower edge of the dark lateral band. Venter immaculate lime green. *Adolfus alleni*: ground colour brown or olive, with a broad or fine dark vertebral stripe. Two black-edged, lime-green or red-brown dorsolateral stripes extend from the posterior edge of the parietals to about the hind limb insertions, and may continue as brown lines onto the tail. The lateral sides of the body are rufous or light brown; the belly varies from orange or orange-pink to blue. *Adolfus jacksoni*: brown to olive on the dorsum of the head, with a continuous mid-dorsal band of the same colour (occasionally light green) and width of the head continuing to the end of the tail. Within the band are randomly scattered black spots or oblique black dashes. The lateral sides of the body are much darker than the dorsum, usually brown but sometimes black, and usually contain several series of

Table 4. Measurements (in mm) of adult species in the genera *Adolfus* and *Congolacerta* **gen. nov.**

Characters	*Adolfus africanus* (4 m, 3 f)	*Adolfus alleni* (1 n, 1 m)	*Adolfus jacksoni* (10 m, 6 f)	*Congolacerta asukului* **sp. nov.** (3 m, 1 f)	*Congolacerta vauereselli* (6 m, 5 f)
SVL (m)	56.95 ± 1.13 (55.7–58.4)	48.0, 46.0	70.46 ± 6.42 (64.0–84.3)	55.40 ± 2.52 (53.7–58.3)	53.42 ± 2.15 (50.0–55.5)
SVL (f)	60.90 ± 0.95 (59.9–61.8)	–	70.28 ± 5.46 (62.3–76.6)	51.9	55.46 ± 3.89 (50.0–60.4)
TL (m)	104.6, 113.6	–	101.3, 112.6	111.4	114.74 ± 3.89 (50.0–60.4)
TL (f)	103.0	–	–	–	112.10 ± 4.10 (109.2–115.0)
SVL/TL	54.93 ± 5.55 (49.0–60.0)	–	56.8, 63.3	52.3	46.95 ± 2.66 (44.4–51.7)
HL	14.36 ± 0.61 (13.4–15.1)	10.0, 10.3	16.33 ± 2.07 (12.4–20.2)	11.35 ± 2.53 (8.4–14.0)	12.61 ± 0.82 (11.1–13.8)
HW	8.74 ± 0.44 (8.2–9.5)	6.4, 6.4	10.63 ± 1.61 (7.8–14.2)	8.18 ± 1.43 (6.5–10.0)	8.12 ± 1.41 (6.8–11.9)
HH	6.21 ± 0.20 (6.0–6.6)	5.3, 5.6	7.19 ± 1.24 (5.6–9.4)	8.18 ± 3.12 (4.8–11.3)	5.57 ± 0.45 (5.0–6.5)
SKL	14.06 ± 0.57 (13.1–14.7)	9.7, 11.0	16.75 ± 2.32 (12.5–20.5)	12.58 ± 1.48 (10.4–13.7)	12.57 ± 0.77 (11.2–13.8)
SEL	6.31 ± 0.43 (5.9–7.0)	3.7, 4.4	6.50 ± 0.83 (5.3–7.7)	4.90 ± 0.62 (4.0–5.4)	5.51 ± 0.47 (4.7–6.1)
ML	11.14 ± 0.48 (10.7–11.8)	8.4, 8.9	12.10 ± 1.45 (9.3–14.1)	10.33 ± 1.46 (8.2–11.5)	10.11 ± 0.74 (8.7–11.0)
SAL	20.76 ± 1.62 (19.0–23.7)	17.9, 17.8	25.74 ± 3.69 (19.5–32.0)	19.47 ± 2.63 (16.2–22.1)	19.98 ± 1.90 (16.4–22.5)
AGD	26.39 ± 2.64 (23.0–30.4)	23.3, 22.7	32.10 ± 4.22 (25.9–40.2)	27.83 ± 0.95 (26.8–28.9)	24.91 ± 2.38 (21.8–29.5)
HML	7.47 ± 0.85 (6.6–8.9)	4.8, 4.5	7.53 ± 1.11 (5.5–9.2)	5.48 ± 0.76 (4.4–6.1)	7.00 ± 1.31 (6.0–10.4)
RUL	7.84 ± 0.22 (7.5–8.1)	4.9, 4.6	7.73 ± 0.97 (6.0–9.1)	5.73 ± 1.17 (4.2–6.9)	7.99 ± 1.35 (6.2–10.7)
FL	10.06 ± 0.51 (9.3–11.0)	5.9, 6.4	10.11 ± 0.96 (8.6–11.9)	6.93 ± 1.10 (5.3–7.7)	8.69 ± 1.10 (7.2–10.6)
TFL	10.20 ± 0.51 (9.3–10.9)	6.0, 6.2	10.01 ± 1.27 (7.6–11.7)	7.10 ± 1.29 (5.2–8.1)	9.06 ± 0.88 (8.2–10.3)
LTL	10.40 ± 0.84 (9.3–11.7)	6.4, 6.5	10.51 ± 1.10 (8.6–12.3)	7.78 ± 1.09 (6.3–8.9)	8.76 ± 0.99 (6.8–9.8)

Data are averages ± one standard deviation, with ranges in parentheses. Abbreviations and measurements are explained in the Material and methods. Snout–vent length (SVL)/tail length (TL) given as percentage data; m, adult male; f, adult female; n, unknown gender. Data for *A. alleni* are taken from single individuals from Mt Elgon (Uganda, 1 n) and the Aberdare Mountains (Kenya, 1 m), which are probably not conspecific.

Table 5. Meristic characters of adult species in the genera *Adolfus* and ***Congolacerta* gen. nov.**

Characters	*Adolfus africanus* (4 m, 3 f)	*Adolfus alleni* (1 n, 1 m)	*Adolfus jacksoni* (10 m, 6 f)	*Congolacerta asukului* (3 m, 1 f)	*Congolacerta vauereselli* (6 m, 5 f)
CS	6	6, 5	6	6	6
FP	15.29 ± 1.11 (14–17)	11, 11	17.27 ± 1.28 (15–19)	13.25 ± 2.22 (11–16)	10.0 ± 1.00 (8–11)
SL	7.14 ± 0.38 (7–8)	6, 5	6.13 ± 0.34 (6–7)	7	6.36 ± 0.51 (6–7)
IL	6	4, 5	6	6	5.91 ± 0.30 (5–6)
SO	4	3, 4	4.06 ± 0.25 (4–5)	3.25 ± 0.50 (3–4)	4.09 ± 0.54 (3–5)
SC	6	5, 3	5.00 ± 0.37 (4–6)	4.75 ± 0.50 (4–5)	5.55 ± 0.82 (4–7)
SG	6.43 ± 0.79 (6–8)	0, 0	3.53 ± 1.06 (2–5)	3.75 ± 0.50 (3–4)	6.36 ± 1.21 (4–8)
ST	4.86 ± 0.90 (4–6)	2, 3	4.81 ± 0.91 (3–6)	4.50 ± 1.00 (3–5)	3.20 ± 0.63 (2–4)
ADS	49.29 ± 10.03 (36–60)	31, 35	61.06 ± 6.61 (51–74)	63.00 ± 4.36 (60–68)	63.36 ± 7.55 (47–73)
PDS	25.43 ± 2.82 (20–28)	19, 22	40.06 ± 2.08 (37–44)	34.25 ± 2.50 (31–37)	39.82 ± 4.14 (32–44)
DSR	24.14 ± 1.22 (23–26)	19, 22	40.25 ± 2.38 (35–44)	31.25 ± 2.22 (28–33)	39.64 ± 5.41 (31–48)
DSN	48.00 ± 3.46 (42–53)	48, 46	95.38 ± 4.51 (90–105)	81.00 ± 5.42 (73–85)	73.18 ± 9.39 (54–84)
VR	6	6, 6	6	6	6
VN	23.14 ± 0.90 (22–24)	26, 25	27.34 ± 2.37 (24.5–31.5)	25.88 ± 1.65 (24–28)	22.55 ± 0.96 (21.5–24.0)
CDS- 11th scale	15.43 ± 0.98 (14–16)	21, 21	24.31 ± 1.25 (22–27)	23.25 ± 1.71 (21–25)	19.67 ± 2.50 (16–24)
CDS- 15th scale	15.14 ± 1.07 (14–16)	21, 21	24.00 ± 1.27 (21–26)	23.50 ± 1.73 (21–25)	18.13 ± 1.81 (16–21)
SDF1	8.14 ± 1.07 (7–10)	7, 6	8.25 ± 0.58 (7–9)	6.50 ± 0.58 (6–7)	7.64 ± 0.67 (7–9)
SDF2	13.17 ± 0.98 (12–14)	10, 9	13.31 ± 0.87 (12–15)	10.75 ± 0.50 (10–11)	11.55 ± 0.82 (11–13)
SDF3	16.71 ± 1.38 (15–18)	14, 12	18.00 ± 1.16 (16–20)	14.33 ± 1.16 (13–15)	15.00 ± 1.55 (13–17)
SDF4	16.71 ± 0.76 (16–18)	12, 12	19.44 ± 1.37 (17–22)	15.50 ± 0.58 (15–16)	16.91 ± 0.94 (16–19)
SDF5	11.57 ± 0.54 (11–12)	8, 9	12.38 ± 1.03 (11–14)	10.00 ± 1.41 (9–12)	10.46 ± 0.69 (9–11)
SDT1	8.29 ± 0.76 (7–9)	8, 6	8.69 ± 1.08 (6–10)	7	8.09 ± 0.54 (7–9)
SDT2	12.67 ± 1.03 (11–14)	11, 10	13.44 ± 0.89 (11–15)	10.75 ± 0.50 (10–11)	11.46 ± 1.13 (10–13)
SDT3	16.00 ± 0.58 (15–17)	15, –	18.79 ± 1.37 (17–21)	15.25 ± 0.50 (15–16)	15.27 ± 1.49 (12–17)
SDT4	19.00 ± 0.58 (18–20)	19, 18	23.64 ± 1.69 (21–27)	19.25 ± 0.50 (19–20)	20.18 ± 1.99 (17–22)
SDT5	13.71 ± 0.76 (13–15)	12, 11	16.13 ± 0.92 (15–17)	12.50 ± 0.58 (12–13)	13.73 ± 1.27 (12–16)

Data are averages ± one standard deviation, with ranges in parentheses. Abbreviations are explained in the Material and methods; m, male; f, female; n, unknown gender. Data for *A. alleni* are taken from single individuals from Mt Elgon (Uganda, 1 n) and the Aberdare Mountains (Kenya, 1 m), which are probably not conspecific.

white or blue, black-edged ocelli, the upper-most and most lateral of which are usually arranged in longitudinal rows and may comprise scattered blue and black scales. The venter is sometimes spotted but more frequently immaculate, and varies from yellow to dull blue (Spawls *et al*., 2002), or bright orange in breeding males from Tanzania (W. R. B., pers. observ.). Poblete (2002) described a Kenyan specimen with an 'army green' dorsum with black, irregular medial dots and flanks with black lateral stripes that were spotted with a luminescent cyan colour.

