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# A new species of chameleon (Squamata: Chamaeleonidae) from the Aberdare Mountains in the central highlands of Kenya

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## Abstract

We describe a new species of chameleon, *Trioceros kinangopensis* **sp. nov.**, from Kinangop Peak in the Aberdare mountains, central highlands of Kenya. The proposed new species is morphologically and genetically distinct from other member of the *bitaeniatus*-group. It is morphologically most similar to *T. schubotzi* but differs in the lack of sexual size dimorphism, smaller-sized females, smoother, less angular canthus rostrales, smaller scales on the temporal region and a bright orange gular crest in males. Mitochondrial DNA indicates that the proposed new taxon is a distinct lineage that is closely related to *T. nyirit* and *T. schubotzi*. The distribution of *T. kinangopensis* **sp. nov.** appears to be restricted to the afroalpine zone in vicintiy of Kinangop Peak and fires may pose a serious threat to the long-term survival of this species.

**Key words:** endemism, East Africa, phylogenetics, rift vally, species diversity, systematics

## Introduction

The highlands of East Africa represent a regional hotspot for chameleon species diversity in mainland Africa. Five genera and over fifity species are present in the region, the majority of which are restricted to montane biotopes (Spawls *et al.* 2002, Tilbury 2010). Surveys of some of the more remote and biologically understudied mountain ranges in the region continue to reveal hitherto undiscovered species diversity (Menegon *et al.* 2002, Necas *et al.* 2003, Necas *et al.* 2005, Mariaux & Tilbury 2006, Menegon *et al.* 2009, Necas 2009, Necas *et al.* 2009, Krause & Böhme 2010, Lutzmann *et al.* 2010, Stipala *et al.* 2011). Molecular techniques have also been used to investigate several groups of East African chameleons that have a complex taxonomic history, providing valuable insights into their the phylogenetic relationships and the historical geological and climatic processes that have driven their diversification (Matthee *et al.* 2004, Measey & Tolley 2011, Tolley *et al.* 2011). Molecular studies have also revealed that many geographically widespread species with fragmented distributions contain deep phylogenetic splits, indicating prolonged periods of isolation among populations and the presence of cryptic species (Matthee *et al.* 2004, Mariaux & Tilbury 2006, Mariaux *et al.* 2008, Menegon *et al.* 2009, Barej *et al.* 2010, Stipala *et al.* 2011).

Among the East African chameleons the genus *Trioceros* is a species diverse lineage that has been included in several phylogenies (Townsend & Larson 2002, Raxworthy *et al.* 2002, Tilbury & Tolley 2009, Krause & Böhme 2010, Stipala *et al.* 2011) but is in need of further detailed investigation. Within the genus is a sub-clade known as the *bitaeniatus*-group (Rand 1963) that consists of small bodied, live-bearing species with montane distributions. They are a morphologically distinctive group that display the following characteristics: prominent tubercular cranial crests including a raised parietal crest, which forms a triangular casque at the back of the head; prominent dorsal and gular crests; and heterogeneous body scalation. A few species possess a single, short rostral process and one species, *T. jacksonii*, possesses three long annular horns. The taxonomic history of the *bitaeniatus*-group is complex and has been subject to several major revisions with conflicting views on species and sub-species groupings (Werner 1911, Mertens 1966, Rand 1963). A detailed study of the external morphology of the *bitaeniatus*-group by Rand (1963)

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resulted in the recognition of six species, which has since been accepted by most authors (Broadley & Howell 1991, Klaver & Böhme 1997, Spawls *et al.* 2002, Tilbury 2010), although two subspecies have been elevated to full species (Necas 1999). More recently, several new species have been described that have also been assigned to the group (Tilbury 1991, Tilbury 1998, Necas *et al.* 2003, Necas *et al.* 2005, Krause & Böhme 2010, Stipala *et al.* 2011). Molecular studies support the monophyly of the *bitaeniatus*-group and identify all described species as separate monophyletic evolutionary lineages (Koreny 2006, Tilbury & Tolley 2009).

The continued discovery of new chameleon species across the highlands of East Africa provided the motivation for a project to investigate chameleon species diversity in the central and western highlands of Kenya. We conducted extensive surveys of afromontane and afroalpine habitats and also adjacent anthropogenic landscapes. During these surveys we visited the inaccessible Kinangop Peak at the southern end of the Aberdare range. It can only be reached after a tough two-day trek through dense bamboo and steep hilly terrain. At the peak we experienced strong winds, heavy cloud cover and hail storms. However, during a short break in the weather and a brief period of sunshine we were able to collect a series of small chameleons that emerged at the tops of bushes to bask. In this paper we compare the Kinangop Peak specimens with other members of the *bitaeniatus*-group and based on their morphological and molecular distinctiveness describe them here as a new species.

## Material and methods

### Field survey techniques

We visited the Kinangop Peak area for three days between 23rd and 26th February 2007. We surveyed afroalpine vegetation between 3000–3800m, conducting searches during the day and also at night using torches. Specimens were held in cloth bags and later killed with chloroform and preserved using a 4% formalin solution, before being finally stored in 70% ethanol. All specimens are held in the National Museums of Kenya, Nairobi.

### Morphological analysis

In addition to specimens collected during the field surveys we examined preserved material of all described species in the *bitaeniatus*-group from the following museum collections: National Museums of Kenya (NMK), Natural History Museum, London (BMNH) and Zoological Research Museum Alexander Koenig in Bonn (ZFMK). The total number of specimens examined of each species were: *T. bitaeniatus* (14), *T. conirostratus* (2), *T. ellioti* (31), *T. hanangensis* (2), *T. hoehnelii* (52), *T. kinangopensis* **sp. nov.** (13), *T. kinetensis* (4), *T. marsabitensis* (2), *T. narraioca* (14), *T. ntunte* (2), *T. nyirit* (24), *T. rudis* (22), *T. schoutedeni* (description only, de Witt 1965), *T. schubotzi* (24), *T. sternfeldi* (7). Material examined is listed in Appendix I. Collecting localities of all specimens are shown in Figure 1 and the number of males and females from each locality are given in Table 1.

We made an initial assessment of the external morphology of Kinangop Peak specimens and other species in the *bitaeniatus*-group and selected the following external morphological characters: parietal crest curvature (straight/ weakly curved/ strongly curved), parietal crest angle (relative to mouth line—low/ moderately elevated/ steep), parietal crest width (narrow/ swollen posteriorly), temporal scale size (fine/ large) and convexity (flat/ convex), rostral horn (absent/ single conical scale/ short, rounded and scale covered/ pointed and annular), horn orientation (anterior/ dorsal), gular region scale size (relative to flanks) and convexity (flat/ convex), gular crest development (absent/ short/ long), dorsal crest development (low/ medium/ high), dorsal crest scale pattern (homogeneous/ heterogeneous), body scale pattern, not including lateral row tubercles (homogeneous/ heterogeneous), lateral rows tubercles (number of rows/ size of tubercles relative to flank scales), para-parietal crests position relative to other cranial crests (e.g. forked anteriorly and in contact with supra-orbital crests, running parallel to parietal, etc).

The Kinangop Peak specimens were morphologically most similar to *T. schubotzi* from Mt. Kenya, therefore we decided to conduct a more detailed comparison of morphological variation among specimens from the two massifs. In addition to the characters listed above we recorded variation in the following characters: profile of the snout (sloping/ angular), rugocity of the scales on the cranial crests (smooth/ denticulate), snout-vent length (SVL) (distance from the mouth tip to the vent); and tail length (distance from opening of the vent to tip of tail). We analysed differences in SVL between the two massifs and between the sexes using a General Linear Model (GLM) and

Analysis of Variance (ANOVA). We also incorporated sex into the model to investigate sexual size dimorphism. Relative tail length was investigated using Analysis of Covariance (ANCOVA) with SVL used as the covariate.

**TABLE 1.** Species and numbers of males and females from each collecting locality used in the morphological analysis (see map in Figure 1).

