Integrative taxonomy and phylogeography of *Colomys* and *Nilopegamys* (Rodentia: Murinae), semi-aquatic mice of Africa, with descriptions of two new species

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Received 18 May 2020; revised 10 August 2020; accepted for publication 23 August 2020

The semi-aquatic African murine genera *Colomys* and *Nilopegamys* are considered monotypic and thought to be closely related to one another. *Colomys* occurs across forested regions of equatorial Africa, whereas *Nilopegamys* is known only from the Ethiopian holotype, making it among the rarest mammalian genera in the world – and possibly extinct. Using morphological and genetic data, we reassess the taxonomy of *Colomys* and *Nilopegamys*. A multilocus phylogeny with outgroups demonstrates that *Nilopegamys* is sister to *Colomys*. In addition, we recognize at least four morphologically diagnosable and genetically distinct species within *Colomys*: *C. eisentrauti* (elevated from subspecies and restricted to north-west Cameroon), *C. goslingi* (with a more restricted range than previously reported) and two new species (one from Liberia and Guinea and one from central and southern Democratic Republic of the Congo and Angola). We also review the status of four other taxa currently recognized within *Colomys goslingi* (*bicolor*, *denti*, *goslingi* and *ruandensis*) and demonstrate that these names lack phylogenetic and/or morphological support. Finally, we discuss potential biogeographic barriers that may have played a role in the evolution of *Colomys* and *Nilopegamys*, emphasizing the importance of rivers in both facilitating and, possibly, limiting dispersal within these genera.

ADDITIONAL KEYWORDS: antique DNA – morphometrics – phylogenetics – rivers – species delimitation – sub-Saharan Africa – systematic.

INTRODUCTION

Forested regions of sub-Saharan Africa have exceptionally high levels of endemism and biodiversity, but they are threatened due to a variety of anthropogenic activities (Myers *et al.*, 2000; Takem-Mbi, 2013; Laurance *et al.*, 2017; Tyukavina *et al.*, 2018). These regions include forests of the West African Atlantic coast, the Congo Basin, the Ethiopian Highlands, the Albertine Rift, the Eastern Arc Mountains and the Kenyan Highlands. Rodents are relatively poorly studied components of many of these ecosystems, and rodent diversity is almost certainly underestimated by current checklists (Monadjem *et al.*, 2015). Various

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[Version of record, published online 8 October 2020; http://zoobank.org/ urn:lsid:zoobank.org:pub:77081E09-855A-4A09-AA7E-1A178D122D3B]

studies have demonstrated both a high degree of endemism at the species-level (Kerbis Peterhans *et al.*, 1998; Clausnitzer & Kityo, 2001; Katuala *et al.*, 2005; Kaleme *et al.*, 2007; Plumptre *et al.*, 2007) and phylogeographic structure within species (Nicolas *et al.*, 2008a, 2020; Demos *et al.*, 2014b, 2015; Šumbera *et al.*, 2018; Mizerovská *et al.*, 2019). Moreover, many new rodents from African forested regions have been described in the past decade using an integrative approach that combines morphological and genetic data (Nicolas *et al.*, 2008b, 2010; Denys & Aniskine, 2012; Demos *et al.*, 2014a; Kerbis Peterhans *et al.*, 2020).

The rodent subfamily Murinae is hyperdiverse, with at least 704 recognized species and comprising approximately 10% of all mammal species (Burgin *et al.*, 2018). Within the Praomyini group of African murines (Lecompte *et al.*, 2002), two semi-aquatic genera have yet to be re-evaluated using an integrative approach: the 'stilt mouse' or 'wading mouse' *Colomys goslingi* Thomas & Wroughton, 1907 and the Ethiopian amphibious rat *Nilopegamys plumbeus* Osgood, 1928. Given the exceptionally wide range of *Colomys goslingi* (Dieterlen, 1983, 2013), with collecting records extending from Liberia to Kenya and south to Angola, this taxon may include undescribed species.

Thomas & Wroughton (1907) named the genus *Colomys* based on the Greek root for 'limb', referring to its elongate, 'stilt-like' hindfeet. This is in contrast to Carleton & Musser's (2005) interpretation of *Colomys* as a mouse that separates or sifts food (*colo* is Latin for 'sift' or 'strain') – which it may well do – but Thomas and Wroughton were unaware of its behaviour. A single species (*C. goslingi*) was described based on one specimen collected in present-day Democratic Republic of the Congo (DRC). Thomas and Wroughton noted the superficial similarity between *C. goslingi* and two other semi-aquatic African murid rodents with long feet: *Deomys* Thomas, 1888 and *Malacomys* Milne-Edwards, 1877. Thomas (1912) named a second species in the genus when he described *C. bicolor* from a single specimen from lowland, south-eastern Cameroon, which was distinguished from *C. goslingi* by its darker colour, larger skull size and longer nasals. Later, St. Leger (1930) named *C. goslingi denti* based on two specimens from the Kenyan Highlands, distinguished primarily by light-coloured tails. St. Leger also noted that the size difference between *C. bicolor* and *C. goslingi* disappeared when larger series, from what is now the eastern DRC, were examined and suggested that *C. bicolor* might be more appropriately considered a subspecies of *C. goslingi*. However, she noted that the one trait that could differentiate *Colomys bicolor* was its distinctly longer and more oval-shaped braincase. In his checklist of African mammals, Allen (1939) classified all three previously described taxa as subspecies of *C. goslingi*, a treatment that has not changed (Dieterlen, 2013; Monadjem *et al.*, 2015).

Osgood (1928) described a new genus and species of semi-aquatic rodent, *Nilopegamys plumbeus*, based on a single specimen caught in a highland tributary of the Blue Nile draining Lake Tana in Ethiopia. This remarkable specimen had adaptations indicative of an aquatic lifestyle, including thick pelage, large hindfeet and reduced ear pinnae, similar to (but not as extreme as) the semi-aquatic *Ichthyomys* rodents of Amazonia. Although Allen (1939) and, later, Ellerman (1941) retained *Nilopegamys* as a distinct genus, subsequent authorities, starting with Hayman (1966), synonymized it within *Colomys*. Hayman did not examine the type specimen and instead relied on notes and photographs from W. Verheyen (Hayman, 1966). Contributing to the taxonomic confusion, Osgood's original description was wanting since he did not have access to specimens of *Colomys* and did not compare the two genera.

Dieterlen (1983) was the first to systematically revise *Colomys* (*s.l.*), retaining a monotypic genus (*C. goslingi*) with six subspecies: *bicolor*, *denti*, *eisentrauti* (a new subspecies from montane Cameroon), *goslingi*, *plumbeus* and *ruandensis* (a new subspecies from the Albertine Rift). *Colomys g. eisentrauti* was distinguished from *C. g. bicolor* from nearby lowland Cameroon by its larger size and subtle pelage characters. *Colomys g. ruandensis* was diagnosed as the smallest member of the genus. A subsequent and detailed analysis based on phenetic characters re-elevated *Nilopegamys* to its former status as a monotypic genus, still represented by the single type specimen (Kerbis Peterhans & Patterson, 1995).

The ecology and behaviour of *Colomys* and *Nilopegamys* remain poorly understood. The lone *Nilopegamys plumbeus* specimen was trapped on a weed-bordered path on a stone islet exiting a small stream; it has never been observed alive. Its stomach contents had a 'fishy smell' (Fuertes & Osgood, 1936), suggesting that it included fish in its diet. The better known *Colomys* is almost always trapped near small streams, with the occasional specimen caught near swamps [Dieterlen & Statzner (1981) and pers. obs.]. Kingdon (1974) observed that *C. goslingi* forages in water while standing on its stilt-like hindlegs, keeping its vibrissae draped on the water surface (Dieterlen & Statzner, 1981: figs 2, 3) and pouncing on detected prey. Dieterlen and Statzner further examined stomach contents from *C. goslingi* trapped in present-day eastern DRC, Rwanda and South Sudan, and found that aquatic macro-invertebrates composed the majority of its diet. They also trapped a live male in the eastern DRC and later observed its behaviour in captivity over a two-year period in Dieterlen's lab in

Germany. In captivity, the animal was active at night and would hunt for live worms, tadpoles and guppies in a shallow basin filled with a few centimetres of water, behaving just as described by Kingdon (1974). It avoided deeper water, leading Dieterlen & Statzner (1981) to infer that the species forages on macro-invertebrates and small vertebrates in the wild by a combination of sifting through flowing water and actively hunting in the shallows.

In this study, we perform the first comprehensive re-evaluation of *Colomys* (*s.l.*) using genetic data from specimens across their known range. We also provide the first molecular phylogeny that includes *Nilopegamys*, one of the few remaining mammalian genera yet to be included in any phylogenetic analysis. By re-evaluating all of the taxa associated with *Colomys* using morphological and genetic evidence, we describe two new species, elevate a subspecies to species status, provide a revised description of *Colomys goslingi* with a reduced range and provide a key to the identification of *Nilopegamys* and the species of *Colomys*. We also discuss biogeographic barriers and avenues that may have been important in driving speciation events within this African radiation of semi-aquatic mice.

MATERIAL AND METHODS

Specimens, morphology and morphometrics

We examined specimens from the American Museum of Natural History, New York, USA (AMNH); British Museum Natural History, London, UK (BMNH); Carnegie Museum of Natural History, Pittsburgh, USA (CMNH); Eswatini National Museum of Natural History, Kwaluseni, Eswatini (EMNH); Field Museum of Natural History, Chicago, USA (FMNH); Louisiana State University Museum of Natural Science, Baton Rouge, USA (LSUMZ); Palaeontological Collection at the Natural History Museum, Berlin, Germany (MB); Stuttgart State Museum of Natural History, Stuttgart, Germany (SMNS); Museum of South Bohemia, České Budějovice, Czech Republic (CB); and Zoological Research Museum Alexander Koenig, Bonn, Germany (ZFMK). Additional specimens from the Medical Ecology Centre, Johannesburg, South Africa (MECJ), Royal Museum of Central Africa, Tervuren, Belgium (RMCA) and the University of Antwerp, Belgium (RUCA) were not available for morphological analyses but were considered in our discussion of geographic distributions and three RUCA specimens with sequence data on GenBank were included in our phylogenetic analyses, explained below. Complete specimen information is recorded in Supporting Information, File S1, Table S1.