Distinctive internal features: Tongue surface mainly squamate; tongue colour in alcohol dark; a continuous ulnar nerve present but connected to the brachial trunk by a bridge in the lower arm (except *A. africanus*, which has a variable ulnar nerve pattern); exit of oviducts into genital sinus dorsal; female genital sinus unlobed (Arnold, 1989a).

Hemipenis: Size relatively large; intramuscular portion of hemipenial armature not deeply cleft; medial side of hemipenial armature not reduced; size of hemipenial clavulae large; shape of hemipenial clavulae simple (Arnold, 1989a).

Ecology: Adolfus africanus is known from primary Guineo-Congolean forest (580–2200 m) and has been observed basking in dappled sunlight on fallen tree limbs, trunks and exposed roots within a few metres of ground clearings in forest (only a few were observed on tree trunks above 3 m from the ground), suggesting that this species is primarily an inhabitant of undergrowth (Spawls *et al*., 2002; Köhler *et al*., 2003). It has been collected in highly disturbed forest in north-eastern DRC (E. G., C. K., & M. M. A., pers. observ.) and Kenya (Köhler *et al*., 2003). *Adolfus alleni* is known from alpine moorland, heather and *Hagenia–Hypericum* zones from 2700–4500 m, and is more terrestrial than other members of the genus, living in tussock grass and open patches in between (Spawls *et al*., 2002). *Adolfus jacksoni* is known from clearings, forest edges, gallery forest, and disturbed habitats, even occurring in the middle of the city of Bukavu (DRC) on slopes that have been cleared of forest for centuries (E. G., C. K., & M. M. A., pers. observ., Schaller, 1964), and in suburban gardens in Arusha, Tanzania (W. R. B., pers. observ.). The species has been recorded from 450–3000 m (Spawls *et al*., 2002).

Reproduction: No reproductive data are available for *A. africanus* or *A. alleni*, but *A. jacksoni* has been observed nesting communally in crevices on exposed vertical road cut walls, and lays clutches of three to five eggs (Spawls *et al*., 2002). Goldberg (2009) con-

firmed the range of clutch size for *A. jacksoni* as three to five eggs (mean = 4.1 ± 0.90 standard deviation), noted reproductively active males and females at opposite ends of the year (February–March and September), and documented evidence of multiple clutches in females.

Remarks: Several morphological features (e.g. osteology, hemipenis) are shared with *Gastropholis*, but not other Equatorial African genera (Table 3), lending support for the weakly supported placement of *Gastropholis* as sister to *Adolfus* in our phylogenetic analyses (Figs 1, 2).

CONGOLACERTA GREENBAUM, VILLANUEVA, KUSAMBA, ARISTOTE & BRANCH GEN. NOV.

Type species: Lacerta vaurereselli Tornier, 1902.

Etymology: A feminine name derived from Democratic Republic of the Congo, where the genus occurs along most of the eastern montane border (Albertine Rift), and *lacerta*, a lizard.

Synonymy

1. *Lacerta* Linnaeus, 1758 (part); Tornier, 1902. Zoologische Anzeiger 25:701 [*Lacerta vaurereselli*].
2. *Algiroides* Duméril & Bibron, 1839 (part); Peracca 1917. Atti della Reale Accademia delle Scienze di Torino 52:351 [*Algiroides boulengeri*].
3. *Adolfus* Sternfeld, 1912 '1913' (part); Arnold 1973. Bulletin of the British Museum (Natural History), Zoology 25:357 [*Adolfus vaurereselli*].

Content: Congolacerta asukului sp. nov. (described below); *Congolacerta vaurereselli* (Tornier, 1902).

Distribution: Occurs from the Lendu Plateau (west of Lake Albert in DRC) along the Albertine Rift and its foothills through Uganda, Rwanda, and Tanzania as far south as the Kabobo Plateau at the border of South Kivu and Katanga Provinces, DRC (Spawls *et al*., 2002; Appendix 2).

Diagnosis: Several mensural, meristic, and qualitative characters that diagnose *Congolacerta* are shown in Tables 3–5, including: modest SVL (50–58 mm); dorsoanterior border of quadrate bone rounded; size of long free ribs immediately posterior to thoracic ribs very elongated; posterior border of medial loop of clavicle present and thickened; small to very small postfemoral mite pockets present (Arnold, 1986b); intramuscular portion of hemipenial armature deeply cleft anteriorly; shape of hemipenial clavulae complexly lobed; female genital sinus bilobed;

habitat forest clearings and grasslands; and ventral coloration usually unpigmented (*C. vauereselli*) or yellow with black or brown blotches (*C. asukului*).

Description

Size and proportions: Relatively modest-sized member of the Equatorial African group of lizards (50–58 mm SVL), with no sexual dimorphism and a modest-sized tail (SVL/TL = 44–52%; Tables 4–5) that is cylindrical without lateral fringes.

Skull: Congolacerta vauereselli premaxilla without anterior boss; postfrontal and postorbital bones fused; shape of squamosal bone slender; squamosal and parietal not in contact; dorsoanterior border of quadrate bone rounded; temporal osteoderms absent; maxilla not extending to coronoid notch; and 14 scleral ossicles in each eye (Arnold, 1989a).

Postcranial skeleton: Average number of presacral vertebrae in males 25 or fewer (both species); *C. vauereselli* has six to seven long free dorsal ribs immediately posterior to thoracic ribs; very elongated long free dorsal ribs immediately posterior to thoracic ribs, about twice the length of other free dorsal ribs; posterior border of medial loop of clavicle present and thickened; and transverse process of anterior autotomic caudal vertebrae directed roughly laterally (Arnold, 1989a).

Scaling: Contact between postnasal and supranasal scales below level of nostril absent; two loreal scales on each side; supraciliary granules present; lower eyelid opaque and covered with relatively small scales; parietal scales without lateral corner erosion; temporal scaling relatively fine; keeling on temporal scales variable, but usually absent; keeling on collar scales absent; granules beneath collar scattered or absent; dorsal scales somewhat enlarged; micro-ornamentation of dorsal scales smooth; flank scales in close contact; four complete rows of ventral body scales and an outer row on each side that is strongly reduced anteriorly; keeling on ventrals absent; preanal scale entire and without keeling; no keeling on scales beneath limbs; row of femoral pores long, extending almost to knee (*C. asukului*) or shortened row of femoral pores, well separated from the knee (*C. vauereselli*); scales bearing femoral pores not or only slightly projecting, close together in males; hind toes without fringes; no pad of spinous scales on dorsum of tail base (Arnold, 1989a). In contrast to Arnold, we did not observe a gular fold on any specimens of *C. vauereselli*, and only faint indications of a gular fold on four adult specimens of *C. asukului*.

Colouring: Congolacerta vauereselli: the dorsum of the head is light yellow to copper bronze with a continuous mid-dorsal band of the same colour and width of the head continuing to the end of the tail. Within the mid-dorsal band are small dark brown to black spots, sometimes forming a vertebral stripe. The lateral sides of the body are reddish brown, edged in black above, with one or two series of white, black-edged ocellar spots. A cream or white streak extends from the cheek to the side of the neck and passes through the ear opening. Venter usually immaculate and unpigmented. Colouring of *C. asukului* is generally similar to that of *C. vauereselli* (one major exception is yellow ventral pigmentation with black or brown blotches), and details are given in the species description below.

Distinctive internal features: Congolacerta vauereselli tongue surface mainly squamate; tongue colour in alcohol dark; a 'Varanidae' ulnar nerve pattern with no continuous independent ulnar nerve and all fibres to lower limb passing through the branchial trunk; exit of oviducts into genital sinus dorsal; female genital sinus bilobed (Arnold, 1989a).

Hemipenis: Congolacerta vauereselli size relatively large; intramuscular portion of hemipenial armature very deeply cleft anteriorly; medial side of hemipenial armature not reduced; size of hemipenial clavulae large; shape of hemipenial clavulae complexly lobed (Arnold, 1989a).

Ecology: Congolacerta vauereselli is found in clearings and openings within Guineo-Congolian forests from 1000–2675 m. Little is known of its natural history, but based on observations made in Bwindi National Park (Uganda), Spawls *et al.* (2002) suggested that it is likely to be similar to *A. africanus*. *Congolacerta asukului* is known from high elevations (> 2650 m) grasslands of the Itombwe Plateau, and has been found in small burrows amongst tussocks of grass.

Reproduction: No reproductive data are available for either species of *Congolacerta*.

Remarks: Several mensural, meristic, qualitative, and molecular divergence characters distinguish the Itombwe population of *Congolacerta* from its congener *C. vauereselli*. The Itombwe population is described as a new species below.

CONGOLACERTA ASUKULUI GREENBAUM, VILLANUEVA, KUSAMBA, ARISTOTE & BRANCH SP. NOV.

ASUKULU'S GRASS LIZARD

Holotype: UTEP 20263 (field no. EBG 2025, Figs 3A, B, 4), an adult male, from footpath south of Rurambo village, Itombwe Plateau, South Kivu Province (SKP),

Figure 3. Photographs of *Congolacerta* in life. Dorsal (A) and ventral (B) view of *Congolacerta asukului* holotype UTEP 20263 [adult male, 58.3 mm snout–vent length (SVL)], dorsal view (C) of *C. asukului* paratype UTEP 20265 (adult male, 53.7 mm SVL), dorsal view (D) of *C. asukului* paratype UTEP 20267 (subadult male, 42.7 mm SVL), and dorsal (E) and ventral (F) view of *Congolacerta vaureselli* UTEP 20289 (adult male, 54.4 mm SVL).

DRC (2°59′39″S, 28°52′34″E, 2876 m; see Figs 5, 6). Collected *c.* 08:00 h on 23.v.2009 by M. M. A., E. G., C. K., Wandege Mastaki Moninga, Maurice Luhumyo, and Asukulu M'Mema.

Paratopotype: UTEP 20264 (field no. EBG 2028), a subadult male, with same date, locality, collectors, and circumstances of capture as holotype.