| Species | Locality ID | Locality | Males | Females |
|---|---|---|---|---|
| *schoutedeni* | 1 | Mt. Kabobo, Democratic Republic of Congo | 1 | 0 |
| *rudis* | 2 | Virunga Mountains, Uganda | 4 | 4 |
| *ellioti* | 3 | Ruwenzori Mountains, Uganda | 1 | 2 |
| *rudis* | 3 | Ruwenzori Mountains, Uganda | 9 | 5 |
| *conirostratus* | 4 | Imatong Mountains, Sudan | 1 | 0 |
| *kinetensis* | 4 | Imatong Mountains, Sudan | 2 | 2 |
| *conirostratus* | 5 | Loima Hills, Kenya | 1 | 0 |
| *nyirit* | 6 | Mtelo massif, Kenya | 4 | 4 |
| *nyirit* | 7 | Sondang, Cherangani Hills, Kenya | 3 | 2 |
| *nyirit* | 8 | Kaptalamwa, Cherangani Hills, Kenya | 5 | 6 |
| *hoehnelii* | 9 | Mt. Elgon (3500m), Kenya | 4 | 4 |
| *ellioti* | 10 | Kabarua forest station, Mt. Elgon, Kenya | 1 | 1 |
| *bitaeniatus* | 11 | Elgeyo forest station, Kenya | 0 | 3 |
| *hoehnelii* | 12 | Eldoret, Uasin Gishu District, Kenya | 3 | 2 |
| *ellioti* | 13 | Nandi forest, Kenya | 12 | 10 |
| *hoehnelii* | 14 | Nabkoi forest station, Kenya | 5 | 3 |
| *ellioti* | 15 | Kericho forest station, Kenya | 1 | 1 |
| *ellioti* | 16 | Nyangores forest station, Kenya | 1 | 1 |
| *hoehnelii* | 16 | Nyangores forest station, Kenya | 1 | 1 |
| *hoehnelii* | 17 | Sururu forest station, Kenya | 4 | 4 |
| *bitaeniatus* | 18 | Entasekera, Nguruman escarpment, Kenya | 1 | 1 |
| *narraioca* | 19 | Mt. Kulal, Kenya | 6 | 8 |
| *marsabitensis* | 20 | Mt. Marsabit, Kenya | 2 | 0 |
| *ntunte* | 21 | Mt. Nyiru, Kenya | 1 | 1 |
| *bitaeniatus* | 22 | Maralal, Samburu District, Kenya | 0 | 3 |
| *hoehnelii* | 23 | Ngare Ndare forest, Mt. Kenya, Kenya | 2 | 2 |
| *schubotzi* | 24 | Mt. Kenya moorland, Kenya | 2 | 2 |
| *schubotzi* | 25 | Chogoria route, Mt. Kenya | 4 | 0 |
| *hoehnelii* | 26 | Naro Moru Met. Station (3000m), Mt. Kenya | 2 | 0 |
| *schubotzi* | 27 | Sirimon route, Mt. Kenya | 9 | 7 |
| *hoehnelii* | 28 | Nyahururu, Nyandarua District, Kenya | 3 | 1 |
| *hoehnelii* | 29 | Kiandogoro Moorland, Aberdare Mtns, Kenya | 4 | 4 |
| *kinangopensis* **sp. nov.** | 30 | Mt. Kinangop, Aberdare Mountains | 8 | 5 |
| *hoehnelii* | 31 | Limuru, Kiambu District, Kenya | 3 | 0 |
| *bitaeniatus* | 32 | Magadi Road, Kajiado district, Kenya | 2 | 2 |
| *sternfeldi* | 33 | Mt. Kilimanjaro, Tanzania | 0 | 2 |
| *sternfeldi* | 34 | Mt. Meru crater, Tanzania | 2 | 3 |
| *hanangensis* | 35 | Mt. Hanang, Tanzania | 1 | 1 |
| *bitaeniatus* | 36 | Mwanza, Tanzania | 2 | 0 |

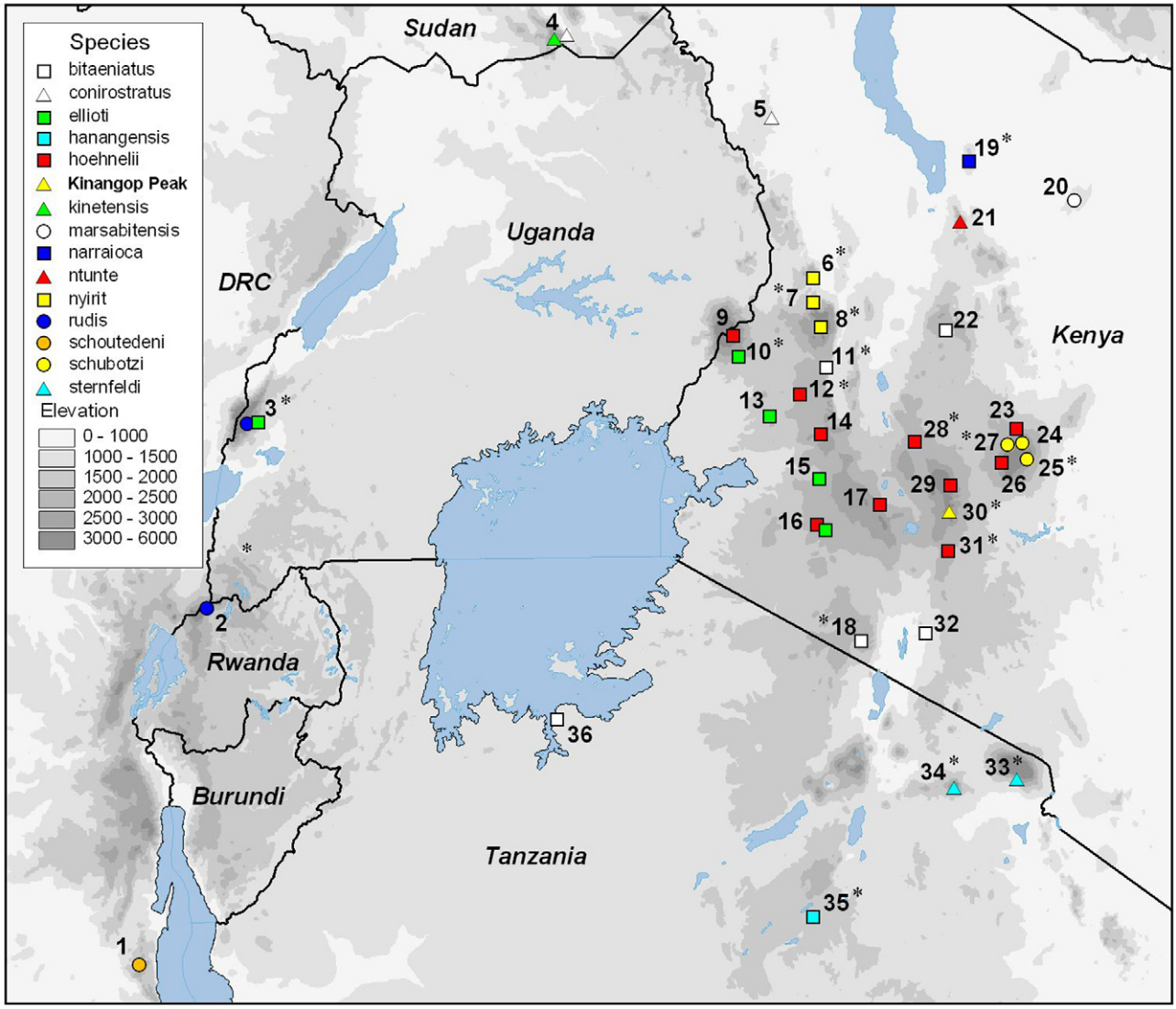


**FIGURE 1.** Collecting localities of specimens used in the morphological analysis. Numbers of specimens from each locality given in Table 1, Appendix II. An * indicates collecting localities used in the molecular analyses.

## Molecular analysis

We investigated genetic differentiation and phylogenetic relationships among species in the *bitaeniatus* group using two mitochondrial markers, partial 16S rRNA and the protein coding region ND4, plus adjacent tRNAs. Both markers have proved informative in studies investigating species diversity and phylogenetic relationships among species in snakes (Wuster *et al.* 2008), other groups of lizards (Albert *et al.* 2007, Leache & McGuire 2006) and within the Chamaeleonidae (Tolley *et al.* 2004, Matthee *et al.* 2004, Mariaux & Tilbury 2006, Boumans *et al.* 2007, Mariaux *et al.* 2008, Tilbury & Tolley 2009, Gehring *et al.* 2010, Glaw *et al.* 2012). The 16S marker has been widely used in molecular studies of Chameleonidae and enabled us to include several additional species from the *bitaeniatus* group in our analyses.

**Source material.** Mitochondrial DNA sequences were obtained for 10 of the 14 described species in the *bitaeniatus*-group: *T. bitaeniatus, T. conirostratus, T. ellioti, T. hanangensis, T. hoehnelii, T. jacksonii, T. narraioca, T. nyirit, T. rudis, T. schubotzi* and *T. sternfeldi*. *Trioceros melleri* and *Chamaeleo dilepis* were used as outgroups. Novel DNA sequences were generated from tissues collected during field surveys. Additional 16S sequences were obtained from GenBank. Species names, collecting localities and GenBank accession numbers of specimens used in the phylogenetic analyses are listed in Table 2.

**TABLE 2.** Specimens used in the phylogenetic analyses: species names, collecting localities, Field tag IDs and GenBank accession numbers for 16S and ND4 sequences.

| | | | GenBank accession numbers | |
|---|---|---|---|---|
| Species | Collecting locality | Field tag ID | 16S | ND4 |
| *C. dilepis* | Entasekera, Nguruman Escarpment, Kenya | JAS209 | JN161104 | JN165389 |
| *T. bitaeniatus* | Elgeyo forest station, Elgeyo escarpement | JAS404 | JN161102 | JN165387 |
| *T. bitaeniatus* | Elgeyo forest station, Elgeyo escarpement | JAS405 | JX046727 | JX046737 |
| *T. bitaeniatus* | Tenges forest station, Tugen Hills | JAS226 | JN161103 | JN165388 |
| *T. conirostratus* | Mtelo massif, Kenya | JAS256 | JX046728 | JX046738 |
| *T. conirostratus* | Mtelo massif, Kenya | JAS258 | JX046729 | JX046739 |
| *T. ellioti* | Cherangani forest station, Cherangani Hills | JAS255 | JN161105 | JN165390 |
| *T. ellioti* | Kabarua forest station, Mt. Elgon | JAS402 | JX046730 | JX046740 |
| *T. ellioti* | Kabarua forest station, Mt. Elgon | JAS403 | JN161106 | JN165391 |
| *T. hanangensis* | Mt. Hanang, Tanzania | - | DQ397283 | - |
| *T. hanangensis* | Mt. Hanang, Tanzania | - | DQ397284 | - |
| *T. hanangensis* | Mt. Hanang, Tanzania | - | FJ717781 | - |
| *T. hoehnelii* | Eldoret, western highlands | JAS414 | JN161107 | JN165392 |
| *T. hoehnelii* | Nyahururu, Central Highlands | JAS033 | JN161112 | JN165397 |
| *T. jacksonii* | Nairobi | CjNBI1 | JN161116 | JN165401 |
| *T. kinangopensis* **sp. nov.** | Mt. Kinangop, Aberdare Mountains | 41661 | JX046732 | JX046742 |
| *T. kinangopensis* **sp. nov.** | Mt. Kinangop, Aberdare Mountains | 41663 | JX046733 | JX046743 |
| *T. kinangopensis* **sp. nov.** | Mt. Kinangop, Aberdare Mountains | 41665 | JX046734 | JX046744 |
| *T. kinangopensis* **sp. nov.** | Mt. Kinangop, Aberdare Mountains | 41667 | JX046735 | JX046745 |
| *T. melleri* | unknown | - | AB474916 | AB474916 |
| *T. narraioca* | Mt. Kulal, Kenya | - | DQ397298 | - |
| *T. nyirit* | Kaptalamwa, Cherangani Hills | JAS243 | JN161117 | JN165402 |
| *T. nyirit* | Tenderwa, Cherangani Hills | TEND1 | JN161122 | JN165407 |
| *T. nyirit* | Tenderwa, Cherangani Hills | TEND2 | JN161123 | JN165408 |
| *T. nyirit* | Tenderwa, Cherangani Hills | TEND4 | JN161125 | JN165410 |
| *T. nyirit* | Mtelo massif. Kenya | JAS264 | JN161120 | JN165404 |
| *T. nyirit* | Mtelo massif. Kenya | JAS265 | JN161121 | JN165405 |
| *T. rudis* | Ruhiza, Ruwenzori Mountains, Uganda | - | DQ397223 | - |
| *T. rudis* | Bwindi, Uganda | - | DQ923811 | - |
| *T. rudis* | Bwindi, Uganda | - | DQ397285 | - |
| *T. schubotzi* | Sirimon route (3000m), Mt Kenya | JAS083 | JN161127 | JN165412 |
| *T. schubotzi* | Sirimon route (3000m), Mt Kenya | JAS084 | JX046736 | JX046746 |
| *T. schubotzi* | Chogoria route (3000m), Mt Kenya | schCH | JX046731 | JX046741 |
| *T. sternfeldi* | Mt. Meru, Tanzania | 3ST | JN161128 | JN165413 |
| *T. sternfeldi* | Mt. Meru, Tanzania | 4ST | JN161129 | JN165414 |
| *T. sternfeldi* | Mt. Kilimanjaro, Tanzania | - | DQ397287 | - |