We used the following 15 craniodental measurements in millimetres (Carleton & Van der Straeten, 1997): greatest skull length (GSL); condyle–incisive length (CI); greatest zygomatic breadth (ZB); breadth of the braincase measured across the parietal flanges behind the zygomatic arches (BBC); breadth across the occipital condyles (BOC); least interorbital breadth (IO); breadth of the rostrum (BR); length of the bony palate (LBP); length of the incisive foramen (LIF); length of upper diastema (LD); length of nasals (LN); breadth of the zygomatic plate (BZP); length of auditory bulla, oblique to tooth row (LAB); coronal (rather than alveolar) length of the maxillary toothrow (CLM); and width of the first upper molar (WM1). Due to missing data, two measurements (GSL and LN) were not used in the morphometric analyses, as explained below. In order to estimate relative age and ontogenetic growth, we adopted dental wear stages from Verheyen & Bracke (1966). Juvenile, subadult and young adult specimens were excluded from analyses based on dental wear, body size and sexual maturity. The lone exceptions are the holotype specimens of the two new species described below (young adults). Specimens deposited at FMNH and LSUMZ after 1990 were either prepared as skins and skeletons or fixed in formalin and later transferred to 70% ethanol. A subsample of tissue was taken from these specimens at time of capture and preserved in ethanol pending final transfer to cryogenic storage at –180 °C. For ten important specimens collected prior to 1990 (including the holotype of *N. plumbeus*; Supporting Information, File S1, Table S1), we attempted to extract and sequence 'antique' DNA (Roberts *et al.*, 2011; McDonough *et al.*, 2018) from clips of skin or dried tissue on skulls. Specimens were broadly sampled across the known range of *Colomys* and *Nilopegamys*; all known collecting localities are included in Figures 1 and 2.

Principal components analysis (PCA) and discriminant function analysis (DFA) of 13 log-transformed craniodental variables (GSL and LN were excluded to increase sample size) were carried out to assess morphometric variation and to visualize the morphometric distinctiveness of named and putative species and subspecies for 59 specimens of *Colomys* and the holotype of *Nilopegamys plumbeus* (*N. plumbeus* included in PCA only). Principal components were extracted from a variance–covariance matrix, and canonical variates were extracted from the DFA analyses. Loadings (correlations) of these variables are given as Pearson product-moment correlation coefficients between the extracted principal components or canonical variates. Two sets of species pairs were tested for significant cranial variation using

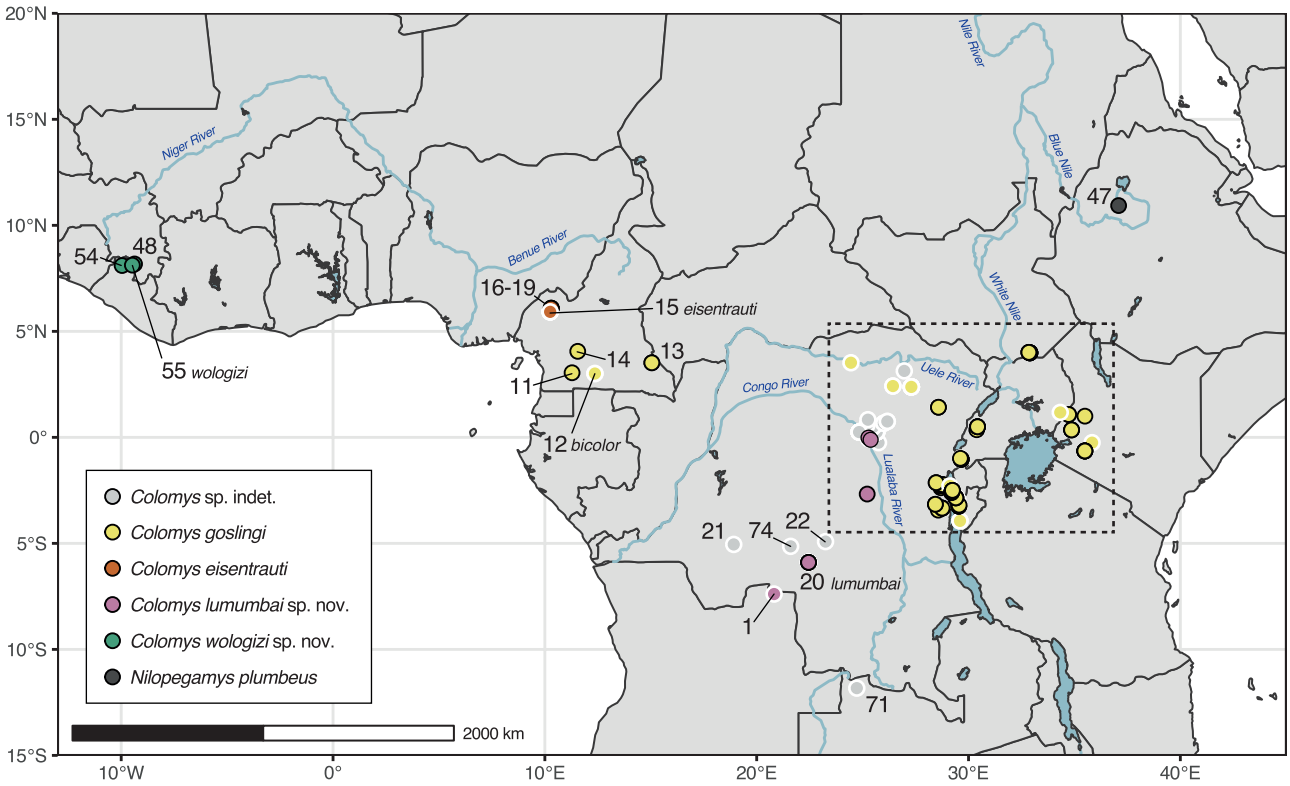

Figure 1. Map of *Colomys* and *Nilopegamys* collecting localities. Symbols with black borders denote specimens included in our phylogenetic analyses; symbols with white borders denote specimens lacking genetic data. Numbers near symbols denote unique collecting localities (Supporting Information, File S1, Table S1). Colomys .Holotype localities are indicated with the taxon name next to the locality number. The area indicated by the dotted lines is shown in further detail in Figure 2.

one-way analysis of variance (ANOVA) and Dunn's post hoc test with sequential Bonferroni correction for 13 log-transformed craniodental variables. Standard summary statistics were generated from univariate measurements for all 15 craniodental variables. All statistical morphometric analyses were performed in the software PAST (Hammer *et al.*, 2001).

DNA EXTRACTION, POLYMERASE CHAIN REACTION (PCR) AND SEQUENCING

We processed fresh tissue samples and conducted subsequent procedures in two different laboratories: one in the United States and one in South Africa. DNA was extracted from fresh tissues using a DNeasy Blood and Tissue Kit (Qiagen) in the United States and a QIAamp DNA Investigator Kit (Qiagen) in South Africa. For antique DNA, we followed the sample washing and DNA extraction protocol described in Giarla & Voss (2020). All antique DNA extractions and PCR reactions took place in a separate laboratory space where amplified mammalian DNA is not present and within a benchtop isolation hood with UV sterilization. Three mitochondrial genes [cytochrome *b* (*Cytb*), cytochrome *c* oxidase I (*COI*) and NADH dehydrogenase subunit 2 (*ND2*)] and two nuclear loci [an intron from glutamate decarboxylase 1 (*GAD1*) and an exon from recombination activating gene 1 (*RAG1*)] were selected for amplification. For fresh tissues, previously published primers were used to amplify these loci. For antique DNA, we designed new sets of primers in GENEIOUS R9 (Biomatters) using Primer3 (Untergasser *et al.*, 2012) to amplify 200–400 bp overlapping regions. We designed primers against conserved regions in consensus sequences derived from a geographically representative set of *Colomys* sequences. All primers used in this study are available in Supporting Information, File S1, Tables S2 and S3.

For samples analysed in the United States, each PCR mixture contained 13 µL of GoTaq Green Master Mix (Promega), 9 µL of water, 1 µL of each 10 µmol/L primer solution and 1 µL of sample DNA. A negative control reaction, where no DNA was added, was conducted for each separate PCR mixture. The reaction mixture was PCR amplified using an initial 2 min melting phase at 95 °C; then 40 cycles of 30 s at 95 °C, 30 s at an annealing temperature between 49–58 °C, and 60 s at 72 °C; then 5 min at 72 °C.