Other paratypes: UTEP 20265 (field no. EBG 2082, Fig. 3C), an adult male, collected by M. M. A., E. G., and C. K. 25.v.2009 at Komesha village, Itombwe Plateau, SKP, DRC (3°5′13″S, 28°48′36″E, 2891 m); UTEP 20266 (field no. EBG 2114), an adult female, collected by M. M. A., E. G., and C. K. 26.v.2009 at Mugegema village, Itombwe Plateau, SKP, DRC (3°4′9″S, 28°46′5″E, 2765 m); UTEP 20267–68 (field nos. EBG 1715–16), one adult male and one subadult

male, collected by E. G., W. M. M., M. M. A., C. K., M. L., and A. M. 30.vi.2008 at Ruhuha, Itombwe Plateau, SKP, DRC (3°22′43″S, 29°0′46″E, 2886 m).

Diagnosis: Congolacerta asukului can be distinguished from all other species in the Equatorial African group of lacertids by the following combination of characters: (1) medium body size (SVL 53.7–58.3 for adult males; 51.9 in one adult female); (2) dorsum brown, rusty brown or tan with several dark brown to black blotches forming a vertebral line from occipital to first quarter of tail, and a dark brown line with cream or greyish white blotches extending from lateral side of rostral through eye and flanks to lateral side of tail; (3) moderate numbers of femoral pores (11–16); (4) low numbers of supraciliary granules (three to four); (5) moderate numbers of dorsal
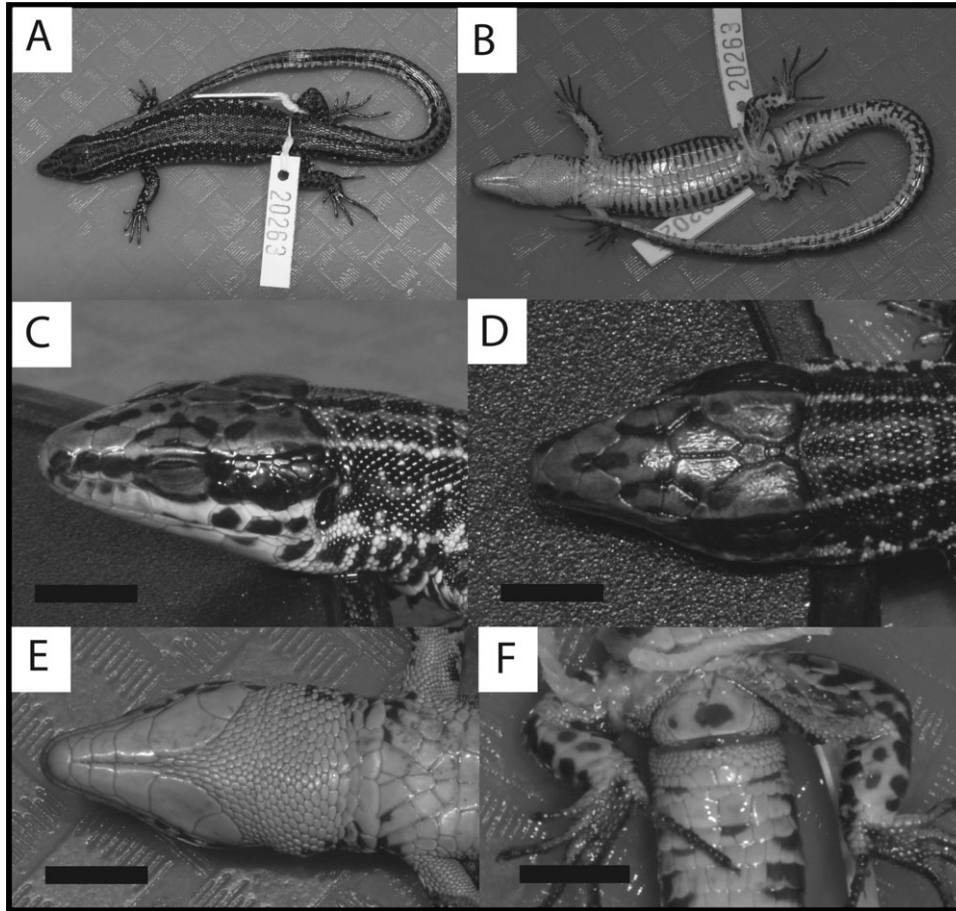
Figure 4. Photographs of the holotype of ***Congolacerta asukului* sp. nov.** (UTEP 20263, adult male, 58.3 mm snout–vent length) after preservation. Dorsal (A) and ventral (B) view of whole specimen, lateral (C), dorsal (D), and ventral (E) view of head, and ventral view of cloacal region (F) illustrating femoral pores. Scale bars = 0.5 cm.

scale rows at midbody (28–33); (6) moderate numbers of dorsal scales in a longitudinal row from occipital to posterior insertion of hind limb (73–85); (7) high numbers of ventral scales from collar to preanal (24–28); (8) high numbers of caudal scale rows at 15th scale (21–25); (9) smooth dorsal scales; and (10) yellow ventral coloration with black or brown blotches.

Differential diagnosis from similar species: As the genera *Adolfus* and *Congolacerta* have similar external morphology, the new species is diagnosed from all species in each genus. *Congolacerta asukului* differs from its partially sympatric and phenotypically similar congener *C. vaureseli* (Fig. 3E, F) by a higher SVL/TL ratio of 52.3 (vs. 44.4–51.7), a smaller HML (4.4–6.1 vs. 6.0–10.4), a smaller TFL (5.2–8.1 vs. 8.2–10.3), a higher number of femoral pores (11–16 vs. 8–11), a smaller number of supraciliary granules (3–4 vs. 4–8; Fig. 7), a smaller number of dorsal scale rows at midbody (28–33 vs.

31–48), a higher number of VN (24–28 vs. 21.5–24), a higher number of caudal scales at the 15th scale row (21–25 vs. 16–21), a smaller number of subdigital lamellae on digits 1 (6–7 vs. 7–9), 2 (10–11 vs. 11–13), and 4 (15–16 vs. 16–19), dorsal scale keeling (smooth vs. keeled), ventral pigmentation (yellow with black or brown blotches vs. usually unpigmented), and habitat (montane grassland vs. forest clearings and openings). *Algiroides boulengeri*, Peracca 1917, described from Fort Portal, Uganda (east of Ruwenzori Mountains) was synonymized with *C. vaureseli* by Loveridge (1957: 229), with which it shares keeled dorsal scales and a strip of metallic bronze in the middle seven to eight longitudinal scale rows (Peracca, 1917), and is clearly not conspecific with *C. asukului*. Most examined specimens of *C. vaureseli* have unpigmented venters, but UTEP 20295 (adult male) from the Kabobo Plateau (most basal population of this species in all analyses, Figs 1, 2) has a yellow venter with some black blotches concentrated on the lateral margins.
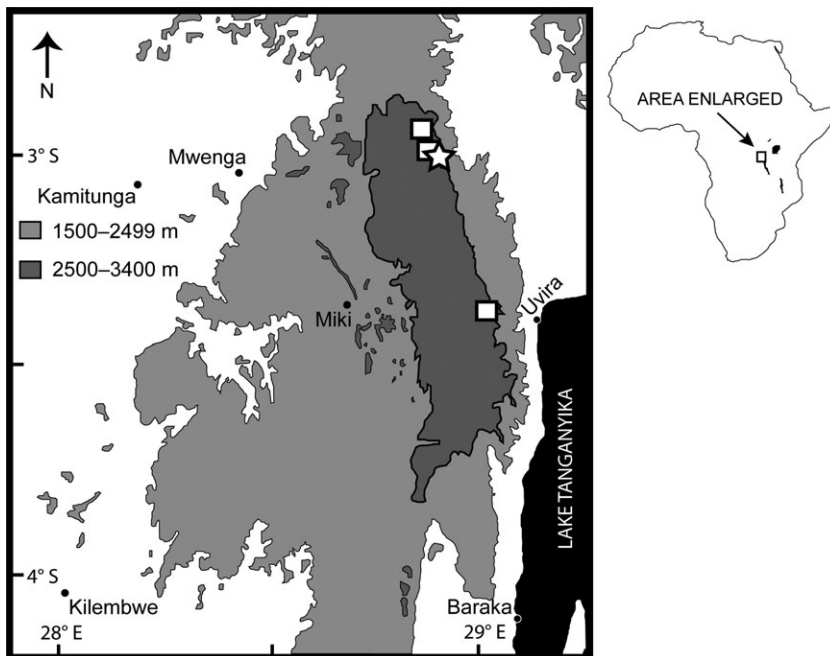
Figure 5. Map of the Itombwe Plateau, showing collection localities for *Congolacerta asukului* **sp. nov.** (open squares). The type locality is indicated by a star symbol.

Figure 6. Photograph of the type locality of *Congolacerta asukului* **sp. nov.**, showing grassland habitat with rocky outcrops.
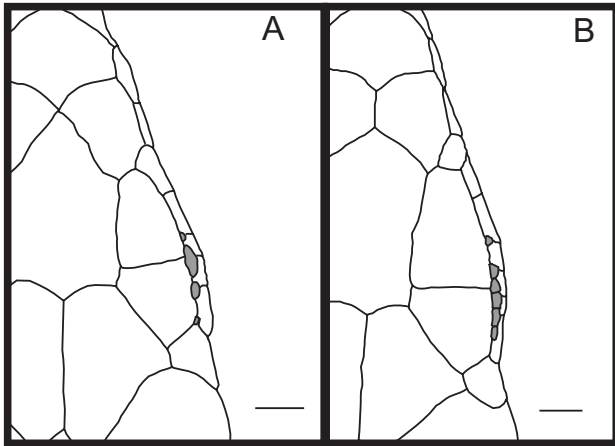
Figure 7. Dorsal views of the heads of **Congolacerta asukului sp. nov.** (holotype, UTEP 20263) and *Congolacerta vaureselli* (UTEP 20291). Supraciliary granules are shaded in grey. Scale bars = 1 mm.

The new species differs from *A. africanus* in having a smaller SEL (4.0–5.4 vs. 5.9–7.0), a smaller HML (4.4–6.1 vs. 6.6–8.9), a smaller RUL (4.2–6.9 vs. 7.5–8.1), a smaller FL (5.3–7.7 vs. 9.3–11.0), a smaller TFL (5.2–8.1 vs. 9.3–10.9), a smaller LTL (6.3–8.9 vs. 9.3–11.7), a smaller number of supraciliaries (4–5 vs. 6), a smaller number of supraciliary granules (3–4 vs. 6–8), a higher number of dorsal scale rows at midbody (28–33 vs. 23–26), a higher number of DSN (73–85 vs. 42–53), a higher number of VN (24–28 vs. 22–24), a higher number of caudal scales at the 11th and 15th scale rows (21–25 vs. 14–16), fewer numbers of subdigital lamellae for each digit (Table 5), dorsal scale keeling (smooth vs. strongly keeled), ventral coloration (yellow with black or brown blotches vs. green), and habitat (montane grassland vs. forest clearings and openings).