**Laboratory methods.** Genomic DNA was extracted from tissues using a standard protocol of Proteinase K digestion and salt extraction (Palumbi *et al*. 1991) and visualised on a 1% agarose gel. We amplified two portions of the mitochondrial genome using the Polymerase Chain Reaction (PCR): approximately 750 b.p. of partial 16S ribosomal RNA and 850 b.p. of partial NADH Dehydrogenase Subunit 4 (ND4) and adjacent tRNAs (tRNAhis, tRNAser, tRNAleu), using the following the laboratory protocols. The ND4 marker was amplified using the prim-

ers ND4 and LEU (Forstner *et al.* 1995) and 16S marker using primers L1921 (Fu 2000), L2206 and H3056 (Honda *et al.* 2003). Approximately 10–40ng of total genomic DNA was used as template for the PCR in a final volume of 20µl containing: a thermophilic buffer (50mM KCl, 10mM Tris–HCl, pH 9.0), 2mM $MgCl_2$, 0.5µM of each primer, 0.4mM dNTPs, and 1.25 Units of Taq polymerase. The cycle profile included an initial denaturing step at 95 ºC for 2 min, followed by 42 cycles of 95 ºC for 45s, 58 ºC (ND4) or 56 ºC (16S) for 45s and 72 ºC for 2 min, with a final extension of 72 ºC for 5 min. PCR products were checked on a 1% agarose gel, then purified with EZNA Cycle Pure PCR Clean-up kits. The concentration of the purified PCR product was determined for optimal sequencing using a SpecroMax spectrophotometer. PCR fragments were directly sequenced for both strands using the BigDye cycle sequencing kit (Applied Biosystems), and an ABI 377 automated sequencer. Chromatograms were read using Geneious Pro 4.0 and a consensus sequence generated from the forward and reverse primer sequences.

**Sequence alignment.** Sequences were aligned with ClustalW (Thompson *et al*. 1994) as a plug-in to Geneious Pro, using the default settings. The protein-coding gene ND4 was translated into amino-acid sequences using ORF Finder (http://www.bioinformatics.org/sms2/orf_find.html) (Stothard 2000) to check for unexpected stop codons, and no indels were present, either of which would indicate pseudogene sequences (Zhang & Hewitt 1996).

**Phylogenetic analysis.** Phylogenetic analyses were conducted using Maximum Parsimony (MP) and Bayesian Inference (BI) methods. Distance matrices were computed with MEGA 5 (Tamura *et al.* 2011). For MP we used PAUP* 4.0b10 (Swofford 2002). Prior to conducting a MP analysis we concatenated 16S and ND4 genes and conducted a partition homogeneity test, as implemented in PAUP* 4.0b10 (Swofford 2002) to test for conflicting phylogenetic signal. MP analyses were performed as an unweighted heuristic search with TBR branch swapping and 1000 random addition sequence replicates. Gaps were treated as fifth character as they have been shown to contain useful phylogenetic signal, particularly at lower taxonomic levels (Kawakita *et al.* 2003). Support for internal nodes was estimated using non-parametric bootstrap searches (Felsenstein 1985) with 1000 pseudo-replicates, 25 random addition sequence replicates each and SPR branch-swapping. Nodes with at least 70% bootstrap support were considered to indicate strong support with a 95% probability of the clade being correct (Hillis & Bull 1993, Felsenstein 2004).

Bayesian analyses were carried out using Markov Chain Monte Carlo (MCMC) randomization in MrBayes 3.1 (Ronquist & Huelsenbeck 2003). We ran multiple Bayesian analyses under different data partitioning strategies. Data partitions were selected based on marker (16S and ND4) and functional role e.g. coding versus non-coding regions and codon position for protein coding regions. We determined the most appropriate model of nucleotide substitution for each data partition using the program MrModelTest v2.2 (Nylander *et al.* 2004) and AIC to select the best-fit model. For each partitioning strategy we ran two independent analyses consisting of four Markov chains that ran for $10x10^6$ generations, sampled every 10,000 generations, with a maximum likelihood starting tree, using default priors with the exception of changes necessary to set models of evolution and ‘‘prset ratepr’’ set as ‘‘variable’’ and using the "unlink" command to allow partitions to evolve at heterogeneous rates. The programme Tracer 1.4 (Rambaut & Drummond 2007) was used to determine ‘burn-in’ and the first 250 trees were discarded, the remaining trees used to generate a 50% majority rule consensus tree. Support for individual clades was assessed based on Bayesian posterior probabilities (Pp), and clades with $Pp \geq 95\%$ were considered to be strongly supported (Huelsenbeck & Rannala 2004). We assessed whether different partitioning strategies were better than an un-partitioned analysis using Bayes factors, as described in the MrBayes 3.1 manual (Ronquist *et al.* 2005) and discussed in Brandley *et al.* (2005), Nylander *et al.* (2004) and Brown & Lemon (2007).

## Results

### Morphological analysis

Specimens from Kinangop Peak differ in their external morphology from all other species in the *bitaeniatus*-group (Table 3) based on the following combination of characters: absence of a rostral process, a low straight casque, a short gular crest (orange in males), heterogeneous body scalation with two prominent rows of enlarged tubercles on each flank. The Kinangop Peak specimens are most similar to *T. schubotzi* but differ from them in the following characters: the canthus rostralis form a sloping snout without a short rostral process or bump and are smooth in profile, scales on temporal region are only moderately enlarged bordering the orbit and graduate in size posteriorly to become indistinguishable from those on the body; females same size as males (sexual-size dimorphism present in *T. schubotzi*).

**TABLE 3.** External morphologyical variation among species in the *bitaeniatus* group.

| Species | Parietal crest curvature | Parietal crest angle | Parietal crest width | Temporal scales (size & convexity) | Rostral process |
|---|---|---|---|---|---|
| *kinangopensis* sp. nov. | straight | low | narrow posteriorly | fine-mod enlarged/ convex | absent |
| *schubotzi* | straight | low | narrow posteriorly | large/ convex | absent or v short |
| *sternfeldi* | straight/ weakly curved | mod elevated | swollen posteriorly (not all specimens) | large/ convex | absent |
| *hanangensis* | straight/ weakly curved | mod elevated | narrow posteriorly | large/ convex | absent |
| *rudis* | straight | low | narrow posteriorly | large/ mod convex | absent |
| *ellioti* | straight | low-mod elevated | narrow posteriorly | small-mod enlarged/ flat | absent |
| *schoutedeni* | straight | low | narrow posteriorly | no data | absent |
| *ntunte* | straight | low | narrow posteriorly | large/ convex | absent |
| *nyirit* | straight/ weakly curved | mod elevated | narrow posteriorly | large/ convex | prominent/ scale-covered |
| *hoehnelii* | strongly curved | steep | narrow posteriorly | large/ flat-convex | prominent/ scale-covered |
| *narraioca* | strongly curved | steep | narrow posteriorly | large/ mod convex | prominent/ scale-covered |
| *bitaeniatus* | straight | low | narrow posteriorly | mod enlarged/ flat | absent |
| *conirostrata* | straight | low | narrow posteriorly | mod enlarged/ flat | single conical scale |
| *kinetensis* | straight | low | narrow posteriorly | large/ weakly convex | absent |
| *marsabitensis* | re-curved | low | narrow posteriorly | mod large/ flat | prominent/ annular |
| *jacksonii* | straight-moderately curved | mod elevated | narrow posteriorly | large/ convex | long/ annular |