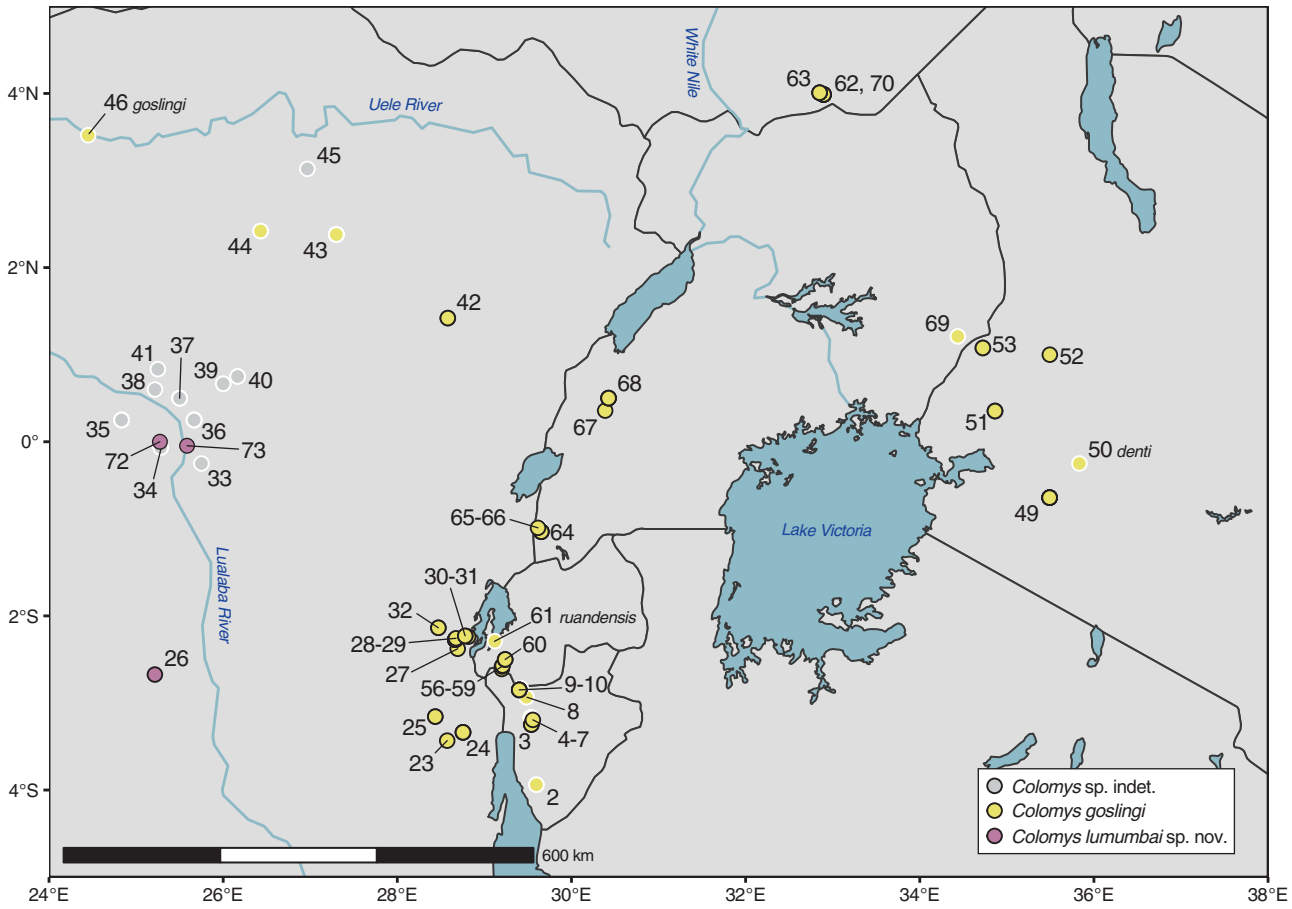

Figure 2. Map of *Colomys* localities from East Africa. Symbols with black borders denote specimens included in our phylogenetic analyses; symbols with white borders denote specimens lacking genetic data. Numbers near symbols denote unique collecting localities (Supporting Information, File S1, Table S1). Colomys Holotype localities are indicated with the taxon name next to the locality number.

Polymerase chain reaction product size was verified on a 1% agarose gel. Polymerase chain reaction products were purified using ExoSAP-IT (ThermoFisher) and sent to GENEWIZ (South Plainfield, NJ) for Sanger sequencing in both directions. For samples analysed in South Africa, amplification of the respective gene regions was carried out in separate PCR reactions consisting of 1× DreamTaq Green PCR Master Mix (ThermoFisher), 0.4 µmol/L of each primer and approximately 20 ng template DNA in a total volume of 20 µL. The temperature profile was as follows: an initial denaturation at 95 °C for 2 min, 35 cycles of 95 °C for 30 s, 55–60 °C for 30 s, and 72 °C for 1 min, followed by a final extension at 72 °C for 10 min. Successful PCR products were purified with Exonuclease I and FastAP (Thermo Fisher). Gene fragments were sequenced in both directions using the BigDye Terminator v.3.1 Cycle Sequencing Kit (ThermoFisher) and visualized on a 3500 Genetic Analyzer (Applied Biosystems).

Chromatograms were edited and assembled in GENEIOUS. For antique DNA samples, individual amplicons were subjected to a nucleotide BLAST search (Altschul *et al.*, 1990) against the nonredundant database of GenBank to check for contaminating DNA. Once contamination was ruled out, amplicons for a given antique DNA sample were assembled to a reference *Colomys goslingi* sequence from the appropriate locus.

Phylogenetics and molecular species delimitation

For each locus, outgroup sequences were downloaded from GenBank (Supporting Information, File S1, Table S4). Outgroups included seven closely related murine genera belonging to the *Praomys* group (Lecompte *et al.*, 2002), along with the more distantly related *Mus musculus* Linnaeus, 1758. Sequences from three *Colomys* specimens from otherwise

unsampled localities in Tshopo Province, DRC, were also downloaded from GenBank (Supporting Information, File S1, Table S4). All sequences for each locus were aligned in GENEIOUS using MAFFT 7 (Katoh & Standley, 2013). Protein-coding sequences were translated and examined by eye to check for premature stop codons and frameshifts. Uncorrected sequence divergences (*p*-distances) between and within species were calculated for *Cytb* using MEGA X 10.1.7 (Kumar *et al.*, 2018). Alignments were concatenated in GENEIOUS and the concatenated dataset was divided by locus and (when applicable) codon position. Different partitioning schemes and nucleotide substitution models were tested using PartitionFinder2 (Lanfear *et al.*, 2017) and ranked according to the Bayesian information criterion (BIC).

We inferred maximum-likelihood (ML) phylogenies in IQ-TREE (Trifinopoulos *et al.*, 2016) using three concatenated datasets: (1) all loci, (2) only mitochondrial loci and (3) only nuclear loci. We assigned the best-fitting partitioning scheme from PartitionFinder2 but allowed IQ-TREE to fit substitution models for each data subset. To assess nodal support, 1000 ultrafast bootstrap replicates (Hoang *et al.*, 2018) were performed. We inferred a Bayesian phylogeny in MrBayes 3.2.6 (Ronquist *et al.*, 2012) using only the complete concatenated dataset of both mitochondrial and nuclear loci. We applied the best-fitting partitioning scheme and substitution models from PartitionFinder2. We ran the two independent tree searches for 1×10^7 Markov chain Monte Carlo (MCMC) generations and assessed convergence for all parameters in TRACER 1.7 (Rambaut *et al.*, 2018).

We conducted a molecular species delimitation analysis on the ML phylogeny (all loci) using the multi-rate Poisson tree processes method in mPTP (Kapli *et al.*, 2017). We estimated the minimum branch length threshold in our ML tree and ignored branch lengths below it. Next, we conducted a ML delimitation analysis in mPTP, allowing for a unique coalescent rate for each delimited species. We estimated mean support for the ML delimitation using ten MCMC runs, each for 1×10^6 generations. Convergence between both MCMC runs was assessed using the mean standard deviation of delimitation support values.

Finally, we inferred a time-calibrated species tree in BEAST 2.6 (Bouckaert *et al.*, 2019) using the StarBEAST2 algorithm (Ogilvie *et al.*, 2017). We removed all outgroups, except for *Mus musculus*, and assigned individuals to species based on the mPTP results. We tested nucleotide substitution models for each locus in jModelTest2 (Darriba *et al.*, 2012), ranking according to the BIC and applied the best-fitting model to each locus. We linked clock rates across the three mitochondrial loci and applied a strict clock to each partition, checking the 'estimate' box for each clock partition. We time-calibrated the analysis by applying a uniform prior of 0.01–0.03 substitutions per site per lineage per millions of years on the mitochondrial clock partition, a range that reflects the increased rate of mitochondrial sequence evolution in murine rodents (Wu & Li, 1985; Arbogast *et al.*, 2002; Hardy *et al.*, 2013). All other priors and settings were left at their default values. We ran the MCMC chain for 1×10^8 generations, sampling every 10 000 steps. We discarded the first 10% of trees as burn-in and checked for convergence in TRACER.

RESULTS

DNA SEQUENCE CHARACTERISTICS

We obtained DNA sequences from five genetic loci across 85 specimens (4647 bp in total; GenBank accession numbers are listed in Supporting Information, File S1, Table S5). Excluding outgroups, 22.8% of our concatenated alignment (all loci) was missing data due to PCR or sequencing failures. Polymerase chain reaction and sequencing success were lower for the ten antique DNA samples (49.8% missing), but in nearly all cases with successful PCR, a single contiguous sequence was obtained. Only two *Cytb* sequences had internal gaps: CMNH 42469 was missing one 5-bp portion of internal sequence and CMNH 42470 was missing two portions (5 bp and 25 bp). Polymerase chain reaction amplicons of antique DNA were assembled successfully with no bases in disagreement. All BLAST searches for individual antique DNA PCR amplicons matched most closely to *Colomys* sequences or, for loci with no *Colomys* sequence yet published on GenBank, to closely related genera (e.g. *Hylomyscus* Thomas, 1926 or *Zelotomys* Osgood, 1910). This allowed us to rule out contamination from more distant relatives. For the alignment that included all outgroups and all loci, PartitionFinder selected a best-fitting partitioning scheme with eight data subsets; nucleotide substitution models for each subset were estimated in PartitionFinder and IQ-Tree (Supporting Information, File S1, Table S6). DNA sequence alignments for all loci are included in Supporting Information, File S2.

PHYLOGENETICS AND MOLECULAR SPECIES DELIMITATION

The MrBayes MCMC analysis of our concatenated dataset (all loci) converged successfully, with all parameters achieving effective sample sizes (ESS) greater than 1000. The Bayesian and ML phylogenies are identical at deeper nodes in the tree (excluding relationships among outgroups), with minor differences for shallower relationships. As such, only the ML

topology is shown (Fig. 3; both trees available in Newick format in Supporting Information, File S2). Maximum-likelihood trees based on analysis of concatenated mitochondrial loci or concatenated nuclear loci are also identical at deeper nodes in the tree, although two taxa are missing from the concatenated nuclear tree due to PCR failure (Supporting Information, File S1, Figs S1, S2; both trees available in Newick format in Supporting Information, File S2). All trees indicate that *Nilopegamys plumbeus* is sister to *Colomys* (*s.s.*) with all outgroup taxa being placed outside of *Nilopegamys* and *Colomys* with strong support (Fig. 3; outgroup taxa not shown here, but retained in tree files, are included in Supporting Information, File S2). *Nilopegamys* differs from the other *Colomys* clades with *p*-distances of 7.9–9.1% (Table 1). The genus *Colomys* is strongly supported as monophyletic.