The new species differs from our two examined specimens of *A. alleni* in having two loreals (vs. one), supraciliary granules (present vs. absent), dorsal scale shape (rhombic vs. lanceolate), dorsal scale keeling (smooth vs. strongly keeled), granules beneath the collar (present vs. absent), and ventral coloration (yellow with black or brown blotches vs. orange, orange-pink, or blue). The new species also has larger numbers of anterior, posterior, and mid-dorsal scale rows, femoral pores, and subdigital lamellae under toe IV (Table 5). Arnold (1989a: table 2) noted several interesting mensural, meristic, and qualitative differences amongst three allopatric populations of *A. alleni*, which suggests that our two samples from Mt Elgon (Uganda) and the Aberdare Mountains (Kenya) are likely not to be conspecific (Appendix 2).

The new species differs from *A. jacksoni* in having a smaller SVL (53.7–58.3 vs. 64.0–84.3), smaller SEL (4.0–5.4 vs. 5.3–7.7), smaller FL (5.3–7.7 vs. 8.6–11.9),

a smaller number of femoral pores (11–16 vs. 15–19), a smaller number of PDS (31–37 vs. 37–44), a smaller number of DSR (28–33 vs. 35–44), a smaller number of DSN (73–85 vs. 90–105), a smaller number of subdigital lamellae of several fingers and toes (Table 5), flank colour pattern (spots vs. ocelli), and habitat (montane grassland vs. forest clearings and openings). The new species is not known to tolerate anthropogenically disturbed habitats in the same manner as *A. jacksoni*.

Description of holotype: Measurements of the holotype are provided in Table 6. Rostral separated from frontonasal by supranasals; nostril surrounded by supranasal, postnasal and first supralabial; supralabials seven (fourth largest) and infralabials six on each side; supraoculars three on each side, the posterior-most ones much smaller than others; supraciliaries five on each side, first supraciliary largest and continuing to dorsum of head to contact first supraocular (probably fused to former first supraocular), relative lengths 1 > 2 > 5 > 4 > 3; second supraciliary in contact with first supraocular, posterior three supraciliaries separated from posterior supraoculars by two (left) or four (right) supraciliary granules; postnasal one, followed by two loreals at each side, anterior loreal smaller than posterior one; two prefrontals separated by medial contact of frontal and frontonasal; frontal hexagonal, contacting supranasals, postnasals, anterior loreals, prefrontals, and frontal; frontoparietals two and connected; parietals two, separated by two interparietals (anterior interparietal largest) and occipital; supratemporals five on each side, the first one largest; temporal scales non-imbricate, much larger than scales posterior to ear opening; six pairs of chin shields, anterior-most three pairs in contact medially; faint indication of gular fold; collar with seven plates, granules present beneath collar; dorsal scales on body enlarged, imbricate, smooth, and rhombic, extending anteriorly beyond forelimbs on to neck, slightly larger than lateral scales at midbody, much larger than lateral scales near limb insertions; 61 anterior dorsal scale rows, 37 posterior dorsal scale rows, 32 scale rows at midbody; 85 scales counted longitudinally from occipital to the posterior margin of hind limb on middle-left and middle-right rows, respectively; lateral body scales at midbody smooth and rhombic, arranged in disorder; lateral body scales at limb insertions small, smooth, and granular, arranged in disorder; small postfemoral mite pockets present (containing larvae of trombiculid mites); ventral scales rectangular, smooth, in six longitudinal rows at midbody, median and outer longitudinal rows smaller than others, outer-most rows incomplete and smooth; 26 (left) and 25 (right) scales counted longitudinally from collars to preanal on middle-most two rows; preanal

Table 6. Continuous (mm) and meristic variation amongst six specimens of ***Congolacerta asukului*** sp. nov.

Character	UTEP 20263, m	UTEP 20268, m	UTEP 20265, m	UTEP 20266, f	UTEP 20267, s	UTEP 20264, s	Average	SD
SVL	58.3	54.2	53.7	51.9	42.7	47.2	51.33	5.56
TL	111.4	–	–	–	–	–	–	–
HL	14.0	12.8	8.4	10.2	9.9	11.3	11.10	2.04
HW	10.0	8.0	8.2	6.5	6.3	6.9	7.65	1.39
SAL	22.1	21.0	18.6	16.2	15.6	16.8	18.38	2.67
AGD	28.3	27.3	26.8	28.9	20.4	23.6	25.88	3.26
HML	6.1	5.5	5.9	4.4	4.9	4.5	5.22	0.72
RUL	6.9	5.5	6.3	4.2	4.1	5.1	5.35	1.12
FL	7.3	7.4	7.7	5.3	5.6	5.6	6.48	1.09
TFL	8.1	7.6	7.5	5.2	6.6	6.8	6.97	1.03
FP	14	16	12	11	15	13	13.50	1.87
SO	3	4	3	3	4	3	3.33	0.52
SC	5	5	5	4	6	4	4.83	0.75
SG	4	4	3	4	1	3	3.17	1.17
ST	5	5	5	3	4	5	4.50	0.84
DSR	32	32	28	33	32	32	31.50	1.76
DSN	85	83	73	83	79	82	80.83	4.31
VN	25.5	26	24	28	23	24.5	25.17	1.75
SDF4	16	15	15	14	15	16	15.17	0.75
SDT4	19	19	20	19	19	20	19.33	0.52

Abbreviations and measurements are explained in the Material and methods; m, adult male; f, adult female; s, subadult male; SD, standard deviation. Tail length (TL) data is not provided for specimens with broken or regenerated tails.

single, ovoid, enlarged, and smooth; 14 femoral pores on each side; scales on anterior and dorsal surfaces of forelimbs enlarged, smooth and imbricate; scales on posterior and ventral surfaces of forelimbs mostly small and granular, with two rows of enlarged, smooth, and imbricate scales; two rows of enlarged, smooth, and imbricate scales on anteroventral side of hind limbs, the other areas with small, smooth, granular scales; relative lengths of appressed fingers IV > III > II = V > I; subdigital lamellae seven (left) – seven (right), 11–11, 14–15, 16–16, 10–9 on fingers I, II, III, IV, and V, respectively; relative lengths of appressed toes IV > III > V > II > I; subdigital lamellae eight (left) – seven (right), 11–11, 15–16, 19–19, 13–13 on toes I, II, III, IV, and V, respectively; tail long (191% of SVL) and complete, covered with strongly keeled scales on lateral and dorsal sides, in 33 rows at base, decreased to 24 rows at 15th scale.

Coloration in life: From photographs of holotype before preservation (Figs. 3A, B). Dorsal ground colour brown to rusty brown with several dark brown to black blotches on the head scales, mid-dorsal area (forming a vertebral line from occipital to first quarter of tail), limbs, and tail. A narrow line of cream to white spots forms a border between the dorsum and flanks from the parietals to the insertion of the hind limb. A dark brown line with cream blotches extends from the lateral side of the rostral through the eye and flanks to the lateral side of the tail. Lateral side of snout and neck (below dark brown line) cream with dark brown blotches. Chin shields white, remainder of venter light yellow anteriorly, becoming increasingly darker yellow posteriorly, with dark brown to black blotches on the lateral sides of the venter and limbs. Coloration in preservative (70% ethanol) similar to coloration in life.

Variation: Variation of mensural and meristic data in the paratypes of *C. asukului* is shown in Table 6. The holotype is the only specimen with separated prefrontals; the prefrontals are in broad contact in UTEP 20267–68 and 20266, and the prefrontals are in narrow contact in UTEP 20264 and 20265. Three specimens (UTEP 20265–67) have only one interparietal; the interparietal in UTEP 20266 is unusually elongate, and is about 2.5 times longer than wide. Coloration in life of UTEP 20265 (Fig. 3C) differed from the holotype in having a tan dorsal ground colour, and greyish white flanks below the dark brown lateral stripe. Coloration in life of UTEP 20267 (Fig. 3D) differed from the holotype in having rusty

brown head plates, and an olive brown ground colour on the remainder of the dorsum.

Ecology and natural history: Congolacerta asukului is a diurnal species that occurs in high-elevation (> 2650 m) grasslands (often near rocky outcrops) of the Itombwe Plateau (Figs. 5, 6) in the Albertine Rift Montane Forest ecoregion as defined by Burgess *et al*. (2004). At least two individuals were observed basking on rocks, and one individual was captured after it retreated to a small burrow amongst tussocks of grass. Laurent (1964) described this habitat as high-elevation meadows that are common amongst swamps, rivers, and subalpine scrub forests, which are dominated by tree heathers and other Ericaceae (Doumenge, 1998).

Etymology: The new species is named in honour of Itombwe native Asukulu M'Mema, an aspiring zoologist and conservationist who was our colleague and guide through the Itombwe Plateau in 2008 and 2009, when all the known specimens of *C. asukului* were collected. Asukulu was killed during his investigation into the killing of a gorilla on 22 August 2009 in Mulombozi village (on the route between Miki and Mwenga) in the western slopes of the Itombwe Plateau. For his service to conservation in Africa, he was posthumously honoured with the Medail de Bravoure from the Alexander Abraham Foundation in 2010.

Conservation: Congolacerta asukului is currently known from four localities, which have a total extent of occurrence of about 550 km². Because of mining activity, widespread cattle/goat grazing (E. G., C. K., & M. M. A., pers. observ.), and dry-season burning of grasslands for agriculture (C. K., pers. observ.), the area, extent and quality of the grassland habitat is declining. Applying the IUCN Red List criteria IUCN (2001) to *C. asukului* results in a classification of endangered, EN B1ab(iii).

DISCUSSION

Using the Bayesian phylogenetic analysis program TreeTime, Hipsley *et al*. (2009) estimated that the common ancestor of Eremiadini lacertids dispersed to north-western Africa via small island chains from Europe in the mid- to late Eocene, substantially earlier than the previous estimates of *c*. 14 Mya by Pavlicev & Mayer (2009). Separation of the 'Saharo-Eurasian' and 'Ethiopian' lineages (equivalent to clades B_1 and B_2 of Mayer & Pavlicev, 2007) occurred shortly thereafter. Given the pattern we recovered for the Equatorial African group of lacertids near the base of the Eremiadini clade, it is likely that the

genera *Adolfus*, *Congolacerta*, *Gastropholis*, and *Holaspis* diverged from each other shortly after the group's arrival in Central Africa, either in the late Eocene or the Miocene. The Miocene was a relatively dry period marked by expansion of grasslands (Lovett *et al*., 2005), and is synchronous with orogeny of the Albertine Rift, which began forming via doming in the early Miocene (Vande weghe, 2004; Partridge, 2010).