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**TABLE 3.** (continued)

| Species | Horn orientation | Gular scales (size/ convexity) | Gular crest length | Dorsal crest height | Dorsal crest pattern (heterogeneity/ grouping) |
|---|---|---|---|---|---|
| *kinangopensis* sp. nov. | n/a | coarse with rows of convex tubercles | short | low to medium | uneven/ groups of 4 |
| *schubotzi* | n/a | coarse with rows of convex tubercles | short | low to medium | uneven/ groups of 4 |
| *sternfeldi* | n/a | coarse with rows of convex tubercles | short | low to medium | weakly differentiated/ groups of 4 |
| *hanangensis* | n/a | coarse with rows of convex tubercles | short | medium | uneven/ groups of 4 |
| *rudis* | n/a | fine | medium-long | low | uneven/ groups of 4 |
| *ellioti* | n/a | fine | short | low to medium | weakly differentiated |
| *schoutedeni* | n/a | no data | short | low | uneven/ groups of 4 |
| *ntunte* | n/a | weakly enlarged | very short | low | uneven/ groups of 4 |
| *nyirit* | anterior | coarse with rows of convex tubercles | short-long | medium to high | uneven/ groups of 3 or 4 |
| *hoehnelii* | dorsal | moderately enlarged | long | medium to high | uneven/ groups of 4 |
| *narraioca* | dorsal | coarse with rows of convex tubercles | short | low to medium | uneven/ groups of 4 |
| *bitaeniatus* | n/a | moderately enlarged | short | low to medium | uneven/ groups of 4 |
| *conirostrata* | anterior | fine | short | low | uneven/ groups of 4 |
| *kinetensis* | n/a | fine | short | low | uneven/ groups of 4 |
| *marsabitensis* | anterior | moderately enlarged | short | low | uneven/ groups of 4 |
| *jacksonii* | anterior | moderately enlarged | absent | high | single or paired large scales, separated by undifferentiated scales |

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**TABLE 3.** (continued)

| Species | Body scale heterogeniety | Lateral rows (number of rows/ size of tubercles) | Para-parietal crests |
|---|---|---|---|
| *kinangopensis* sp. nov. | heterogenous | double/ large | meets supraorbitals but obscured by extensive interorbital convex scales |
| *schubotzi* | heterogenous | double/ large | meets supraorbitals but obscured by extensive interorbital convex scales |
| *sternfeldi* | heterogenous | double/ moderate-large | meet supraorbitals |
| *hanangensis* | heterogenous | double/ moderate-large | meets supraorbitals in most specimens but not all i.e. Mt. Hanang |
| *rudis* | homogeneous-weakly heterogeneous | single, rarely double,/ small | do not meet supraorbitals |
| *ellioti* | homogeneous-weakly heterogeneous | single or sometimes double/ small | do not meet supraorbitals - three parallel ridges between the orbits |
| *schoutedeni* | homogeneous | single/ small | do not meet supraorbitals |
| *ntunte* | homogeneous-weakly heterogeneous | single or double/ small-moderate | forked anterio-laterially in one and indistinct in another |
| *nyirit* | heterogeneous | double/ moderate-large | often meets supraorbitals posteriorly |
| *hoehnelii* | heterogeneous | double/ moderate-large | often indistinct and do not meet supraorbitals |
| *narraioca* | heterogeneous | single or double/ small-moderate | often indistinct, may or may not meet supraorbitals |
| *bitaeniatus* | heterogeneous | double/ moderate-large and flat | do not meet supraorbitals |
| *conirostrata* | heterogeneous | double/ moderate-large | start high on the parietal crest at shallow angle to parietal |
| *kinetensis* | heterogeneous | double/ small | |
| *marsabitensis* | heterogeneous | double/ moderate-large | meet supraorbitals |
| *jacksonii* | heterogeneous | absent | do not meet supraorbitals |

The canthus rostralis in *T. schubotzi* are raised to give the snout a square profile and form a short rostral process in some individuals. The scales on the canthus rostrales are also larger in *T. schubotzi*, giving the crests a serrated outline in most specimens. In *T. schubotzi* the temporal region is covered by enlarged scales, weakly or moderately convex and distinctly larger than the scales on the nape. Figures 2 and 6 illustrate the differences in head morphology between Kinangop Peak specimens and the closely related *T. nyirit* and *T. schubotzi*.

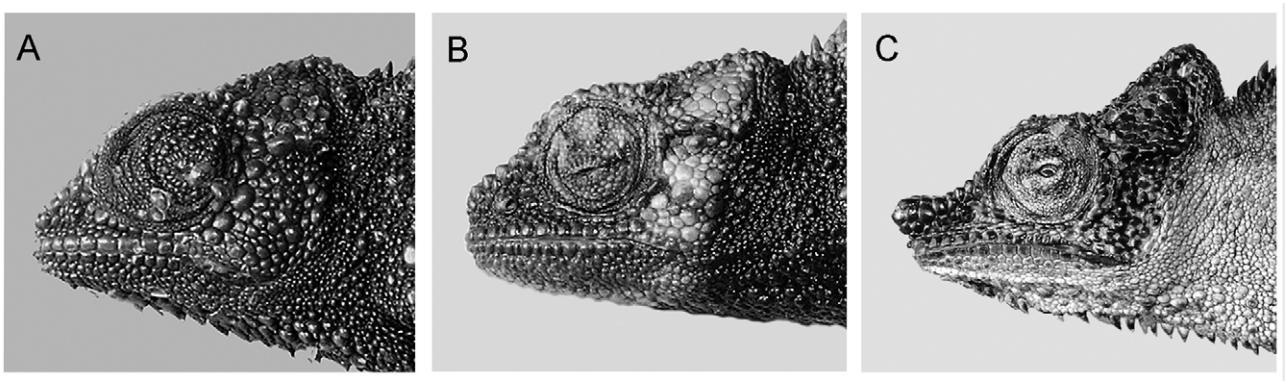


**FIGURE 2.** Male head morphology. A— male (NMK L/3071/12), Kinangop Peak; B—*T. schubotzi* (NMK L/2325), Mt. Kenya; C—*T. nyirit*, Cherangani Hills (NMK L/3166/1). *T. nyirit* differs from Kinangop Peak specimens in having a prominent rostral process and elevated casque. *T. schubotzi* differs from the Kinangop Peak specimens in having an angular snout profile, present as a short rostral process in many individuals, and enlarged scales across the entire temporal region.

A GLM of SVL revealed that the 'massif*sex' interaction term was highly significant ($F_{3,30}$=8.51, p<0.001), therefore we investigated differences in SVL between massifs and between sex independently. Males did not significantly differ in SVL between massifs ($T_{1,21}$=2.58, p=0.12) but females were significantly different ($T_{1,9}$=8.11, p=0.02). Sexual-size dimorphism was not evident in the Kinangop Peak specimens ($T_{1,10}$=0.28, p=0.61) but was highly significant for *T. schubotzi* ($T_{1,20}$=13.6, p=0.0014) (Figure 3).

Relative tail length (RTL) was also investigated using a GLM with SVL as a covariate. The massif*sex interaction term was not significant ($F_{1,28}$=0.03, p=0.85) and RTL did not significantly differ between massifs ($F_{1,28}$=0.08, p=0.78) or between the sexes ($F_{1,28}$=0.77, p=0.39).

## Molecular analysis

**Sequence variation.** Average genetic (uncorrected pairwise) distance among specimens from Kinangop Peak was <0.1%. Uncorrected p-distances between Kinangop Peak specimens and other described species in the *bitaeniatus*-group ranged from 1.7–6.6% for 16S and 3.7–8.2% for ND4 (Table 4). Genetic distances among described species in the *bitaeniatus*-group ranged from 1.7–6.2% for 16S and 5.8–9.5% for ND4.

**Phylogenetic analysis.** The final sequence alignment consisted of 1555 base pairs (726 b.p. of 16S and 829 b.p. of ND4 and adjacent tRNAs). Translation of the sequences revealed no unexpected indels or stop codons. Of the 1555 b. p., 474 were variable and 291 were parsimony-informative. The partition homogeneity test revealed no conflicting phylogenetic signal (p=0.82) and therefore 16S and ND4 markers were concatenated and analysed together. The MP analysis produced a single most parsimonious tree. The Bayesian analysis was run using different partitioning strategies and Bayes Factors did not strongly support any of the partitioned analyses over an unpartitioned analysis using GTR + I + G as the model of nucleotide substitution. Both Bayesian and MP trees produced almost identical topologies in the majority rule consensus trees (Figure 4) with the exception of a polytomy in the Bayesian tree that is resolved in the MP tree, although boostrap values are low at the relevant nodes. Species assigned to the *bitaeniatus* group form a strongly supported clade.

The phylogenetic relationships among species in the *bitaeniatus* group are not fully resolved, although the Kinangop Peak specimens represent a strongly supported monophyletic lineage that together with *T. schubotzi* and *T. nyirit* forms a strongly supported sub-clade within the *bitaeniatus* group. *T. nyirit* is paraphyletic with respect to the Kinangop Peak specimens, although this relationship is only weakly supported.