In addition to *Nilopegamys*, mPTP diagnosed four other clades as distinct species with mean support values greater than 0.99 across the ten runs: (1) a group of 73 specimens broadly distributed north and east (i.e. the right bank) of the Congo River, spanning from lowland Cameroon to Kenya, which we refer to as *Colomys goslingi*; (2) a group of four specimens from the highlands of north-western Cameroon that corresponds to the nominal taxon *eisentrauti*, redescribed below as *C. eisentrauti*; (3) a group of three specimens from Liberia and Guinea corresponding to a new species (***C. wologizi* sp. nov.**) described below; and (4) a group of seven specimens from central and southern DRC corresponding to a new species (***C. lumumbai* sp. nov.**) described below.

Colomys eisentrauti is strongly supported as being sister to *C. wologizi*; the two clades differ from each other with a *Cytb p*-distance of 2.2% (Table 1). Likewise, *C. goslingi* is strongly supported as sister to *C. lumumbai* with a *p*-distance of 3.8% (Table 1). *Colomys goslingi* includes the taxa *bicolor* (lowland Cameroon), *denti* (Kenya, South Sudan and eastern Uganda), *ruandensis* (Burundi, Rwanda and western Uganda) and *goslingi* (north-eastern DRC). Only *bicolor* and *denti* form well-supported clades.

For the time-calibrated species tree analysis in BEAST, best-fitting nucleotide substitution models for each locus (with no intra-locus partitioning) are identified in jModelTest: GTR+G for *COI* and *Cytb*, HKY+G for *ND2*, and K80 for GAD and *RAG1*. The BEAST analysis converged successfully, with ESS values over 1000 for all parameters. The resulting species tree has maximum support (PP = 1.0) for all nodes and illustrates the same species-level relationships as the concatenated analyses (Fig. 4; Newick-formatted tree available in Supporting Information, File S2). This time-calibrated species tree indicates that *Nilopegamys* split from *Colomys* approximately 2.35 Mya [95% highest posterior density interval (HPDI): 1.8–3.0 Mya], with speciation events within *Colomys* occurring between 1.44 and 0.38 Mya.

Morphology

Morphometrics: Morphometric results illustrate the distinctiveness of the five putative species delimited by mPTP (Figs 5, 6; Tables 2–5). There is minor overlap between *Colomys wologizi*, *C. lumumbai* and *C. goslingi*, but *C. eisentrauti* and *Nilopegamys plumbeus* occupy distinct regions of PCA morphospace and do not overlap with any other taxon (Fig. 5). In contrast, four subspecies within *C. goslingi* (*bicolor*, *denti*, *goslingi* and *ruandensis*) exhibit substantial overlap in PCA morphospace. The two new species are distantly separated along the first principal component, which also separates *C. goslingi* and *N. plumbeus* (Fig. 5). The second principal component separates *C. eisentrauti* from the other three *Colomys* species and *N. plumbeus.* More specifically, *C. wologizi* is distinguished on the basis of small skull size (CI), narrow zygomatic plate (BZP) and short bony palate (LBP; Table 2). On the other hand, the broad and convex zygomatic plate (BZP; Table 2) of *C. lumumbai* distinguishes it from all other taxa, except for the largest taxon in our study, *N. plumbeus*. In addition to being the largest member of the genus (CI; Table 2), *C. eisentrauti* has a long snout, reflected here in its long incisive foramina and diastema (LIF and LD; Table 2). In the PCA scatterplot, *N. plumbeus* and *C. lumumbai* are readily distinguished from other species along the first principal component of craniodental variables (Fig. 5), although there is a slight overlap between *C. lumumbai* and the two *C. goslingi* subspecies, *C. g. bicolor* and *C. g. ruandensis*. The second principal component readily distinguishes *C. eisentrauti* from all other named and putative *Colomys* taxa. On the basis of the PCA, the putative *C. goslingi* subspecies *bicolor*, *denti*, *goslingi* and *ruandensis* are indistinguishable. Overall, the largest loading along the first principal component was breadth of zygomatic plate (BZP) and the largest loading on the second principal component was length of incisive foramen (LIF; Table 3).

Results of the discriminant function analysis (DFA) plotted as the first and second canonical variates (CVs) are generally similar to that inferred by results of the PCA; the primary difference being the distinct region of DFA morphospace occupied by *C. wologizi* (Fig. 6). Overall, individual specimen scores projected on the first and second canonical variates form four non-overlapping constellations of points (Fig. 6). The first canonical variate distinguishes *C. goslingi* from *C. lumumbai*. The second canonical variate readily distinguishes *C. wologizi* from *C. eisentrauti*. Overall, the largest loadings along the first canonical variate

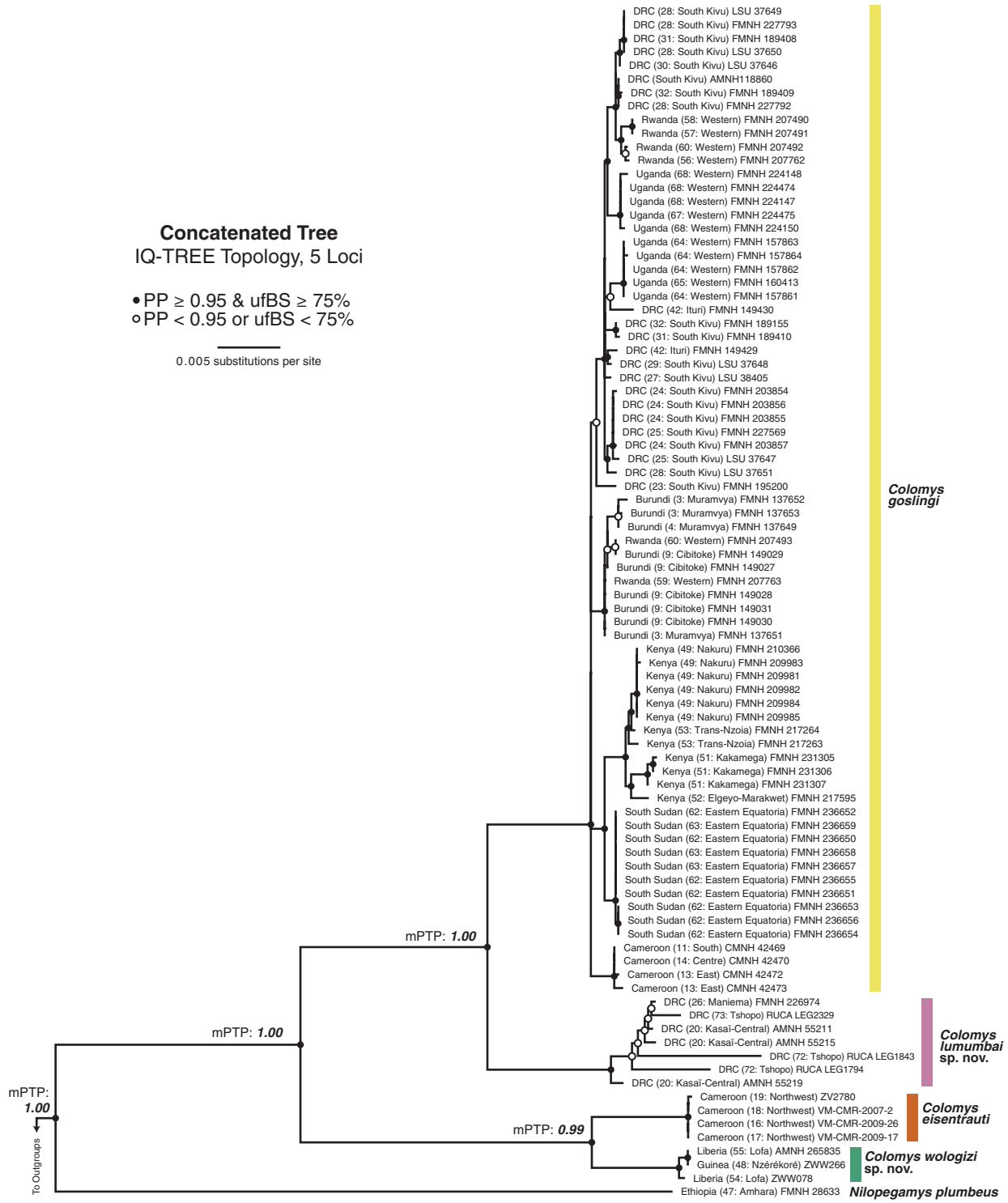

Figure 3. Phylogeny inferred in IQ-TREE based on analysis of five concatenated loci: *Cytb*, *COI*, *ND2*, GAD and *RAG1*. Symbols at nodes denote both Bayesian posterior probabilities (PP) from MrBayes and ultrafast bootstrap support (ufBS) from IQ-TREE. Mean support values for species delimitation are displayed in bold italics next to the four nodes with descendant species delimited by mPTP. Tips of the phylogeny are labeled with specimen information: country [unique locality number from Supporting Information, File S1, Table S1: highest-level administrative division (region, province, county, or state)] and unique specimen identifier. Outgroups have been removed. Full tree available in Newick format in Supporting Information, File S2.

Table 1. Uncorrected Cytb p-distances among (numbers below diagonal) and within (bolded numbers on diagonal) *Colomys* and *Nilopegamys* calculated in MEGA X

	Taxon	[1]	[2]	[3]	[4]	[5]
[1]	*Colomys goslingi*	**0.004**				
[2]	*Colomys eisentrauti*	0.068	**0.001**			
[3]	*Colomys lumumbai*	0.038	0.071	**0.015**		
[4]	*Colomys wologizi*	0.060	0.022	0.062	**0.002**	
[5]	*Nilopegamys plumbeus*	0.079	0.091	0.087	0.089	**n/a**

were condylo-incisive length (CI) and breadth of zygomatic plate (BZP); the largest loadings on the second canonical variate were length of bony palate (LBP) and breadth of braincase (BBC; Table 4). Results of one-way analysis of variance (ANOVA) carried out on the four species of *Colomys* are presented in Table 5. Post hoc pairwise comparison using Dunn's test indicated that nine of 13 variables are statistically significant in the comparison of *C. eisentrauti* and *C. wologizi* (Table 5), and three of 13 variables are statistically significant in the comparison of *C. goslingi* and *C. lumumbai* (BR, BZP and LAB; Table 5).