As *C. asukului* is known from a small area (550 km²) at the highest elevations of the Itombwe Plateau, potential negative effects from global warming are of paramount concern. In general, the African continent has warmed by 0.5 °C since 1900, but global climate models for future temperature and precipitation trends are problematic (Hulme *et al*., 2005). Hernes *et al*. (1995) and Ringius *et al*. (1996) constructed climate change scenarios that predicted equatorial African countries would warm by 1.4 °C by the 2050s. Hulme *et al*. (2001) also constructed climate change scenarios that predicted a 0.2–0.5 °C/ decade increase in temperature, with the least amount of warming in equatorial latitudes and coastal environments. These authors examined the intermodel range of their global climate models to assess their levels of agreement, and found the smallest range over northern Africa and the equator, suggesting that warming estimates for equatorial Africa are relatively robust. However, estimates of the magnitude and direction of future rainfall changes in Africa are not precise, because models have not accounted for the roles of land-cover change, and dust and biomass aerosols in inducing regional climate changes (Hulme *et al*., 2005). This is especially relevant to Itombwe, where human activity during Africa's World War (Prunier, 2008) destroyed large areas of natural habitat on the plateau (E. G., C. K., & M. M. A. pers. observ.).

Alward, Detling & Milchunas (1999) noted that average annual minimum temperatures (T_{MIN}) have increased at twice the rate of average annual maximum temperatures at a global scale. These authors analysed a 23-year data set from a montane grassland long-term ecological research site in Colorado (USA), and demonstrated that increased T_{MIN} was correlated with decreased net primary production by the dominant C_4 grass, rendering the habitat more susceptible to invasion by exotic species and less tolerant of drought and grazing. If similar effects are occurring at Itombwe, it is likely that the high-elevation grassland habitat will be devastated, possibly leading to the extinction of *C. asukului*. Moreover, in a study that focused on the potential effects of global climate change on Mexican lizards, Sinervo *et al*. (2010) noted that extinction risk was significantly related to low latitudinal and altitudinal range limits, where thermal physiology and/or eco-

logical interactions limit species, especially viviparous species in cool, montane habitats. Although *C. asukului* is probably oviparous, it is restricted to a limited latitudinal and elevation range in a cool, montane habitat, rendering it especially vulnerable to extinction risk from global warming.

Recognition of the genus *Congolacerta* adds another distinct evolutionary lineage to a long list of taxa that are endemic to the Albertine Rift mountains in eastern DRC, Uganda, Rwanda, Burundi, and Tanzania (Plumptre *et al.*, 2007). Overall, the Albertine Rift contains more than half of continental Africa's bird species (Omari *et al.*, 1999), and nearly 40% of its mammal species (Plumptre *et al.*, 2007), including endangered mountain gorillas (*Gorilla beringei*; Schaller, 1964; Eckhart & Lanjouw, 2008). Many of these high-elevation forests are threatened by deforestation, and on a global scale, montane forests make up 12% of existing tropical forests worldwide, but are being cleared at twice the rate of the global average (Sodhi, Brook & Bradshaw, 2007).

Amongst other Albertine Rift sites, Itombwe (under consideration for a national park) has the most threatened species of amphibians (Laurent, 1964, 1983; Evans *et al.*, 2008; Stuart *et al.*, 2008; Roelke *et al.*, 2011), and the second-highest number of endemic amphibians (most not recorded for 60 years), rendering it amongst the most important sites for amphibian conservation in continental Africa (Burgess *et al.*, 2004). Two amphibian genera, *Laurentophryne*, Tihen, 1960 and *Chrysobatrachus*, Laurent, 1951, are endemic to Itombwe, and the latter genus is only found above 2400 m, with a peak in activity during the dry season (Laurent, 1951, 1964). *Congolacerta asukului* underscores the high levels of reptile endemism of the plateau – Itombwe also contains large numbers of endemic and threatened plants, butterflies, birds, and mammals (Louette, 1990; Omari *et al.*, 1999; Plumptre *et al.*, 2003). This diversity is remarkable given the superficial herpetological exploration of the plateau; Laurent (1954) mentioned only two reptiles from the upper plateau of Itombwe (2500–3000 m), including taxa in the lizard genera *Trioceros* (Chamaeleonidae) and *Leptosiaphos* (Scincidae).

In October 2006, parts of the Itombwe Plateau were recognized as the Réserve Naturelle d'Itombwe (RNI), by decree of the Ministry of Environment, Conservation of Nature and Tourism (C. K., pers. comm.). An administration with a managing warden was established for RNI in 2008, but armed militias have impeded conservation efforts (E. G., C. K., & M. M. A., pers. observ.). The reserve faces severe anthropogenic pressure from a growing human population (Barnes & Lahm, 1997), and park rangers are not yet established to ameliorate poaching and deforestation (elephants were probably extirpated recently), which is currently not monitored. Based on preliminary vegetation surveys, Doumenge (1998) remarked that Itombwe is, 'undoubtedly the second most important, if not the most important, location of highland forests in continental Africa'. As multiple, additional new species of amphibians and reptiles await description (E. G., unpubl. data), it is likely that Itombwe's importance as a centre of endemism and conservation concern will increase as biological exploration continues.

ACKNOWLEDGEMENTS

REFERENCES

Adolphs K. 2006. *Bibliotheca Cordyliformium*. St. Augustin, Germany: Squamata Verlag.

Alward RD, Detling JK, Milchunas DG. 1999. Grassland vegetation changes and nocturnal global warming. *Science (Washington, DC)* 283: 229–231.

Arnold EN. 1973. Relationships of the Palaearctic lizards assigned to the genera *Lacerta, Algyroides* and *Psammodromus* (Reptilia: Lacertidae). *Bulletin of the British Museum (Natural History), Zoology Series* **25:** 291–366.

Arnold EN. 1986a. The hemipenis of lacertid lizards (Reptilia: Lacertidae): structure, variation and systematic implications. *Journal of Natural History* **20:** 1221–1257.

Arnold EN. 1986b. Mite pockets of lizards, a possible means of reducing damage by ectoparasites. *Biological Journal of the Linnean Society* **29:** 1–21.

Arnold EN. 1989a. Systematics and adaptive radiation of Equatorial African lizards assigned to the genera *Adolfus, Bedriagaia, Gastropholis, Holaspis* and *Lacerta* (Reptilia: Lacertidae). *Journal of Natural History* **23:** 525–555.

Arnold EN. 1989b. Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology. *Bulletin of the British Museum (Natural History), Zoology Series* **55:** 209–257.

Arnold EN. 1998. Structural niche, limb morphology and locomotion in lacertid lizards (Squamata, Lacertidae); a preliminary survey. *Bulletin of the Natural History Museum of London, Zoology* **64:** 63–89.

Arnold EN, Arribas O, Carranza S. 2007. Systematics of the Palaearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. *Zootaxa* **1430:** 1–86.

Barnes RFW, Lahm SA. 1997. An ecological perspective on human densities in the central African forests. *Journal of Applied Ecology* **34:** 245–260.

Barraclough TG, Davies TJ. 2005. Predicting future speciation. In: Purvis A, Gittleman JL, Brooks T, eds. *Phylogeny and conservation. Conservation biology 8*. Cambridge: Cambridge University Press, 400–418.

Bastin Y, Beeckman H, Cornelissen E, Fernandez Alonso M, Gansemans J, Huysmans C, Janssens B, Kennes E, Lavreau J, Louette M, Maniacky J, Omasombo J, Tack L, Tréfois P, Van Bockhaven V, Van Schuylenbergh P, Vanhee H. 2004. *Nature and culture in the Democratic Republic of Congo*. Tervuren: Royal Museum for Central Africa.

Bauer AM, de Silva A, Greenbaum E, Jackman TR. 2007. A new species of day gecko from high elevation in Sri Lanka, with a preliminary phylogeny of Sri Lankan *Cnemaspis* (Reptilia: Squamata: Gekkonidae). *Mitteilungen Aus Dem Museum Für Naturkunde in Berlin. Zoologische Reihe* **83** (Sonderheft)**:** 22–32.

Barbour T. 1914. Some new Reptiles. *Proceedings of the New England Zoological Club* **4:** 95–98.

Boulenger GA. 1899. Descriptions of two new lizards from the interior of British East Africa. *Proceedings of the Zoological Society of London* **1899:** 96–98.

Boulenger GA. 1906. Additions to the herpetology of British East Africa. *Proceedings of the Zoological Society of London* **1906:** 570–573.

Boulenger GA. 1920. *Monograph of the Lacertidae. Volume I*. London: Trustees of the British Museum (Natural History).

Brown RM, Siler CD, Diesmos AC, Alcala AC. 2009. Philippine frogs of the genus *Leptobrachium* (Anura; Megophryidae): phylogeny-based species delimitation, taxonomic review, and descriptions of three new species. *Herpetological Monographs* **23:** 1–44.

Burgess N, Hales JD, Underwood E, Dinerstein E, Olson D, Itoua I, Schipper J, Ricketts T, Newman K. 2004. *Terrestrial ecoregions of Africa and Madagascar: a conservation assessment*. Washington, Covelo and London: Island Press, World Wildlife Fund.

Doumenge C. 1998. Forest diversity, distribution, and dynamique in the Itombwe Mountains, South-Kivu, Congo Democratic Republic. *Mountain Research and Development* **18:** 249–264.

Eckhart G, Lanjouw A. 2008. *Mountain gorillas: biology, conservation and coexistence*. Baltimore, MD: The Johns Hopkins University Press.

Evans BJ, Carter TF, Tobias ML, Kelley DB, Hanner R, Tinsley RC. 2008. A new species of clawed frog (genus *Xenopus*) from the Itombwe Massif, Democratic Republic of the Congo: implications for DNA barcodes and biodiversity conservation. *Zootaxa* **1780:** 55–68.

Felsenstein J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39:** 783–791.

Frederick A. 1910. *In the heart of Africa*. London, New York, Toronto and Melbourne: Cassell and Company, Ltd.

Fu J. 1998. Toward the phylogeny of the family Lacertidae: implications from mitochondrial DNA 12S and 16S gene sequences (Reptilia: Squamata). *Molecular Phylogenetics and Evolution* **9:** 118–130.