**TABLE 4.** Uncorrected average p-distances among species in the *bitaeniatus* group. Lower left = 16S, upper right = ND4.

| Species | *bitaeniatus* | *conirostratus* | *ellioti* | *hoehnelii* | *jacksonii* | *nyirit* | *schubotzi* | *kinangopensis* **sp. nov.** | *sternfeldi* |
|---|---|---|---|---|---|---|---|---|---|
| *bitaeniatus* | | 0.065 | 0.085 | 0.082 | 0.094 | 0.085 | 0.095 | 0.079 | 0.084 |
| *conirostratus* | 0.035 | | 0.085 | 0.073 | 0.088 | 0.073 | 0.086 | 0.068 | 0.071 |
| *ellioti* | 0.043 | 0.030 | | 0.077 | 0.096 | 0.076 | 0.089 | 0.079 | 0.060 |
| *hoehnelii* | 0.048 | 0.030 | 0.028 | | 0.083 | 0.067 | 0.080 | 0.070 | 0.058 |
| *jacksonii* | 0.068 | 0.060 | 0.056 | 0.055 | | 0.090 | 0.100 | 0.082 | 0.085 |
| *nyirit* | 0.039 | 0.035 | 0.031 | 0.034 | 0.060 | | 0.065 | 0.037 | 0.061 |
| *schubotzi* | 0.046 | 0.038 | 0.031 | 0.034 | 0.062 | 0.017 | | 0.060 | 0.069 |
| *kinangopensis* sp. nov. | 0.047 | 0.040 | 0.034 | 0.036 | 0.066 | 0.017 | 0.023 | | 0.059 |
| *sternfeldi* | 0.041 | 0.034 | 0.023 | 0.029 | 0.059 | 0.032 | 0.035 | 0.034 | |

**TABLE 5.** Uncorrected average p-distances among species in the *bitaeniatus* group for 423 b.p. of partial 16S rRNA.

| Species | *narraioca* | *bitaeniatus* | *conirostratus* | *nyirit* | *hoehnelii* | *kinangopensis* **sp. nov.** | *schubotzi* | *sternfeldi* | *ellioti* | *rudis* | *hanangensis* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *bitaeniatus* | 0.027 | | | | | | | | | | |
| *conirostratus* | 0.028 | 0.026 | | | | | | | | | |
| *nyirit* | 0.014 | 0.033 | 0.029 | | | | | | | | |
| *hoehnelii* | 0.016 | 0.036 | 0.027 | 0.020 | | | | | | | |
| *kinangopensis* sp. nov. | 0.020 | 0.042 | 0.033 | 0.011 | 0.026 | | | | | | |
| *schubotzi* | 0.021 | 0.043 | 0.035 | 0.016 | 0.022 | 0.021 | | | | | |
| *sternfeldi* | 0.024 | 0.041 | 0.032 | 0.026 | 0.022 | 0.031 | 0.033 | | | | |
| *ellioti* | 0.020 | 0.037 | 0.028 | 0.022 | 0.018 | 0.027 | 0.024 | 0.019 | | | |
| *rudis* | 0.023 | 0.035 | 0.031 | 0.025 | 0.022 | 0.029 | 0.032 | 0.019 | 0.018 | | |
| *hanangensis* | 0.025 | 0.042 | 0.034 | 0.026 | 0.020 | 0.026 | 0.029 | 0.025 | 0.020 | 0.023 | |
| *jacksonii* | 0.029 | 0.039 | 0.038 | 0.039 | 0.028 | 0.042 | 0.041 | 0.035 | 0.034 | 0.031 | 0.033 |

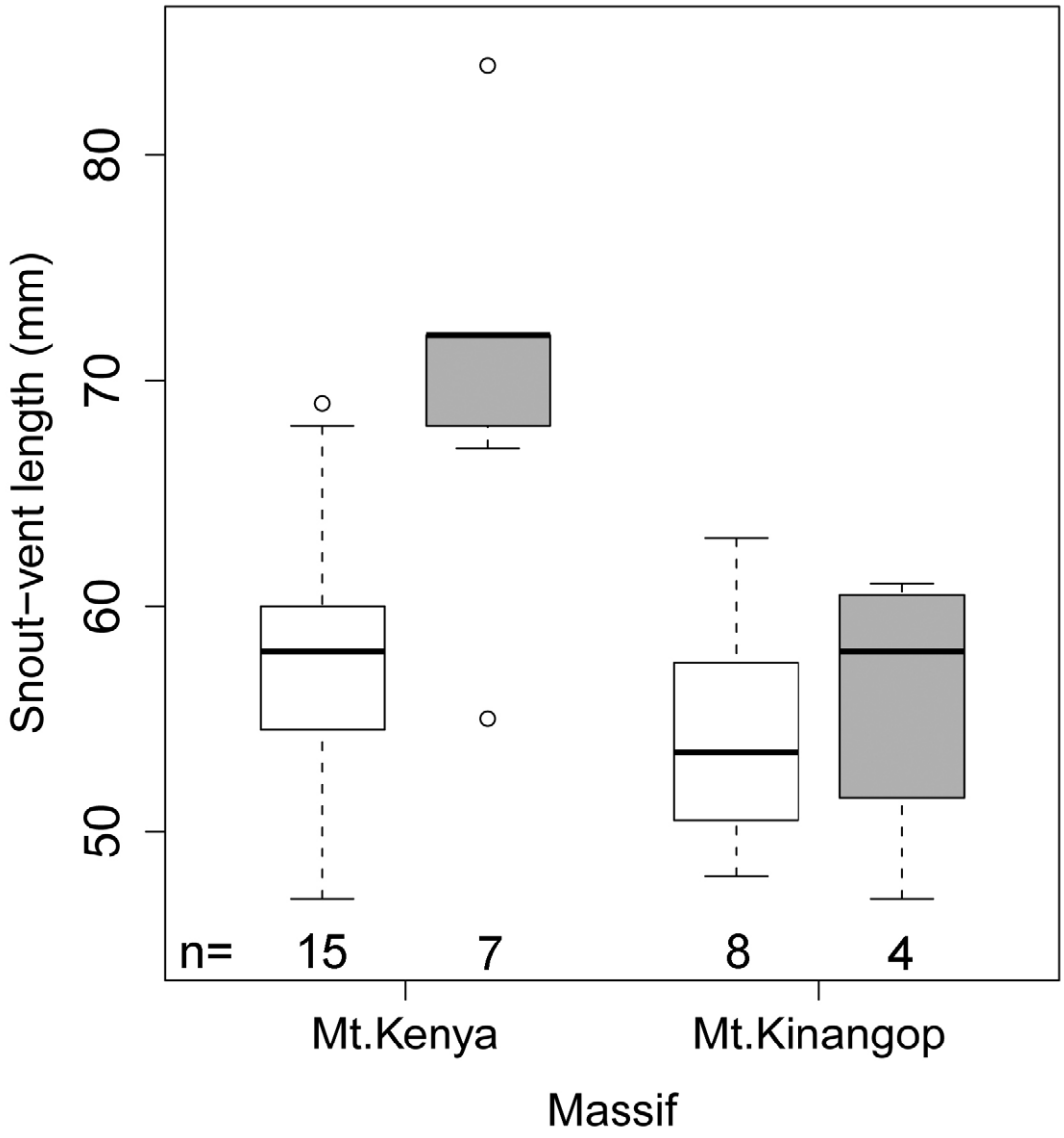


**FIGURE 3.** SVL variation in *T. schubotzi* and *T. kinangopensis* **sp. nov.** among males and females. White boxes = males, grey boxes = females, bold line = median, box limits = 25th and 75th percentiles, whiskers = 5th and 95th percentiles, circles = outliers.

Phylogenetic analysis of the 422 b.p. sequence alignment of the 16S marker included several additional species from the *bitaeniatus* group: *T. hanangensis*, *T. narraioca* and *T. rudis*. The monophyly of the *bitaeniatus* group is not supported in the Bayesian analysis and the phylogenetic relationships among most species are either represented by a large polytomy in the majority-rule consensus trees or have low support values (Figure 5). However, in both MP and Bayesian trees, nodes that represent described species are strongly supported with the exception of *T. rudis*, which was only moderately supported in the Bayesian tree. The sub-clade identifed in the 16S+ND4 tree (Kinangop Peak/ *T. schubotzi*/ *T. nyirit*) has weak support and topologies conflict between Bayesian and MP analyses. However, the Kinangop Peak specimens form a strongly supported monophyletic lineage in both Bayesian and MP trees.

Molecular data were not available for the following species in the *bitaeniatus* group: *T. marsabitensis*, *T. kinetensis*, *T. schoutedeni* and *T. ntunte*. However, unpublished trees generated from sequences of the mitochondrial marker NADH dehydrogenase subunit 2 (ND2) included several of these missing taxa (Koreny 2006). *T. ntunte* is placed in a clade together with *T. schubotzi* and *T. nyirit*, which suggests a close phylogenetic relationship with the Kinangop peak lineage. However, the two populations are geographically isolated and

separated by several hundred kilometers and a substantial ecological barrier, which suggests they are likely to be distinct evolutionary lineages. *T. marsabitensis* is a sister taxon to *T. bitaeniatus* and therefore does not appear to be closely related to the Kinangop peak specimens *T. kinetensis* was placed in a clade with *T. sternfeldi*, *T. ellioti*, *T. hanangensis* and *T. rudis*, which also suggests that it is a distinct evolutionary lineage from the Kinangop Peak specimens. Molecular data were unavailable for *T. schoutedeni.*