Comparing Colomys *and* Nilopegamys: Kerbis Peterhans & Patterson (1995) provided a direct comparison between *Colomys* and *Nilopegamys*. Many of the characters they discussed when distinguishing the two genera can be matched when viewing a large series of *Colomys* from throughout their range (Supporting Information, File S3). We highlight here the most important diagnostic characters for differentiation. Externally, the holotype of *N. plumbeus* differs from *Colomys* in the following traits: shorter ears (Table 6) with white edging (but white edging present in a few *Colomys* as well); broader hindfeet (Kerbis Peterhans & Patterson 1995, Fig. 6); and a midventral

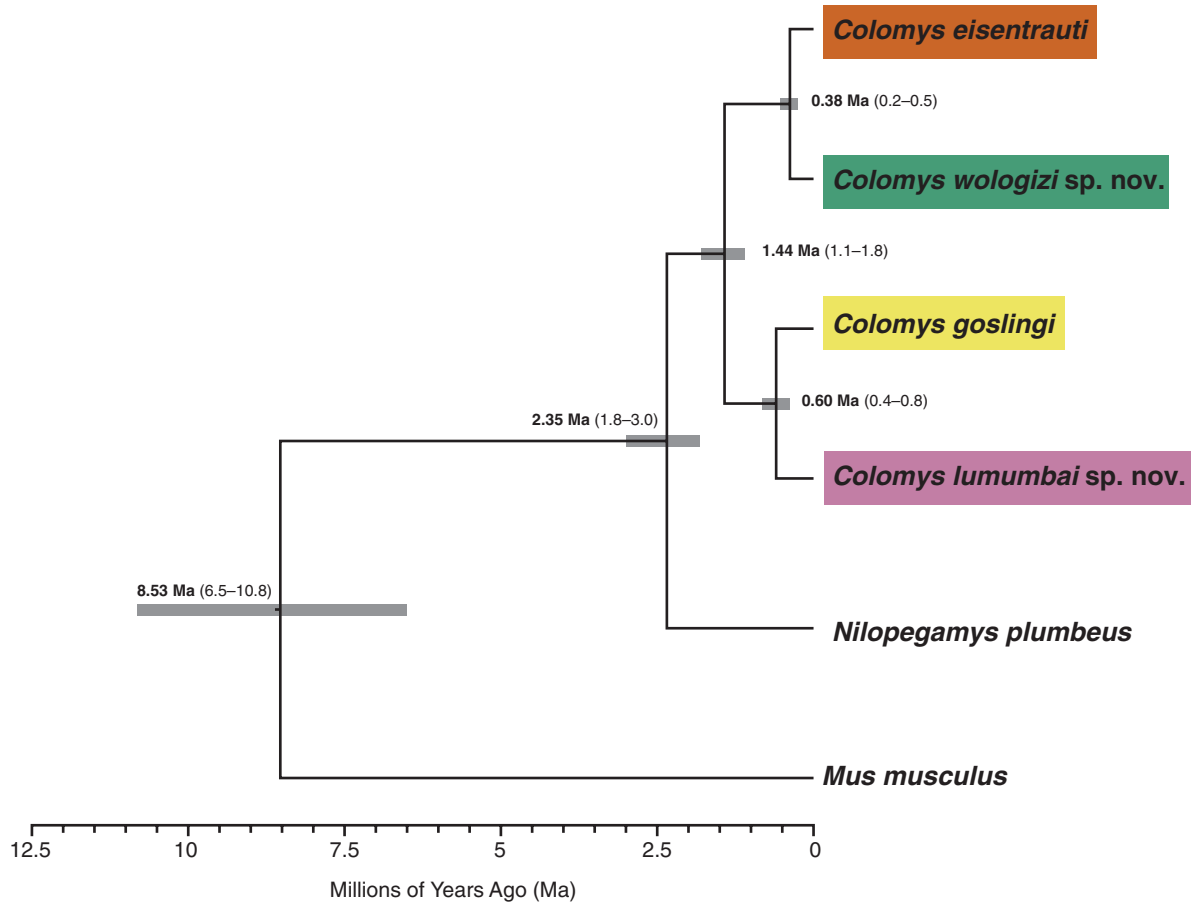

Figure 4. Species tree inferred in BEAST based on analysis of five loci: *Cytb*, *COI*, *ND2*, GAD and *RAG1*. All nodes received posterior probabilities of 1.0. Node labels include divergence time estimates in millions of years (Ma) and gray bars indicate the 95% highest posterior density interval surrounding each estimate.

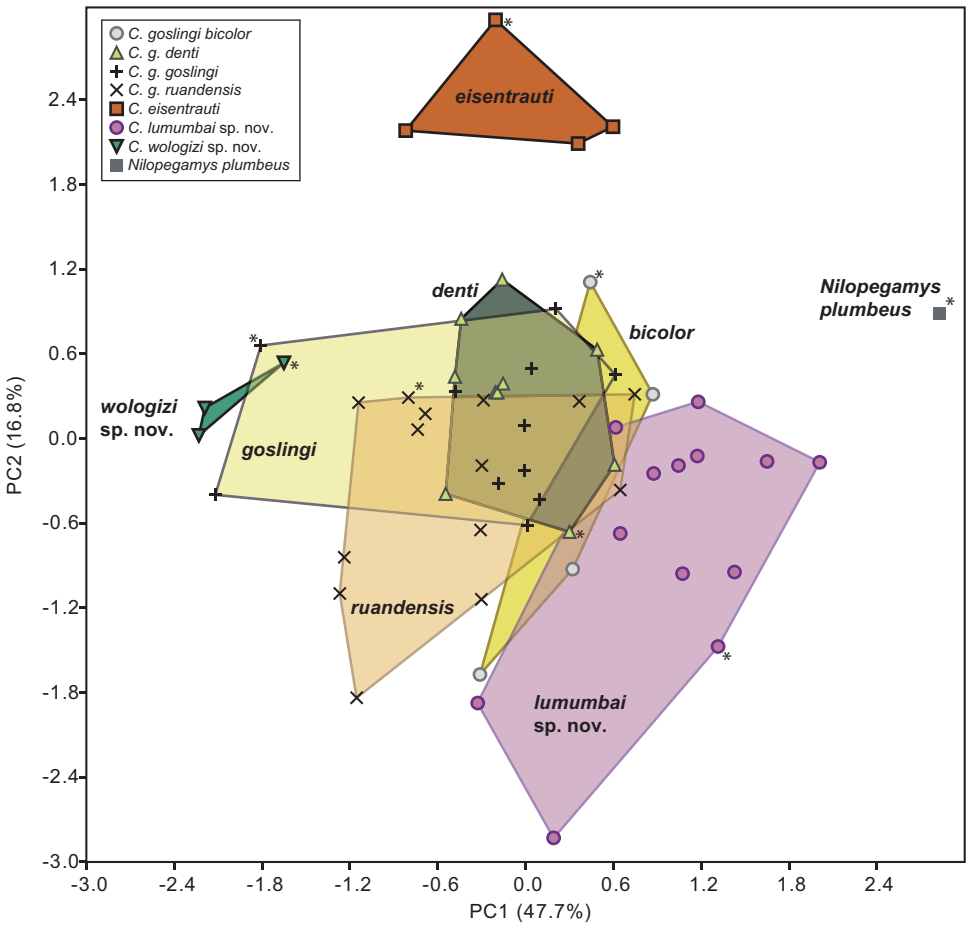

Figure 5. Scatterplot of first and second principal components extracted from principal components analysis (PCA) performed on 13 log-transformed craniodental measurements for *Colomys* and *Nilopegamys*. Asterisks denote holotype specimens (species and subspecies) included in this study.

line of black hairs along most of the tail. Cranially, *Nilopegamys* has a longer diastema (LD); a broader zygomatic plate (BZP; Table 2); larger cranial capacity and larger foramen magnum (Kerbis Peterhans & Patterson 1995; Fig. 7); typically expanded maxillary septum [but see Dieterlen (1983) for variation]; thicker hamular process substantially reducing the size of the subsquamosal fossa (Kerbis Peterhans & Patterson; Fig. 5); complete (vs. fenestrated) mastoid wall (ibid.); and a premaxilla that does not project between incisors. Dental differences include an M1 with four roots and quadrate m3 with two transverse lophs of subequal width. Postcranially, the fibula is fused to the tibia for the distal 40–45% compared to 46.5–51.0% in *Colomys*.

Dieterlen (1983) stated that *Colomys* possesses six plantar tubercles, while Kerbis Peterhans & Patterson (1995) stated that five plantar tubercles are present (in contrast to six in *Nilopegamys*). We have found examples of *Colomys* with six tubercles (27% in specimens from South Sudan, $N = 22$; and in two from Uganda, $N = 3$), but most specimens have five tubercles (Fig. 7).

Members of *Colomys* vary in the shape of the zygomatic plate (Fig. 8; Table 7): anterior rim concave (condition A), anterior rim straight (B), anterior rim slightly convex/curved (C) and anterior rim strongly convex/curved (D). Condition A was only found in *Colomys eisentrauti*, B in *C. wologizi* and in some *C. goslingi*, while C occurred only in *C. goslingi* and D in *C. goslingi*, *C. lumumbai* and in *Nilopegamys*. Although the zygomatic plate of *C. lumumbai* approaches *Nilopegamys* in BZP, only *Nilopegamys* has BZP ≥ 3.0 (Table 2).