Fu J. 2000. Toward the phylogeny of the family Lacertidae – why 4708 base pairs of mtDNA sequences cannot draw the picture. *Biological Journal of the Linnean Society* **71:** 203–217.

Goldberg SR. 2009. Reproduction of Jackson's Forest Lizard, *Adolfus jacksoni* (Squamata: Lacertidae). *African Herp News* **48:** 5–7.

Goldberg SR, Bursey CR. 2009. *Adolfus jacksoni*. Endoparasites. *African Herp News* **48:** 16–17.

Groth JG, Barrowclough GF. 1999. Basal divergences in birds and the phylogenetic utility of the nuclear RAG-1 gene. *Molecular Phylogenetics and Evolution* **12:** 115–123.

Harris DJ. 1999. Molecular systematics and evolution of lacertid lizards. *Natura Croatica* **8:** 161–180.

Harris DJ, Arnold EN, Thomas RH. 1998. Relationships of lacertid lizards (Reptilia: Lacertidae) estimated from mitochondrial DNA sequences and morphology. *Proceedings of the Royal Society B, Biological Sciences* **265:** 1939–1948.

Hernes H, Dalfelt A, Bernsten T, Holtsmark B, Naess LO, Selrod R, Aaheim HA. 1995. *Climate strategy for Africa*. University of Oslo, Norway: CICERO Report 1995:3.

Hillis DM, Bull JJ. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology* **42:** 182–192.

Hipsley CA, Himmelmann L, Metzler D, Müller J. 2009. Integration of Bayesian molecular clock methods and fossil-based soft bounds reveals early Cenozoic origin of African lacertid lizards. *BMC Evolutionary Biology* **9:** 151.

Huelsenbeck JP, Ronquist F. 2001. MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* **17:** 754–755.

Hulme M, Doherty RM, Ngara T, New MG, Lister D. 2001. African climate change: 1900–2100. *Climate Research* **17:** 145–168.

Hulme M, Doherty R, Ngara T, New M. 2005. Global warming and African climate change: a reassessment. In: Low PS, ed. *Climate change and Africa*. Cambridge: Cambridge University Press, 29–40.

IUCN. 2001. *IUCN Red List Categories and Criteria: Version 3.1.* IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK.

Köhler J, Wagner P, Visser S, Böhme W. 2003. New country records of *Adolfus africanus* (Sauria: Lacertidae) – a rain forest lizard with disjunct distribution? *Salamandra* **39:** 241–248.

Kroniger M, in den Bosch HAJ. 2001. Biological data on *Holaspis guentheri laevis* Werner, 1895 obtained from vivarium keeping. *Podarcis* **2:** 72–80.

Laurent R. 1951. Deux reptiles et onze batraciens nouveaux d'Afrique centrale. *Revue de Zoologie et de Botanique Africaines* **44:** 360–381.

Laurent RF. 1954. Aperçu de la biogéographie des batraciens et des reptiles de la région des grand lacs. *Bulletin de la Société Zoologique de France* **79:** 290–310.

Laurent RF. 1964. Adaptive modifications in frogs of an isolated highland fauna in Central Africa. *Evolution* **18:** 458–467.

Laurent RF. 1983. About the herpetofauna of Central African montane forest. In: Rhodin AGJ, Miyata K, eds. *Advances in herpetology and evolutionary biology: essays in honor of Ernest E. Williams*. Cambridge, MA: Museum of Comparative Zoology, 350–358.

Leaché AD, Reeder T. 2002. Molecular systematics of the fence lizard (*Sceloporus undulatus*): a comparison of parsimony, likelihood, and Bayesian approaches. *Systematic Biology* **51:** 44–68.

Lönnberg E. 1907 '1910'. Reptilia and Batrachia. In: Sjöstedt BY, ed. *Wissenschaftliche Ergebnisse der Swedischen Zoologischen Expedition nach dem Kilimandjaro, dem Meru und den umgebenden Massai-steppen Deutsch-Ostafrikas, 1905–1906*. Uppsala, Sweden: Almqvist & Wikksels Boktryckeri-A.-B., Chapter 4, 1–28 + 1 plate.

Louette M. 1990. A new species of nightjar from Zaïre. *Ibis* **132:** 349–353.

Loveridge A. 1957. Check list of the reptiles and amphibians of East Africa (Uganda; Kenya; Tanganyika; Zanzibar). *Bulletin of the Museum of Comparative Zoology* **117:** 153–362 + xxxvi.

Lovett JC, Marchant R, Taplin J, Küper W. 2005. The oldest rainforests in Africa: stability of resilience for survival and diversity? In: Purvis A, Gittleman JL, Brooks T, eds. *Phylogeny and conservation*. New York, NY: Cambridge University Press, 198–229.

Lue K-Y, Lin S-M. 2008. Two new cryptic species of *Takydromus* (Squamata: Lacertidae) from Taiwan. *Herpetologica* **64:** 379–395.

Maddison DR, Maddison WP. 2005. *Macclade: analysis of phylogeny and character evolution*. Sunderland, MA: Sinauer Associates, Inc.

Mayer W, Benyr G. 1994. Albumin-Evolution und Phylogenese in der Familie Lacertidae (Reptilia: Sauria). *Annalen Des Naturhistorischen Museums in Wien* **96B:** 621–648.

Mayer W, Pavlicev M. 2007. The phylogeny of the family Lacertidae (Reptilia) based on nuclear DNA sequences: convergent adaptations to arid habitats within the subfamily Eremiainae. *Molecular Phylogenetics and Evolution* **44:** 1155–1163.

Moore WS. 1995. Inferring phylogenies from mtDNA variation: mitochondrial gene trees versus nuclear gene trees. *Evolution* **49:** 718–726.

Omari I, Hart JA, Butynski TM, Birhashirwa NR, Upoki A, M'Keyo Y, Bengana F, Bashonga M, Bagurubumwe N. 1999. The Itombwe Massif, Democratic Republic of Congo: biological surveys and conservation with an emphasis on Grauer's gorilla and birds endemic to the Albertine Rift. *Oryx* **33:** 301–322.

Page RDM. 2000. Extracting species trees from complex gene trees: reconciled trees and vertebrate phylogeny. *Molecular Phylogenetics and Evolution* **14:** 89–106.

Palumbi S, Martin A, Romano S, McMillan WO, Stice L, Grabowski G. 1991. *The simple fool's guide to PCR. Version 2*. Honolulu, HI: The University of Hawaii.

Partridge TC. 2010. Tectonics and geomorphology of Africa during the Phanerozoic. In: Werdelin L, Sanders WJ, eds. *Cenozoic mammals of Africa*. Berkeley, Los Angeles and London: University of California Press, 3–17.

Pavlicev M, Mayer W. 2006. Multiple copies of coding as well as pseudogene c-mos sequence exist in three lacertid species. *Journal of Experimental Zoology Part B Molecular and Developmental Evolution* **306B:** 539–550.

Pavlicev M, Mayer W. 2009. Fast radiation of the subfamily Lacertinae (Reptilia: Lacertidae): history or methodical artefact? *Molecular Phylogenetics and Evolution* **52:** 727–734.

Peracca MG. 1917. Sopra una nuova specie di Lacertidae del gen. 'Algiroides' dell'Uganda. *Atti Della R. Accademia Delle Scienze Di Torino. Classe Di Scienze Fisiche, Matematiche E Naturali* **52:** 351–354.

Plumptre AJ, Behangana M, Davenport TRB, Kahindo C, Kityo R, Ndomba E, Nkuutu D, Owiunji I, Ssegawa P, Eilu G. 2003. *The biodiversity of the Albertine Rift. Albertine Rift Technical Reports No 3*. Wildlife Conservation Society. http://www.albertinerift.org/Publications/AlbertineRiftTechnicalReportsSeries/tabid/2531/Default.aspx

Plumptre AJ, Davenport TRB, Behangana M, Kityo R, Eilu G, Ssegawa P, Ewango C, Meirte D, Kahindo C, Herremans M, Kerbis Peterhans J, Pilgrim JD, Wilson M, Languy M, Moyer D. 2007. The biodiversity of the Albertine Rift. *Biological Conservation* **134:** 178–194.

Poblete GH. 2002. *Adolfus jacksoni*. Morphology. *African Herp News* **34:** 23–24.

Poe S, Chubb AL. 2004. Birds in a bush: five genes indicate explosive evolution of avian orders. *Evolution* **58:** 404–415.

Posada D. 2008. jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution* **25:** 1253–1256.

Posada D, Buckley TR. 2004. Model selection and model averaging in phylogenetics: advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. *Systematic Biology* **53:** 793–808.

Prunier G. 2008. *Africa's world war: Congo, the Rwandan genocide, and the making of a continental catastrophe*. New York, NY: Oxford University Press.

de Queiroz K. 1998. The general lineage concept of species, species criteria, and the process of speciation. In: Howard DJ, Berlocher SH, eds. *Endless forms: species and speciation*. New York, NY: Oxford University Press, 57–75.

de Queiroz K. 1999. The general lineage concept of species and the defining properties of the species category. In: Wilson RA, ed. *Species: new interdisciplinary essays*. Cambridge, MA: Massachusetts Institute of Technology Press, 49–89.

de Queiroz K. 2007. Species concepts and species delimitation. *Systematic Biology* **56:** 879–886.

Ringius L, Downing TE, Hulme M, Waughray D, Selrod R. 1996. *Climate change in Africa: issues and regional strategy*. Oslo, Norway: CICERO Report No. 1996: 8.

Roelke CE, Greenbaum E, Kusamba C, Aristote MM, Smith EN. 2011. Systematics and conservation status of two distinct Albertine Rift treefrogs, *Leptopelis karissimbensis* and *L. kivuensis* (Anura: Arthroleptidae). *Journal of Herpetology* **45:** 343–351.

Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: bayesian phylogenetic inference under mixed models. *Bioinformatics* **19:** 1572–1574.

Salvi D, Bombi P, Vignoli L. 2011. Phylogenetic position of the southern rock lizard *Australolacerta australis* within the Lacertidae radiation. *African Journal of Herpetology* **60:** 60–69.

Schaller GB. 1964. *The year of the gorilla*. Chicago, IL: The University of Chicago Press.

Schmidt KP. 1919. Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition, 1909–1915. Part I. Turtles, Crocodiles, Lizards, and Chameleons. *Bulletin of the American Museum of Natural History* **39:** 385–624.

Shimodaira H. 2002. An approximately unbiased test of phylogenetic tree selection. *Systematic Biology* **51:** 492–508.