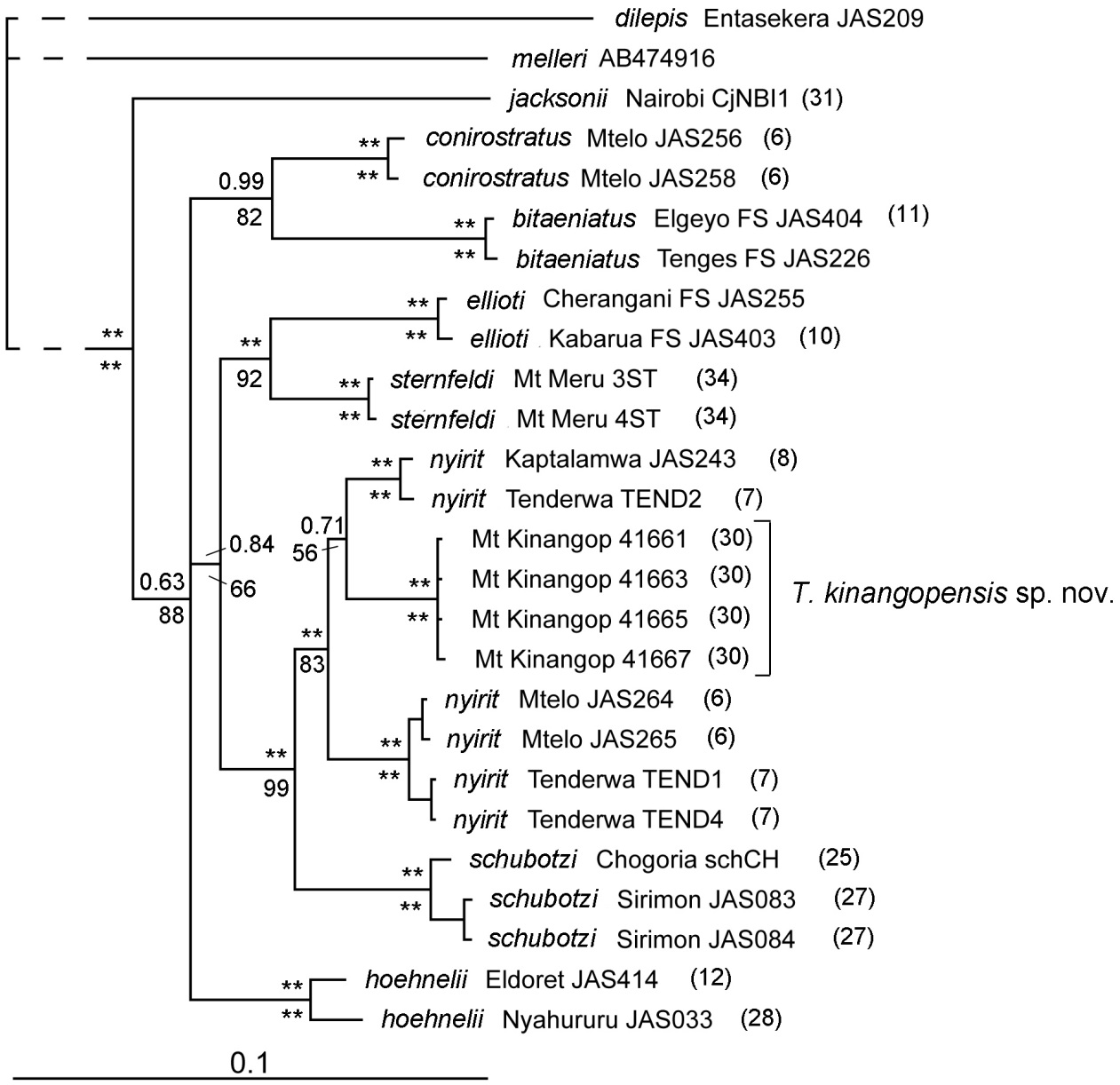


**FIGURE 4.** Phylogenetic relationships among species in the *bitaeniatus*-group. Bayesian majority-rule consensus tree for combined 16S and ND4 markers. Bayesian posterior probabilities above branches, MP boostrap values below branches. ** indicates nodes with Bayesian Pp = 1.0 and MP bootstrap support = 100%. Scale bar indicates the proportion of nucleotide substitutions. Values in parentheses = collecting locality numbers (see Figure 1 and Table 1).

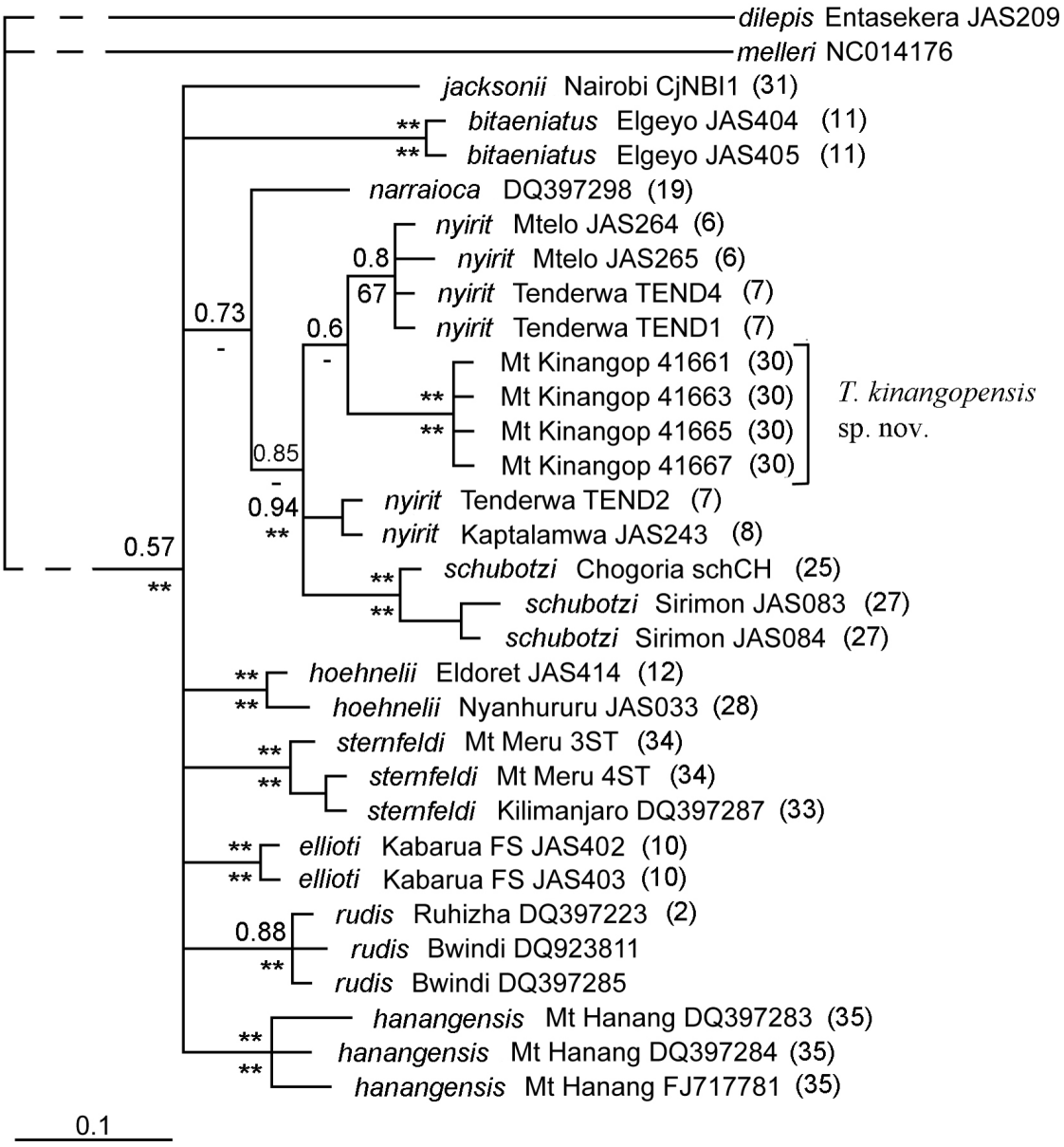


**FIGURE 5.** Phylogenetic relationships among species in the *bitaeniatus*-group. Bayesian majority-rule consensus tree generated from 422bp of partial 16S. Bayesian posterior probabilities above branches, MP boostrap support values below branches. ** indicates supported nodes (Bayesian Pp ≥0.95 and MP ≥70%). Scale bar indicates number of nucleotide substitutions. Missing values indicate conflicting topology between Bayesian and MP trees. Values in parentheses = collecting locality numbers (see Figure 1 and Table 1).

## Systematics

The results of the morphological analyses show that specimens from Kinangop Peak are morphologically distinct from all currently described taxa in the *bitaeniatus* group, although they are morphologically similar to several species. Phylogenetic analyses using mitochondrial markers (16S and ND4) show that the Kinangop Peak specimens form a monophyletic lineage distinct from other taxa in the *bitaeniatus* group. *T. nyirit* is paraphyletic in relation to the Kinangop Peak specimens. Two *T. nyirit* haplotypes occur in the Cherangani Hills, likely the result of secondary contact with the isolated population on the Mtelo massif. However, the Kinangop Peak specimens are morphologically and ecologically distinct from the *T. nyirit* populations and therefore we do not consider them

conspecific, despite the low genetic distance between them. Although not all species from the *bitaeniatus* group were included in our molecular analyses, the results of another study (Koreny 2006) indicate that the Kinangop Peak population is likely to represent a unique mitochondrial lineage distinct from all other species. Therefore, under the General Lineage Species Concept (de Quieroz 1998) or Phylogenetic Species Concept (Cracraft 1983) we propose that the Kinangop Peak population be recognised as a new species, *Trioceros kinangopensis* **sp. nov.**, based on their morphological and genetic distinctiveness, and provide the following taxonomic description.

## Species description

***Trioceros kinangopensis* sp. nov.**
(Figures 2A, 6A/ B/ C/ E)

**Holotype.** NMK 3071/12, adult male, Kinangop Peak (3500m), Aberdare Mountains National Park, Kenya, collected by Jan Stipala and Joash Nyamache on 24th February 2007.

**Paratypes.** 7 males and 5 females. NMK 3071/1, 3–5, 7, 11, males, NMK 3071/ 2, 6, 8–9, females, locality same as holotype; NMK 2536/1, male, NMK 2536/2, female, vicinity of Kinangop Peak.

**Diagnosis.** A small, robust-bodied chameleon that differs from other members of the *bitaeniatus* group in having a combination of the following characters: tail shorter than SVL in both sexes; heterogeneous body scalation (fine body scales with small scattered tubercles and two lateral rows of enlarged tubercles on each flank); low straight casque; short gular crest (orange in males); scales on the temporal region moderately enlarged and graduating in size posteriorly to merge with the body scales; snout with sloping profile and smooth canthus rostrales.