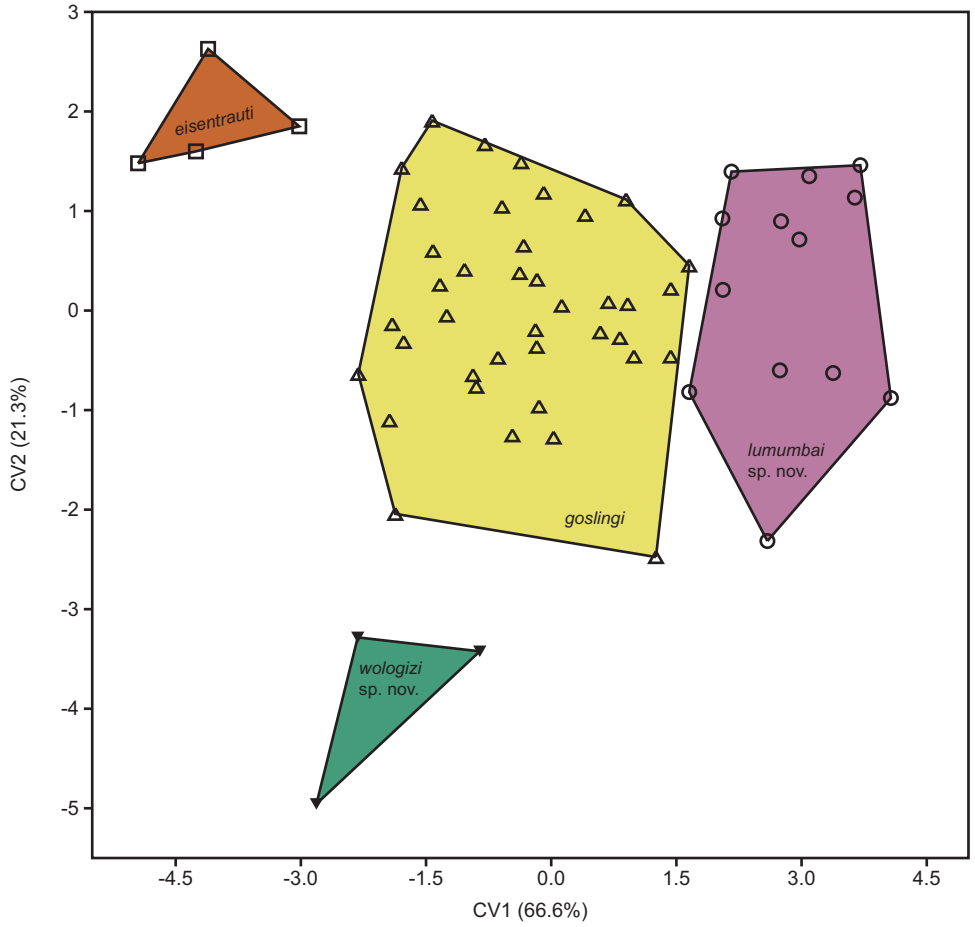

Figure 6. Scatterplot of first and second canonical variates (CV1 and CV2) extracted from discriminant function analysis (DFA) performed on 13 log-transformed craniodental measurements for *Colomys*.

TAXONOMIC ACCOUNTS

COLOMYS WOLOGIZI HUTTERER, MONADJEM & KERBIS PETERHANS, SP. NOV.

ZooBank Life Science Identifier (LSID): urn:lsid:zoobank.org:act:C55CD64A-1AF8-4568-A3AD-1960F9419EF0.

2005 *Colomys goslingi*, Musser & Carleton. In: Wilson & Reeder, eds. *Mammal species of the world: a taxonomic and geographic reference (3rd edn)*, Baltimore: Johns Hopkins University Press, 1307.

2013 *Colomys goslingi*, Dieterlen. In: Happold, ed. *Mammals of Africa, Vol. III: rodents, hares and rabbits*, London: Bloomsbury, 390–393. (part)

2017 *Colomys goslingi*, Denys, Taylor & Aplin. In: Wilson, Lacher Jr. & Mittermeier, eds. *Handbook of the mammals of the world, Vol. 7. Rodents II*. Barcelona: Lynx Edicions, 801–802.

Holotype: AMNH 265835, a young adult female, collected by CPK with large rubber band (original number R. W. Dickerman 21143) on 12 March 1990, in lowland rainforest at the foot of the Wonegizi Mountains, 10.5 km north of, and 1 km east of, Ziggida, Lofa County, Liberia (8.13° N, 9.476° W) at 560 m a.s.l. It was collected during the AMNH Expedition to the Wonegizi Mountains, Liberia, led by R. W. Dickerman. The specimen consists of a stuffed museum study skin with accompanying cranium and mandible; skin and skull are well preserved, except for a small patch of fur missing at venter and some damage of the left ear. Total length 264 mm; tail 134 mm (103% HB); hindfoot (with claw) 34.7 mm and (without claw) 33.3 mm; ear length (fresh) 18 mm and (dry) 15.5 mm. Weight: not available. Skull measurements in Table 2.

Paratypes: EMNH ZWW78, adult male preserved in alcohol, skull extracted, nasals damaged, collected by MLM on 25 May 2019 in lowland rainforest at 541 m a.s.l. near Lisco, Lofa County, Liberia (8.10416° N, 9.95802° W); EMNH ZWW266, adult male preserved in alcohol, skull extracted, nasals damaged, collected by MLM on 19 June 2019 in lowland rainforest at 532 m a.s.l. near Kpoda, Ziama Man and Biosphere Reserve, Nzérékoré Region,

Table 2. Craniodental measurements in millimeters (mean ± SD and range) of four species of *Colomys* and *Nilopegamys plumbeus*. Abbreviated variables are defined in the text

Variable	*C. eisentrauti*	*C. wologizi*	*C. goslingi*	*C. lumumbai*	*Nilopegamys* (*N* = 1)
GSL	35.5 ± 0.9 (34.2–36.2) *N* = 4	31.65 (*N* = 1)	33.2 ± 0.99 (30.6–35.7) *N* = 42 *N* = 42	34.2 ± 1.0 (32.3–35.6) *N* = 16	35.1 (*N* = 1)
CI	32.5 ± 0.38 (31.9–32.7) *N* = 4	29.0 ± 0.92 (28.0–29.6) *N* = 3	30.7 ± 0.82 (28.5–32.4) *N* = 39	30.9 ± 1.63 (26.7–32.7) *N* = 13	33.7 (*N* = 1)
ZB	17.4 ± 0.28 (17.2–17.8) *N* = 4	15.3 ± 0.47 (14.8–15.7) *N* = 3	15.9 ± 0.61 (14.6–16.8) *N* = 39	16.1 ± 0.77 (14.8–17.7) *N* = 13	17.6 (*N* = 1)
BBC	15.7 ± 0.12 (15.6–15.9) *N* = 4	14.4 ± 0.11 (14.2–14.4) *N* = 3	14.6 ± 0.38 (13.9–15.6) *N* = 39	14.7 ± 0.46 (13.7–15.3) *N* = 13	15.40 (*N* = 1)
BOC	8.2 ± 0.28 (7.8–8.4) *N* = 4	7.6 ± 0.04 (7.6–7.6) *N* = 3	7.8 ± 0.30 (7.2–8.6) *N* = 39	7.8 ± 0.23 (7.5–8.2) *N* = 13	9.0 (*N* = 1)
IO	5.1 ± 0.09 (5.0–5.2) *N* = 4	4.7 ± 0.27 (4.4–4.9)	5.0 ± 0.18 (4.6–5.3) *N* = 39	4.9 ± 0.13 (4.6–5.1) *N* = 13	5.2 (*N* = 1)
LN	14.1 ± 0.6 (13.4–14.6) *N* = 4	12.2 (*N* = 1)	12.4 ± 0.66 (10.9–13.7) *N* = 43	13.0 ± 0.5 (12.2–13.7) *N* = 17	13.2 (*N* = 1)
BR	6.6 ± 0.25 (6.2–6.8) *N* = 4	5.9 ± 0.24 (5.6–6.1) *N* = 3	6.1 ± 0.34 (5.4–6.7) *N* = 39	6.6 ± 0.34 (5.9–7.0) *N* = 13	6.7 (*N* = 1)
LBP	6.3 ± 0.13 (6.2–6.5) *N* = 4	5.3 ± 0.45 (4.9–5.8) *N* = 3	6.4 ± 0.32 (5.8–7.0) *N* = 39	6.4 ± 0.31 (5.8–6.8) *N* = 13	6.4 (*N* = 1)
LIF	7.6 ± 0.27 (7.4–7.9) *N* = 4	7.0 ± 0.62 (6.3–7.4) *N* = 3	7.0 ± 0.33 (6.4–7.5) *N* = 39	6.7 ± 0.33 (5.9–7.3) *N* = 13	7.6 (*N* = 1)
LD	9.6 ± 0.21 (9.4–9.9) *N* = 4	8.7 ± 0.26 (8.4–9.0) *N* = 3	9.0 ± 0.40 (8.1–10.1) *N* = 39	9.2 ± 0.51 (8.4–10.0) *N* = 13	10.5 (*N* = 1)
BZP	2.1 ± 0.18 (1.9–2.2) *N* = 4	1.8 ± 0.08 (1.7–1.9) *N* = 3	2.2 ± 0.18 (1.8–2.5) *N* = 39	2.6 ± 0.16 (2.4–2.9) *N* = 13	3.1 (*N* = 1)
LAB	4.4 ± 0.09 (4.3–4.5) *N* = 4	4.2 ± 0.06 (4.2–4.3) *N* = 3	4.4 ± 0.22 (4.1–4.9) *N* = 39	4.7 ± 0.16 (4.5–5.0) *N* = 13	5.0 (*N* = 1)
CLM	5.5 ± 0.21 (5.3–5.8) *N* = 4	4.9 ± 0.06 (4.9–5.0) *N* = 3	5.3 ± 0.20 (4.8–5.9) *N* = 39	5.2 ± 0.22 (4.9–5.7) *N* = 13	5.6 (*N* = 1)
WM	1.9 ± 0.04 (1.9–1.9) *N* = 4	1.8 ± 0.06 (1.8–1.9) *N* = 3	1.8 ± 0.07 (1.7–2.0) *N* = 39	1.8 ± 0.07 (1.7–2.0) *N* = 13	2.0 (*N* = 1)