Shimodaira H, Hasegawa M. 2001. CONSEL: for assessing the confidence of phylogenetic tree selection. *Bioinformatics* **17:** 1246–1247.

Sinervo B, Méndez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans E, Villagrán-Santa Cruz M, Lara-Resendiz R, Martínez-Méndez N, Calderón-Espinosa ML, Meza-Lázaro R, Gadsden H, Avila LJ, Morando M, De La Riva IJ, Sepulveda PV, Rocha CFD, Ibargüengoytía N, Puntriano CA, Massot M, Lepetz V, Oksanen TA, Chapple DG, Bauer AM, Branch WR, Clobert J, Sites JW Jr. 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science (Washington, DC)* **328:** 894–899.

Sodhi NS, Brook BW, Bradshaw CJA. 2007. *Tropical conservation biology*. Malden, MA: Blackwell Publishing.

Spawls S, Howell K, Drewes R, Ashe J. 2002. *A field guide to the reptiles of East Africa: Kenya, Tanzania, Uganda, Rwanda and Burundi*. San Diego, CA: Academic Press.

Stamatakis A. 2006. RAXML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22:** 2688–2690.

Stamatakis A, Blagojevic F, Nikolopoulos D, Antonopoulos C. 2007. Exploring new search algorithms and hardware for phylogenetics: RAxML meets the IBM cell. *Journal of VLSI Signal Processing* **48:** 271–286.

Stamatakis A, Hoover P, Rougemont J. 2008. A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology* **57:** 758–771.

Sternfeld R. 1912 '1913'. Reptilia. In: Schubotz H., ed. *Wissenschaftliche Ergebnisse der Deutschen Zentral-Afrika-Expedition 1907–1908 unter Führung Adolf Friedrichs, Herzogs zu Mecklenberg. Band IV, Zoologie II*. Leipzig: Klinkhardt & Biermann, 197–279 + figs. 1–4 + pl. VI–IX.

Stuart SN, Hoffman M, Chanson JS, Cox NA, Berridge RJ, Ramani P, Young BE, eds. **2008.** *Threatened amphibians of the world*. Barcelona: Lynx Editions, Gland, Switzerland: IUCN, Arlington, VA: Conservation International.

Swofford DL. 2002. *PAUP*4.0b10: phylogenetic analysis using parsimony [*and other methods]*. Sunderland, MA: Sinauer Associates, Inc.

Szczerbak NN. 1975. Katalog afrikanskih Jashchurok. Kiev.

Tornier G. 1902. Herpetologisch Neues aus Ost-Afrika. *Zoologischer Anzeiger* **25:** 700–704.

Vande weghe JP. 2004. *Forests of Central Africa: nature and man*. Pretoria: Ecofac, Protea Book House.

Wiens JJ, Penkrot TA. 2002. Delimiting species using DNA and morphological variation and discordant species limits in spiny lizards (*Sceloporus*). *Systematic Biology* **51:** 69–91.

Wilcox TP, Zwickl DJ, Heath TA, Hillis DM. 2002. Phylogenetic relationships of the dwarf boas and a comparison of Bayesian and bootstrap support measures of phylogenetic support. *Molecular Phylogenetics and Evolution* **25:** 361–371.

Wiley EO. 1981. *Phylogenetics: the theory and practice of phylogenetic systematics*. New York, NY: John Wiley and Sons.

APPENDIX 1

List of specimens, geographical origin, voucher number, and GenBank accession numbers for mitochondrial and nuclear gene sequences used in this study.

Species	Geographical origin	Museum/field voucher number	16S	cyt b	c-mos	RAG1
Acanthodactylus boskianus	Egypt (animal trade)	–	–	–	EF632251	EF632206
Acanthodactylus erythrurus	Morocco: Foret de Cedres (Azrou)	IBES 2917	HQ605790	HQ605832	HQ605874	HQ616540
Acanthodactylus scutellatus	Egypt: Abu Simbel	–	–	–	EF632252	EF632207
Adolfus africanus	DRC: South Kivu Province, Hombo	UTEP 20269	HQ605799	HQ605846	HQ605887	HQ616552
Adolfus africanus	DRC: South Kivu Province, Mashaba	UTEP 20271	HQ605828	HQ605870	HQ605911	HQ616576
Adolfus alleni	Kenya: Aberdares	NM Nairobi	–	HQ605841	HQ605882	–
Adolfus alleni	Kenya: Mt Kenya	ZFMK 82078	HQ605779	HQ605840	–	–
Adolfus jacksoni	DRC: South Kivu Province, Lwiro	UTEP 20276	HQ605792	HQ605842	HQ605883	HQ616548
Adolfus jacksoni	DRC: South Kivu Province, Bitale	UTEP 20279	HQ605793	HQ605843	HQ605884	HQ616549
Adolfus jacksoni	Uganda: Kabale District, Bwindi Impenetrable National Park	CAS 201598	HQ605794	HQ605844	HQ605885	HQ616550
Adolfus jacksoni	Rwanda: North Province, Ruhengeri	CER 227	HQ605826	HQ605868	HQ605909	HQ616574
Adolfus jacksoni	Rwanda: North Province, Ruhengeri	UTA R55679	HQ605827	HQ605869	HQ605910	HQ616575
Adolfus jacksoni	Rwanda: North Province, Buhanga Forest	UTA R56311	HQ605825	HQ605867	HQ605908	HQ616573
Adolfus jacksoni	DRC: South Kivu Province, Kahuzi-Biega National Park	UTEP 20272	HQ605813	HQ605858	HQ605899	HQ616564
Adolfus jacksoni	DRC: South Kivu Province, Kahuzi-Biega National Park	UTEP 20273	HQ605814	HQ605859	HQ605900	HQ616565
Adolfus jacksoni	DRC: Orientale Province, Aboro	UTEP 20283	HQ605806	HQ605852	HQ605893	HQ616558
Adolfus jacksoni	DRC: South Kivu Province, Itombwe Plateau	UTEP 20280	HQ605809	HQ605854	HQ605895	HQ616560
Adolfus jacksoni	DRC: South Kivu Province, Kahuzi-Biega National Park	UTEP 20274	HQ605816	HQ605861	HQ605902	HQ616567
Adolfus jacksoni	DRC: Orientale Province, Aboro	UTEP 20285	HQ605823	HQ605866	HQ605907	HQ616572
Adolfus jacksoni	DRC: Orientale Province, Aboro	UTEP 20282	HQ605811	HQ605856	HQ605897	HQ616562
Adolfus jacksoni	DRC: South Kivu Province, Lwiro	UTEP 20275	HQ605815	HQ605860	HQ605901	HQ616566
Adolfus jacksoni	DRC: South Kivu Province, Lwiro	UTEP 20277	HQ605817	HQ605862	HQ605903	HQ616568
Adolfus jacksoni	DRC: South Kivu Province, Kahuzi-Biega National Park	UTEP 20278	HQ605818	HQ605863	HQ605904	HQ616569
Adolfus jacksoni	DRC: South Kivu Province, Bukavu	UTEP 20281	HQ605805	HQ605851	HQ605892	HQ616557
Adolfus jacksoni	Rwanda: Rukiva	–	–	–	EF632253	EF632208
Adolfus jacksoni	Arusha, Tanzania	761	HQ605785	HQ605839	HQ605881	HQ616547
Algyroides fitzingeri	Italy: Nuoro: Sardinia, Lula, direction to Conca e Crapa, monte Turuddo	Sa 35	HQ605789	–	–	–
Algyroides moreoticus	Greece: Korinthia, Feneos	–	–	–	EF632254	EF632209
Algyroides nigropunctatus	Greece: Preveza, Parga	–	–	–	EF632255	EF632210

APPENDIX 1 *Continued*

Species	Geographical origin	Museum/field voucher number	16S	cyt *b*	c-mos	RAG1
Anatolacerta danfordi	Turkey: Icel, Camliyayla	—	—	—	DQ461743	EF632224
Apathya cappadocica	Turkey: Kayseri, Mt Ercyas	—	—	—	EF632268	EF632223
Archaeolacerta bedriagae	France: Corsica	—	—	—	EF632256	EF632211
Atlantolacerta andreanskyi	Morocco: Oukaimeden	IBES 1699	HQ605787	HQ605830	HQ605872	HQ616538
Congolacerta asukului	DRC: South Kivu Province, Itombwe Plateau	UTEP 20268	HQ605801	—	HQ616585	HQ616577
Congolacerta asukului	DRC: South Kivu Province, Itombwe Plateau	UTEP 20265	HQ605804	HQ605850	HQ605891	HQ616556
Congolacerta asukului	DRC: South Kivu Province, Itombwe Plateau	UTEP 20264	HQ605803	HQ605849	HQ605890	HQ616555
Congolacerta asukului	DRC: South Kivu Province, Itombwe Plateau	UTEP 20263	HQ605802	HQ605848	HQ605889	HQ616554
Congolacerta asukului	DRC: South Kivu Province, Itombwe Plateau	UTEP 20267	HQ605800	HQ605847	HQ605888	HQ616553
Congolacerta asukului	DRC: South Kivu Province, Itombwe Plateau	UTEP 20266	HQ605808	HQ605853	HQ605894	HQ616559
Congolacerta vauereselli	DRC: South Kivu/Katanga Province border, Kabobo Plateau	UTEP 20295	HQ605810	HQ605855	HQ605896	HQ616561
Congolacerta vauereselli	DRC: South Kivu Province, Kahuzi-Biega National Park	UTEP 20289	HQ605795	—	HQ616586	HQ616578
Congolacerta vauereselli	DRC: South Kivu Province, Itombwe Plateau	UTEP 20293	HQ605798	HQ605845	HQ605886	HQ616551
Congolacerta vauereselli	DRC: Uganda: Kabale District, Bwindi Impenetrable National Park	CAS 201613	HQ605797	—	HQ616587	HQ616579
Congolacerta vauereselli	Rwanda: North Province, Bisate	UTA R55658	HQ605824	—	HQ616592	HQ616584
Congolacerta vauereselli	DRC: South Kivu Province, Itombwe Plateau	UTEP 20292	HQ605796	—	HQ616588	HQ616580
Congolacerta vauereselli	DRC: Orientale Province, Aboro	UTEP 20297	HQ605822	HQ605865	HQ605906	HQ616571
Congolacerta vauereselli	DRC: Orientale Province, Aboro	UTEP 20296	HQ605812	HQ605857	HQ605898	HQ616563
Congolacerta vauereselli	DRC: South Kivu Province, Itombwe Plateau	UTEP 20294	HQ605807	—	HQ616589	HQ616581
Congolacerta vauereselli	DRC: Orientale Province, Aboro	UTEP 20298	HQ605821	HQ605864	HQ605905	HQ616570
Congolacerta vauereselli	DRC: South Kivu Province, Kahuzi-Biega National Park	UTEP 20288	HQ605820	—	HQ616591	HQ616583
Congolacerta vauereselli	DRC: South Kivu Province, Kahuzi-Biega National Park	UTEP 20287	HQ605819	—	HQ616590	HQ616582
Dalmatolacerta oxycephala	Croatia: Hvar Island	—	—	—	EF632271	EF632228
Darevskia valentini	Armenia: Rasdan	—	—	—	EF632257	EF632212
Dinarolacerta mosorensis	Montenegro: Durmitor Mts	—	—	—	EF632270	EF632227
Eremias arguta	Ukraine	—	—	—	EF632258	EF632213
Eremias pleskei	Armenia: Ararat region	—	—	—	EF632259	EF632214
Gallotia galloti	Spain: Tenerife Island	—	—	—	EF632260	EF632215
Gastropholis prasina	Tanzania: East Usambaras	760	HQ605781	HQ605835	HQ605877	HQ616543
Gastropholis vittatus	Tanzania: Amani, East Usambaras (captive specimen)	691	HQ605780	HQ605834	HQ605876	HQ616542
Heliobolus lugubris	Namibia: Haruchas	—	—	—	EF632261	EF632216
Heliobolus spekii	Tanzania: Lake Natron	—	—	—	EF632262	EF632217