**Description of holotype**. Adult male, SVL = 58mm, tail = 51mm (total length = 109mm). Head with prominent tubercular head crests, the lateral and parietal crests forming a low triangular casque. The scales on the casque and between the canthal crests are weakly convex and between the supraorbital crests are more strongly convex. The parietal crest forks anteriorly, consisting of two ridges of strongly convex tubercles that meet with the posterior edge of the supraorbital crests. The temporal region is covered in weakly convex scales, larger than on the flanks but smaller than the tubercles on the fore-limbs. A row of larger scales borders the posterior margin of the orbit. The gular region consists of several rows of enlarged, strongly convex tubercles separated from the gular crest by fine scales. The gular crest is made up of short, conical tubercles that continue onto the belly as a much shorter ventral crest that terminates at the vent. The scales on the eye turrets are weakly heterogeneous, fine towards the outer margin with slightly larger, more convex scales around the eye opening.

Body scalation is strongly heterogeneous and consists of fine background scales scattered with slightly larger, convex tubercles. There are two prominent rows of large tubercles on each flank. The lower row runs between the limbs. The upper row starts above the forelimb level with the lateral crest and extends the length of the body, continuing onto the tail as a series of smaller tubercles. The dorsal crest is well-developed and consists of a single row of conical scales that extends the length of the body and continues on to the tail almost to the tip, the scales decreasing in size posteriorly. The scales of the dorsal crest are heterogeneous in size, forming groups of four scales that increase in size posteriorly within each group, the last two scales significantly larger than the ones before them. The upper surfaces of the limbs are covered in numerous enlarged, weakly convex tubercles, although smaller in size than those of the two lateral rows. A large convex tubercle is present on the flank above the point where the forelimb meets the body. The ventral surfaces of the limbs and tail are covered in fine homogenous scales. The hemipenes are not everted.

**Colour in preservation**. The holotype is uniform black.

**Variation in paratypes**. SVL and tail length measurements of all type specimens are given in Table 6 . Mean SVL: males = 54.3mm ± 4.9 (n = 8); females = 56.0mm ± 6.4 (n = 5). Largest male: 117mm total length (SVL = 63mm, tail = 54mm), largest female: total length = 112mm (SVL = 61mm, tail = 51mm).

The size and convexity of the scales in the two lateral rows is variable. In some individuals the tubercles are flat and very large in both rows, in others individuals they are moderately convex, the tubercles of the upper row somewhat smaller and more strongly convex, although always larger than the scattered tubercles on the flanks and limbs. In one individual the gular crest between the legs forms a double row of conical tubercles.

The hemipenes are not everted in any of the male specimens.

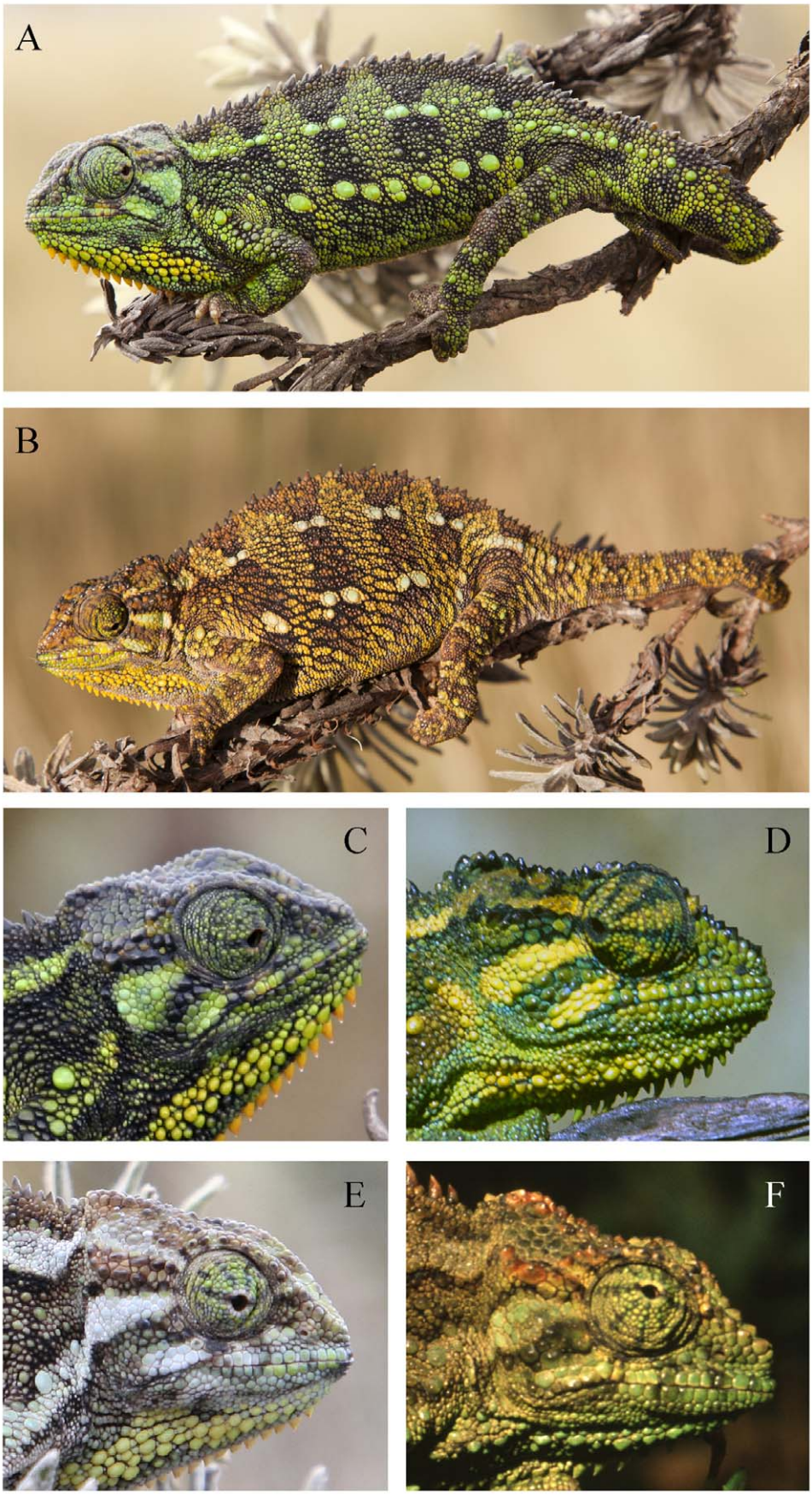


**FIGURE 6.** A—*T. kinangopensis* **sp. nov.**, adult male (holotype); B—*T. kinangopensis* **sp. nov.**, adult female; C—*T. kinangopensis* **sp. nov.**, male; D—*T. schubotzi*, male; E—*T. kinangopensis* **sp. nov.**, female; F—*T. schubotzi*, female.

**TABLE 6.** Morphometric measurements (in millimetres) of the type series of *T. kinangopensis* **sp. nov.**

| Type | Locality | Museum No. | Sex | SVL | Tail length | Head length | Head width |
|---|---|---|---|---|---|---|---|
| holotype | Kinangop peak | NMK3071/12 | male | 58 | 51 | 17.1 | 8.7 |
| paratype | " | NMK3071/1 | " | 52 | 48 | 15.8 | 8.1 |
| " | " | NMK3071/2 | " | 53 | 48 | 16.2 | 9.0 |
| " | " | NMK3071/3 | " | 49 | 41 | 15.6 | 8.4 |
| " | " | NMK3071/5 | " | 63 | 54 | 18.7 | 8.7 |
| " | " | NMK3071/7 | " | 48 | 39 | 17.6 | 9.1 |
| " | " | NMK3071/11 | " | 57 | 49 | 16.7 | 8.7 |
| " | " | NMK2536/1 | " | 54 | 46 | 16.4 | 8.6 |
| " | " | NMK2536/2 | female | 61 | 51 | 19.2 | 10.4 |
| " | " | NMK3071/6 | " | 60 | 48 | 18.4 | 9.3 |
| " | " | NMK3071/8 | " | 47 | 39 | 14.6 | 8.1 |
| " | " | NMK3071/9 | " | 56 | 45 | 17.0 | 8.8 |

**Colour in life**. Males have a background colour of grey, although in some individuals this is replaced with turquoise on the lower half of the body, head, tail and limbs. The flanks, limbs and tail are banded with a lighter yellow-green. Two broad stripes on the cheeks and the lateral rows of enlarged tubercles are also a light yellow-green. The enlarged tubercles on the sides of the throat are bright yellow and the gular crest is a distinctive orange. The eye turrets are grey-turquoise with lighter yellow-green tubercles surrounding the opening.

Females have a background colour of dark brown, a more orange-brown on the dorsal keel and the top of the head. The flanks, legs and tail are banded with grey or pale yellow. The cheek stripes and lateral rows of tubercles are cream or white. The enlarge tubercles on the side of the throat are yellow and the gular crest pale yellow-orange. The eye turrets grey with green tubercles surrounding the opening to the eye.

**Etymology.** *T. kinangopensis* **sp. nov.** is named after the collecting locality, Kinangop Peak at the southern end of the Aberdare Mountains, Kenya.

**Distribution**. *T. kinangopensis* **sp. nov.** appears to be endemic to the Kinangop Peak area at the southern end of the Aberdare Mountains. Specimens were collected between 3500–3600m. At lower elevations (3000–3200m) we found only *T. hoehnelii*. *Trioceros kinangopensis* appears to be absent from afroalpine vegetation in the central Aberdare Mountains between Mutubio and Kiandogoro gates (3000–3150m). We surveyed 13km of roadside vegetation, which included pure tussock-grass moorland, low ericaceous scrub and tall stands of St. John's Wort (*Hypericum revolutum*) and found 50 specimens of *T. hoehnelii* but no *T. kinangopensis* **sp. nov.**. Although Andren (1976) reported *T. schubotzi* (= *T. kinangopensis* **sp. nov.**) from the northern peaks in the Aberdare Mountains, a photograph labelled as *T. schubotzi* clearly shows *T. hoehnelii*. SVL/ tail length ratios in the same paper are within the range of *T. hoehnelii*, which is relatively longer-tailed than either *T. schubotzi* or *T. kinangopensis* **sp. nov.**. Nevertheless, the northern peaks reach a similar altitude to Kinangop Peak (approximately 4000m) and it is possible that *T. kinangopensis* **sp. nov.** may occur there.