Table 3. Variable loadings from principal components analysis (PCA) performed on 13 craniodental measurements of *Colomys* and *Nilopegamys*. Variables are the measurements as defined in the Materials and Methods. PC = principal component

	Correlations	
Variable	PC1	PC2
CI	0.171	0.319
ZB	0.201	0.390
IO	0.033	0.094
BBC	0.095	0.215
CLM	0.120	0.098
BOC	0.131	0.166
BR	0.315	0.237
LBP	0.228	-0.060
LIF	0.060	0.518
LD	0.210	0.364
BZP	0.798	-0.425
LAB	0.217	-0.105
WM1	0.079	0.054
Cumulative % variance	47.7	16.8
Eigenvalue	0. 003845	0.001351

Table 4. Variable loadings from discriminant-function analysis (DFA) performed on 13 craniodental measurements of *Colomys*. Variables are the measurements as defined in the Materials and Methods. CV = canonical variate

	Correlations	
Variable	CV1	CV2
CI	43.613	-1.5858
ZB	-23.049	0.19935
IO	-19.44	24.286
BBC	-21.764	33.697
CLM	-20.193	8.1371
BOC	-10.065	6.669
BR	14.625	2.1212
LBP	-7.1593	34.762
LIF	-29.73	3.0815
LD	-18.42	3.9114
BZP	29.946	-1.6505
LAB	15.273	7.8042
WM1	-15.78	-1.6612
Eigenvalue	3.43	1.096
Cumulative % variance	66.6	87.9

Guinea (8.17779° N, 9.37062° W). Both new specimens were captured using standard funnel traps typically used to capture another semi-aquatic small mammal in the region, the Nimba otter-shrew *Micropotamogale lamottei* Heim de Balsac, 1954 (Monadjem *et al.*, 2019).

Diagnosis: This species is characterized by small dimensions, short tail, gracile forefeet and hindfeet, dark nose tip, short and stout skull, narrow zygomatic plate with a straight anterior margin (Fig. 8) and small molars (Fig. 9B).

Description: Colomys wologizi is a small species with a short tail (134–150 mm; 14 scale rows per cm), short hindfeet (with claw, 33–36 mm) and moderately long ears (18–19 mm). Dorsal fur greyish-brown with some reddish patches (Fig. 10B), followed by a narrow, greyish margin and merging into the pure white ventral pelage. Ears brownish, with a small patch of white hairs behind conches. Snout dark grey. Dorsal and ventral surfaces of forefeet and hindfeet pale brownish; hindfeet with five pads. Whiskers black above and white below, reaching up to 36 mm in length and extending far behind ears. The skull is short (Table 2; Fig. 9B), with short nasals, a short bony palate, short diastema length and a narrow zygomatic plate (Fig. 8). In the type specimen, the incisive foramina penetrate the first lamina of the M1, unlike other members of the genus. Maxillopalatal suture V-shaped, beginning between M1 and M2. Posterior palatal foramina at first lamina of the M2. The length of the upper toothrow (Table 2) is short (5.8–5.9 mm) but overlaps with the lowest values of *C. goslingi*. Least interorbital breadth is smaller than in all other species (Table 2), and the values of breadth of the rostrum, length of upper diastema, and length of auditory bulla are low but partly overlap with *C. goslingi* and the new species *C. lumumbai*.

Comparisons: Compared with its closest geographical and genetic relative, *Colomys eisentrauti*, *C. wologizi* is easily distinguished by its shorter and squatter skull as reflected in a shorter rostrum (LIF and LN), more rounded braincase and proportionately broader IO. Despite the short LIF, the incisive foramina penetrate the first lamina of the M1, unlike the condition found in *C. eisentrauti*. Nasals originate posteriorly beyond front rim of the zygoma, whereas they originate anterior to the zygoma in *C. eisentrauti*. Zygomatic plate straight, sloping slightly forward at base, whereas in *C. eisentrauti* the anterior rim of zygomatic arch is concave and sloping at base (Fig. 8). Vertical height of mandible at coronoid much lower (Fig. 9). Bullae less inflated. Tail and head-body length short (Table 6; Fig. 10B).

Distribution and habitat: The type specimen was collected during the course of herpetological surveys

Table 5. Results of ANOVA for 13 craniodental variables among four species of *Colomys* (*C. eisentrauti*, *C. goslingi*, *C. lumumbai*, *C. wologizi*) followed by results of Dunn's post hoc test of significance between species pairs using sequential Bonferroni correction. Significant values in bold

Craniodental variable	*One-way ANOVA*		*wologizi vs. eisentrauti*	*lumumbai vs. goslingi*
	F	*P*	*P*	*P*
CI	6.284	≤ 0.001	≤ **0.001**	0.112
ZB	8.292	≤ 0.001	≤ **0.001**	0.238
IO	3.994	≤ 0.05	≤ **0.05**	0.076
BBC	9.37	≤ 0.001	≤ **0.01**	0.427
CLM	5.072	≤ 0.01	≤ **0.01**	0.807
BOC	3.253	≤ 0.05	≤ **0.01**	0.721
BR	9.005	≤ 0.001	≤ **0.05**	≤ **0.001**
LBP	12.35	≤ 0.001	≤ **0.05**	0.368
LIF	5.775	≤ 0.01	0.158	0.134
LD	3.865	≤ 0.05	≤ **0.01**	0.194
BZP	25.19	≤ 0.001	0.360	≤ **0.001**
LAB	6.887	≤ 0.001	0.322	≤ **0.001**
WM1	1.103	0.3557	0.184	0.434

by CPK along a small stream in headwaters of the Ngawalo River (Kofron, 1992; Kofron & Schmitt, 1992), at the foot of the Wonegizi Mountains in north-eastern Liberia. The stated distance from Ziggida (alternate spelling Zigida) and the stated latitude/longitude are approximated. The Ngawolo River (may be called also Ngawolo Creek, alternate spelling Ngwolo) is a tributary of the Lawa River that flows south-west into the Lofa River (also known as Little Cape Mount River) emptying into the Atlantic Ocean near Lake Piso. The Wonegizi Range contains the third highest peak in Liberia (BirdLife International, 2020b), and it is proposed for protected area status as the Wonegizi Multi-Use Reserve (Woods, 2019). The mouse was spotted with a headlamp at night running away from the collector (who was in the stream channel) and along a tree branch overhanging the edge of the channel and approximately 1.2 to 1.5 m above it. The bank of the stream channel was steeply sloped and approximately 1.5 to 2 m high. The mouse moved diagonally and upward across several branches, and some of these extended downward, contacting the bottom of the channel. The mouse was shot with a rubber band, in a manner similar to how herpetologists sometimes capture lizards, just as it gained a position beyond the bank. Kofron (1992: 269) described the stream:

Table 6. External measurements (mean ± SD, range and sample size) for *Colomys* and *Nilopegamys plumbeus*. Measurements are in mm and mass is in g.

Variable	*Colomys eisentrauti*	*Colomys wologizi*	*Colomys goslingi*	*Colomys lumumbai*	*Nilopegamys plumbeus*
Total length (TOT)	307 ± 16.9 (279–326) *N* = 6	264 ± 2.0 (262–266) *N* = 3	287.6 ± 12.5 (264–328) *N* = 72	290.8 ± 8.2 (274–299) *N* = 8	328
Head + body length (HB)	128.8 ± 8.0 (116–137) *N* = 6	122 ± 7.2 (116–130) *N* = 3	126.1 ± 8.0 (109–151) *N* = 72	133.8 ± 11.6 (112–146) *N* = 8	148
Tail vertebrae length (TV)	178.2 ± 10.1 (163–189) *N* = 6	142 ± 8.0 (134–150) *N* = 3	161.5 ± 8.5 (143–182) *N* = 72	157.0 ± 12.5 (142–182) *N* = 8	180
Hindfoot length (HF)	39.9 ± 1.2 (38.5–42) *N* = 7	35 ± 1.7 (33–36) *N* = 3	37.6 ± 1.7 (33–42) *N* = 74	36.6 ± 2.4 (32–40) *N* = 8	40
Ear length	18.7 ± 0.8 (18–20) *N* = 6	18.7 ± 0.6 (18–19) *N* = 3	18.7 ± 1.4 (14–22) *N* = 73	21.0 ± 1.4 (20–22) *N* = 2	14.4
Weight (Wt)	72.3 ± 10.0 (62–82) *N* = 3	47.5 ± 0.7 (47–48) *N* = 2	56.4 ± 6.3 (41.5–72) *N* = 61	na	na
TV/HB	1.39 ± 0.1 (1.28–1.45) *N* = 6	1.17 ± 0.1 (1.03–1.29) *N* = 3	1.28 ± 0.1 (1.08–1.57) *N* = 72	1.19 ± 0.20 (1.02–1.63) *N* = 28	1.22