Species	Locality	Field no.				
Hellenolacerta graeca	Greece: Lakonia, Monemvasia	–	–	–	EF632269	EF632225
Holaspis guentheri	DRC: Orientale Province: Yaekela near Yangambi, Congo River	CRT 3660	HQ605784	HQ605538	HQ605880	HQ616546
Holaspis laevis	Tanzania: E. Usambaras	763	HQ605783	HQ605837	HQ605879	HQ616545
Holaspis laevis	Tanzania: Handeni	764	HQ605782	HQ605836	HQ605878	HQ616544
Holaspis laevis	Tanzania: Usambara Mts	–	–	–	EF632263	EF632218
Iberolacerta cyreni	Spain: Avila: Track to Laguna Grande de Gredos	IBES 1010	HQ605788	HQ605831	HQ605873	HQ616539
Iberolacerta horvathi	Austria: Carinthia, Rattendorf	–	–	–	EF632264	EF632219
Iberolacerta monticola	Portugal: Sierra Estrela	–	–	–	EF632265	EF632220
Ichnotropis squamulosa	Mozambique (animal trade)	–	–	–	EF632266	EF632221
Lacerta agilis	Austria: Lower Austria, Weitra	–	–	–	EF632267	EF632222
Latastia longicaudata	Eritrea: Nakfa	–	–	–	EF632272	EF632229
Meroles suborbitalis	Namibia: Rosh Pinah	–	–	–	EF632273	EF632230
Mesalina guttulata	Tunisia: Tamerza	–	–	–	EF632274	EF632231
Mesalina rubropunctata	Egypt: Hurghada	–	–	–	EF632275	EF632232
Nucras lalandii	South Africa: Stellenbosch	–	–	–	EF632276	EF632233
Omanosaura jayakari	United Arab Emirates: Fujayrah	–	–	–	EF632277	EF632234
Ophisops elegans	Greece: Evros, Gianuli	–	–	–	EF632278	EF632235
Parvilacerta parva	Turkey: Malatya	–	–	–	EF632279	EF632236
Pedioplanis undata	Namibia: Nauchas	–	–	–	EF632280	EF632237
Philochortus spinalis	Eritrea: Ghinda	–	–	–	EF632281	EF632238
Phoenicolacerta laevis	Cyprus: Pafos	–	–	–	DQ461715	EF632226
Podarcis muralis	France: Languedoc-Roussillon: Lac du Salut de Vesoles	IBES 1181	HQ605791	HQ605833	HQ605875	HQ616541
Podarcis muralis	Austria: Lower Austria, Gumpoldskirchen	–	–	–	EF632282	EF632239
Poromera fordii	Cameroon: Mt Nlonako	–	–	–	EF632283	EF632240
Psammodromus algirus	Spain: Lerida	–	–	–	EF632284	EF632241
Psammodromus hispanicus	Spain: Barcelona	–	–	–	EF632285	EF632242
Pseuderemias smithi	Kenya: Lake Turkana	–	–	–	EF632286	EF632243
Takydromus amurensis	Russia: Amur Region	–	–	–	EF632287	EF632244
Takydromus sexlineatus	Indonesia (animal trade)	–	–	–	EF632288	EF632245
Teira dugesii	Portugal: Madeira Island	–	–	–	EF632289	EF632246
Timon lepidus	Spain: Alicante	–	–	–	EF632290	EF632247
Timon tangitanus	Morocco: Foret de Cedres (Azrou)	IBES 2892	HQ605786	HQ605829	HQ605871	HQ616537
Tropidosaura gularis	South Africa: SW-Cape	–	–	–	EF632291	EF632248
Zootoca vivipara	Austria: Lower Austria, Schneeberg	–	–	–	EF632292	EF632249

CER, Corey E. Roelke field series; DRC, Democratic Republic of the Congo; IBES and Sa field numbers were kindly provided by Salvador Carranza; CRT field number was kindly provided by Zoltán Nagy and Jos Kielgast; NM Nairobi and field numbers without letters, William R. Branch tissue collection.

APPENDIX 2

SPECIMENS EXAMINED

Adolfus africanus: CAS 54812 (male), Democratic Republic of the Congo (DRC), Medje; CAS 176853 (female), Uganda, Rukungiri District, Impenetrable (Bwindi) Forest Reserve, Buhoma Road, 2 km S of forest reserve boundary, 1°0′35″S, 29°37′14″E, 1585 m; CAS 176858 (female), Uganda, Rukungiri District, Impenetrable (Bwindi) Forest Reserve, Ngoto Swamp, 0°53′7″S, 29°43′46″E, 1280 m; CAS 204389 (male), Uganda, Toro District, Kibale National Park, Makerere University Biological Field Station; UTEP 20269 (male), UTEP 20270 (female), DRC, South Kivu Province, Hombo, 1°50′40″S, 28°26′36″E, 800 m; UTEP 20271 (male), DRC, South Kivu Province, Mashaba village near Irangi, 1°52′28″S, 28°27′6″E, 800 m.

Adolfus alleni: CAS 162680, Uganda, Mt Elgon, Arugot, 2896 m; USNM 49411 (male), Kenya, Aberdare Range summit, 0°19′0″S, 36°37′0″E.

Adolfus jacksoni: CAS 122729 (male), Kenya, Western Province, Kakamega District, Kakamega Forest, near Kaimosi; CAS 152783 (male), Kenya, Nyanza Province, Kisumu District, Chemelil; CAS 201598 (female), Uganda, Kabale District, Bwindi Impenetrable National Park, Institute for Tropical Forest Conservation (Ruhizha), 1°2′47″S, 29°46′28″E, 2362 m; CAS 201610 (female), Uganda, Kabale District, Bwindi Impenetrable National Park, Kabale-Kayonza rd, 1°2′36″S, 29°46′5″E, 2347 m; CAS 204386 (male), Uganda, Masaka District, Lake Nabagabo; UTEP 20272 (male), UTEP 20273 (male), DRC, South Kivu Province, Kahuzi-Biega National Park, Tshivanga, 2°18′46″S, 28°45′18″E, 2200 m; UTEP 20274 (subadult), DRC, South Kivu Province, Mbayo, 2°15′58″S, 28°47′1″E, 1943 m; UTEP 20275 (male), South Kivu Province, Lwiro, 2°14′44″S, 28°48′45″E, 1678 m; UTEP 20276 (subadult), UTEP 20277 (male), DRC, South Kivu Province, Lwiro, 2°14′27″S, 28°50′58″E, 1530 m; UTEP 20278 (female), DRC, South Kivu Province, Kahuzi-Biega National Park, Mugaba, 2°16′3″S, 28°39′43″E, 2264 m; UTEP 20279 (subadult), DRC, South Kivu Province, Bitale, 2°12′28″S, 28°37′46″E, 1770 m; UTEP 20280 (female), DRC, South Kivu Proince, Itombwe Plateau, Kizuka, 3°0′23″S, 28°45′0″E, 2450 m; UTEP 20281 (subadult), DRC, South Kivu Province, Bukavu, 2°30′23″S, 28°51′20″E, 1529 m; UTEP 20282 (female), UTEP 20283 (male), UTEP 20284 (female), DRC, Orientale Province, Aboro, 2°0′59″N, 30°50′0″E, 2088 m; UTEP 20285 (male), UTEP 20286 (male), DRC, Orientale Province, summit of Mt Aboro, 2°0′20″N, 30°31′8″E, 2445 m.

Congolacerta vauereselli: CAS 201613 (subadult), CAS 201614 (female), Uganda, Kabale District, Bwindi Impenetrable National Park, Mubwindi Swamp, NW end, S trail, 1°4′15″S, 29°45′12″E; CAS 204387 (female), Uganda, Toro District, Kibale National Park, Makerere University Biological Field Station, Kanyawara, Lower Camp; UTEP 20287 (subadult), DRC, South Kivu Province, Kahuzi-Biega National Park, Bwindi, 2°16′36″S, 28°39′40″E, 2333 m; UTEP 20288 (male), DRC, South Kivu Province, Kahuzi-Biega National Park, Chinya, 2°16′26″S, 28°39′36″E, 2297 m; UTEP 20289 (male), UTEP 20290 (female), UTEP 20291 (male), DRC, South Kivu Province, Kahuzi-Biega National Park, Mugaba, 2°16′3″S, 28°39′43″E, 2264 m; UTEP 20292 (subadult), DRC, South Kivu Province, Itombwe Plateau, Bishaka, 3°20′27″S, 28°47′39″E, 2208 m; UTEP 20293 (subadult), DRC, South Kivu Province, Itombwe Plateau, *c.* Miki, 3°22′28″S, 28°38′33″E, 1799 m; UTEP 20294 (female), DRC, South Kivu Province, Itombwe Plateau, Mugegema, 3°3′42″S, 28°46′42″E, 2675 m; UTEP 20295 (male), DRC, South Kivu/Katanga Province border, Kabobo Plateau near Kilwemapante, 5°3′13″S, 28°59′30″E, 1993 m; UTEP 20296 (female), UTEP 20297 (male), UTEP 20298 (female), UTEP 20299 (male), DRC, Orientale Province, Aboro, 2°0′59″N, 30°50′0″E, 2088 m.