**Ecology**. *Trioceros kinangopensis* **sp. nov.**. appears to be restricted to the afroalpine zone. Specimens were found in low ericaceous shrubs, which occur in patches in a habitat dominated by tussock-grass with scattered clumps of *Alchemilla* and megaphytic *Lobelia* and *Senecio* spp..

**Conservation status**. The results of our field surveys suggest that *T. kinangopensis* **sp. nov.** may be restricted to elevations above 3500m on Kinangop Peak and its range may be only 10km$^2$. Although the distribution of *T. kinangopensis* **sp. nov.** is completely within the Aberdare National Park, burnt woody remains of ericaceous shrubs suggest that extensive fires have affected the entire peak. Fires are reported to occur annually in the afroalpine zone on Mt. Kenya and may be quite extensive, sometimes burning large areas (>10km$^2$)(Coe 1967, Bongo Woodley, pers. comm.). There are no published reports on the frequency of fires in the afroalpine zone on Kinangop Peak, and the impact of fires on chameleons populations in the afroalpine zone has not been studied. Fires typically result in a total loss of surface vegetation and are likely to lead to the extinction of local chameleon populations in the short-term. The frequency of fires and the ability of chameleons to re-colonise burnt areas may result in chame-

leons being absent from much of their potential range. There may also be other long-term negative effects of fires due to population fragmentation and loss of genetic diversity through extreme population fluctuations. Further research is recommended to learn more about the distribution, ecology and the impact of fires on *T. kinangopensis* **sp. nov.** and *T. schubotzi*. Although little in known about *T. kinangopensis* **sp. nov.**, it has a very restricted distribution and lives in a habitat that is subject to fires. Therefore we suggest that under IUCN guidelines (IUCN 2010) it may be reasonable to categorise *T. kinangopensis* **sp. nov.** as either Endangered (E) or Critically Endangered (CR).

## Discussion

The mtDNA trees in this study place *T. kinangopensis* **sp. nov.** as a sister taxon to the morphologically dissimilar *T. nyirit*, rather than to the morphologically similar *T. schubotzi*. Although statistical support for this relationship is low, the results suggest that the morphological similarity between *T. schubotzi* and *T. kinangopensis* **sp. nov.** may represent morphological convergence. Morphological convergence among unrelated evolutionary lineages has been studied in a wide range of vertebrate organisms (Wiens 1991, Winemiller *et al.* 1995, Ben-Moshe *et al.* 2001), including several lizard families (Carranza *et al.* 2008, Luxbacher & Knouft 2009, Losos 2009) and is frequently correlated with ecological convergence (Karr & James 1975). In chameleons, molecular studies have revealed ecomorphological convergence in head ornamentation within the genus *Bradypodion*, thought to be driven by a combination of sexual and natural selection (Stuart-Fox & Moussalli 2007, Hopkins & Tolley 2011). Another study of morphological and ecological variation across the entire Chamaeleonidae family revealed a significant correlation between limb/ tail length and terrestrial behaviour (Bickel & Losos 2002). In relation to this study, both *T. schubotzi* and *T. kinangopensis* **sp. nov.** are restricted to open shrub habitats, while *T. nyirit* is associated with afromontane forest, suggesting that reduced head ornamentation is correlated with open habitats. However the phylogenetic relationships among these three taxa are not fully resolved in either tree. Furthermore, it may also be premature to draw any conclusions regarding potential ecomorphological convergence based on molecular trees generated using mitochondrial markers. Mitochondrial DNA is maternally inherited and introgression can result in conflicting hypotheses about population histories, species boundaries and phylogeographic events when compared to trees generated using multi-locus nuclear markers (Ballard & Whittock 2004, Gompert *et al.* 2008, Sequiera *et al.* 2008, Rato *et al.* 2010, Hailer *et al.* 2012). The genus *Trioceros* contains a relatively large number of species and many display elaborate horns and crests, making it an interesting group to investigate the evolutionary processes that drive morphological diversification and speciation. However, a fully resolved multi-locus phylogeny is needed, that includes all taxa and broad geographic sampling of widespread species, before hypotheses can be tested.

The description of a new species of chameleon from one of the better studied massifs in Kenyan highlands highlights the potential for further discoveries in the region. Many montane species, such as *T. kinangopensis* **sp. nov.**, are restricted to high elevations and may have escaped the attention of biologists due to their inaccessible habitat. Unusual distribution records for *T. schubotzi* from Mt. Kilimanjaro and the Nguru Mountains (Loveridge 1957) have been discounted by later authors (Klaver & Böhme 1997, Spawls *et al.* 2002). However, photographic evidence of chameleons from Mt. Kilimanjaro and also the Ngorongoro crater highlands suggests that chameleons similar to *T. schubotzi* may represent additional undescribed taxa and warrant investigation.

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**APPENDIX I.** Material Examined.

*T. bitaeniatus:* KENYA: Entasekera, Nguruman escarpment (2000m) (NMK 3030/1-2); Maralal, Samburu District (1900m) (NMK 3065/1-3, ZFMK 70752-3); Elgeyo forest station, Marakwet District (2400m) (NMK 3041/1-3); Magadi Road, Kajiado District (NMK 1953/1-4); TANZANIA: Mwanza, Tanzania (NMK 2154/1-2).

*T. conirostratus*: SUDAN: Lomoriti, southwest Imatong Mountains, Sudan (3500ft) (NMK 1949). KENYA: Alapatui, Loima Hills (ZFMK 84820).

*T. ellioti*: KENYA: Nandi forest, Nandi District (NMK 2653/1-2); Kabarua forest station, Mt. Elgon District (NMK2488/1-4); Chemisia, North Nandi forest (NMK 1271/ 1-20); Nyangores forest station, Bomet District (2280m) (NMK 2995/1-2); Kericho forest station, Kericho District (NMK 2989/1-2). UGANDA: Ibanda, Ruwenzori Mountains (4500ft) (NMK 1078-80), Uganda.

*T. hanangensis*: TANZANIA: Mt. Hanang (ZFMK 82368-9).

*T. hoehnelii:* KENYA: Nabkoi forest station, Uasin Gishu District (NMK 3042/1-8); Sururu forest station, Nakuru District (NMK 3044/1-8); Eldoret, Uasin Gishu District (NMK 3047/ 1-5); Ngare Ndare forest, Mt. Kenya (NMK 3066/1-4); Limuru, Kiambu District (NMK 687-9); Kiandogoro Moorland, Aberdare Mountains (NMK 761-769); Mt. Elgon (3500m), Trans-Nzoia District (NMK 2987/1-9; Nyahururu, Nyandarua District (NMK 2962/1-4); Naro Moru Met. Station

(3000m), Mt. Kenya (NMK2949/1-2); ); Nyangores forest station, Bomet District (2280m) (NMK 2994/1-2); Sururu forest station, Nakuru District (NMK 3044/1-8)

*T. kinangopensis* **sp. nov.**: see species description.

*T. kinetensis*: SUDAN: Talanga forest (ZFMK 29712); Imatong Mountains (ZFMK 25670-1, ZFMK 34531).

*T. marsabitensis.* KENYA: Mt. Marsabit (ZFMK 55602, NMK 2580)

*T. narraioca.* KENYA: Mt. Kulal, Marsabit District (NMK 2521/1-8, ZFMK 73956-62)

*T. ntunte*. KENYA: Mt. Nyiru (ZFMK 74221, ZFMK 82148)

*T. nyirit*. KENYA: southern slopes of Mtelo massif (2200-3100m) (NMK 3166/1-4); Gatau Pass, Mtelo massif (2200-2500m) (NMK 2990/1-3 & 5). Kaptalamwa and Kapiego, Cherangani Hills (2900-3000m) (NMK 2998/1-11); Sondang (3050m), Cherangani Hills (BMNH 1969.2588-9, BMNH 1969.2591, BMNH 1969.2595-6).

*T. rudis*. UGANDA: Ruwenzori trail above Ibanda, Uganda (NMK 1983/1-4); Gorilla reserve, Rwanda (8-10,000ft) (NMK 1151/1-2); Nyakalengijo, Ruwenzori (ZFMK 63219-22). Mt. Ruwenzori (ZFMK 63222 & 63224); east Ruwenzori (ZFMK 66283-4); Uganda Ruwenzori (ZFMK 65182, 64754). Visoke Karasimbi, Virunga National Park (BMNH 1978.1475-7), Mikeno Karasimbi (BMNH 1931.10.3.12-14).

*T. schubotzi*: Mt. Kenya (14,000ft) (BMNH 1932.5.2.110); Mt. Kenya (9500ft) (BMNH 1950.1.2.62); Sirimon route, NWest Mt. Kenya (11,000ft) (NMK1599/1-5); Sirimon route, NWest Mt. Kenya (11,000ft) (NMK 1954/2, 5); Mt. Kenya, Laikipia Disitrct (3588m) (NMK 2325); Old Moses Campsite, Sirimon route, Mt. Kenya, Mt. Kenya N. P. (NMK 2637/1, 2, 4, 6); Sirimon route (moorland) (3000-3200m) (NMK 2971/1-2); Old Moses Campsite, Sirimon route, Mt. Kenya (NMK 3170); Marania (NMK3172/3); Chogoria route, beyond gate (NMK 3196/1-4); Sirimon route (3800m) (NMK3200/1-2); Mt. Kenya (ZFMK 48705).

*T. sternfeldi*. TANZANIA: Mt. Meru crater, Arusha (NMK1300-2); Mt. Meru (ZFMK 82250); Mt. Kilimanjaro (ZFMK 70527-8); Laikinoi, Mt. Meru (BMNH 1958.1.3.23-4).