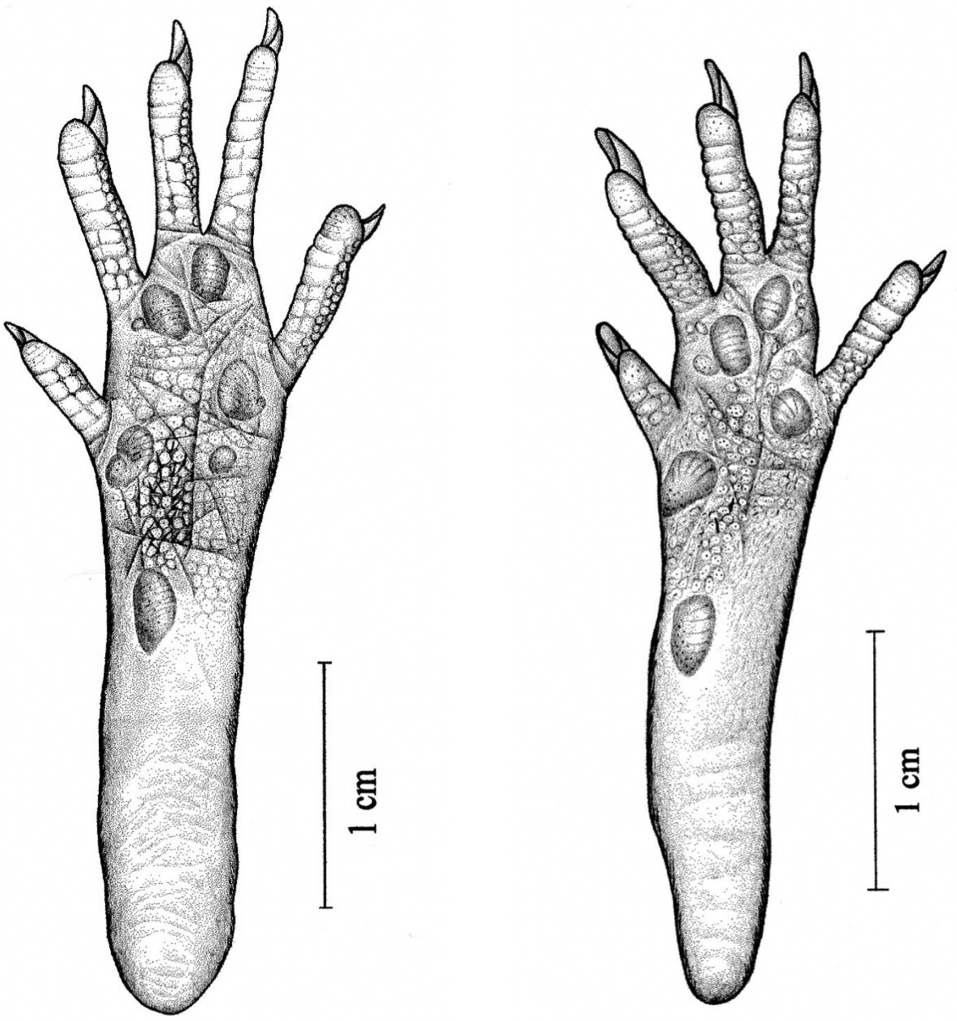

Figure 7. Hindfeet of *Colomys goslingi* with 6 (left, SMNS-Z-MAM-030124) and 5 pads (right, SMNS-Z-MAM-032298). Drawings by I. Ziekur (2006).

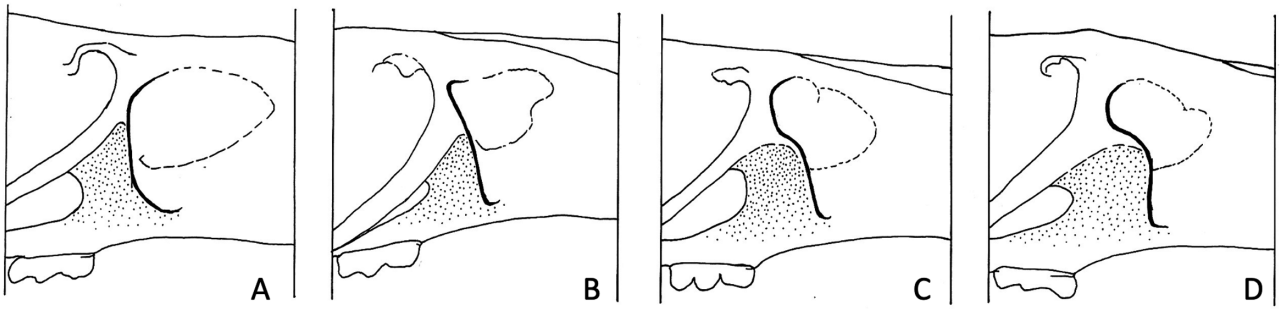

Figure 8. Four states (A–D) of the shape of the zygomatic plate (see Table 7) as shown by specimens of *Colomys* from West to East Africa. A, *C. eisentrauti*, Mt. Lefo, Cameroon (ZFMK 1974.0365); B, *C. goslingi*, Imatong Mts, South Sudan (SMNS-Z-MAM-027685); C, *C. goslingi*, Uwinka, Rwanda (ZFMK 1968.0550); D, *C. goslingi*, Mt. Elgon, Uganda (ZFMK 1999.1086).

'The streambed was loose with stones, the banks undercut with exposed root systems of trees and some fallen trees across the stream. It was the dry season and water flowed slowly, but with an indication of high water levels and torrential currents during the wet season. There were deep pools of dark water with

Table 7. Shape of the zygomatic plate in *Nilopegamys* and in different species and populations of *Colomys*. Character state A: anterior rim concave; state B: anterior rim straight; state C: anterior rim slightly curved; state D: anterior rim strongly curved. Character states illustrated in Figure 8

Population/Species	*N*	A	B	C	D
Nilopegamys plumbeus	1	0	0	0	1
Colomys goslingi (S. Sudan)	18	0	4	14	0
C. goslingi (Mt. Elgon)	3	0	0	0	3
C. goslingi (Kenya)	10	0	1	2	7
C. goslingi (Rwanda)	10	0	5	5	0
C. goslingi (DRC)	27	0	4	21	2
C. goslingi (Cameroon)	11	0	4	7	0
C. eisentrauti	4	4	0	0	0
C. wologizi	3	0	3	0	0
C. lumumbai	1	0	0	0	1
Totals	88	4	21	49	14

leaves and mud on the bottom, and also shallow pools of clear water and rock or sand.' This is the first record of arboreal behaviour in any species of *Colomys*, and it is likely an example of its scansorial ability. The holotype specimen was living in a stream channel with steep banks at the foot of a mountain where water flow ranges from slow and pooled to torrential currents. The ability to use overhanging tree branches would be especially advantageous for escaping the channel during torrential flows of the wet season.

The holotype specimen was first mentioned in a paper on the bats of Liberia: 'A skin and skull of *Colomys* was also obtained, which Dr Guy Musser assures us probably represents a new species and is certainly a major range extension for the genus west from Cameroon' (Koopman *et al.*, 1995: 2). Members of the American Museum of Natural History Expedition to Liberia collected 'for the most part in apparently undisturbed High Forest' (ibid., p. 2). The Liberian specimen remained the only one from West

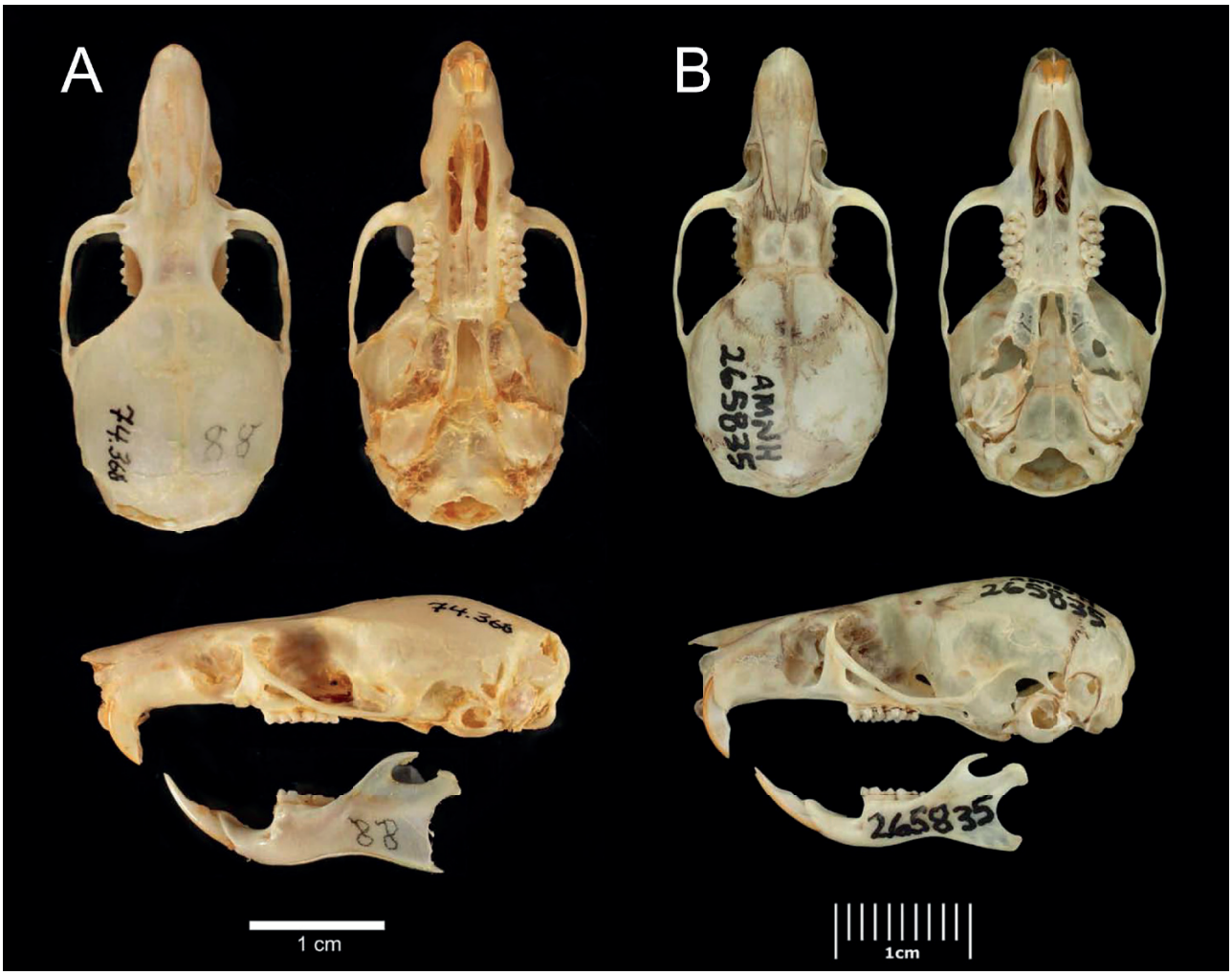

Figure 9. Skulls of (A) *Colomys eisentrauti* (ZFMK 1974.0366, holotype) and of (B) *Colomys wologizi* (AMNH 265835, holotype).

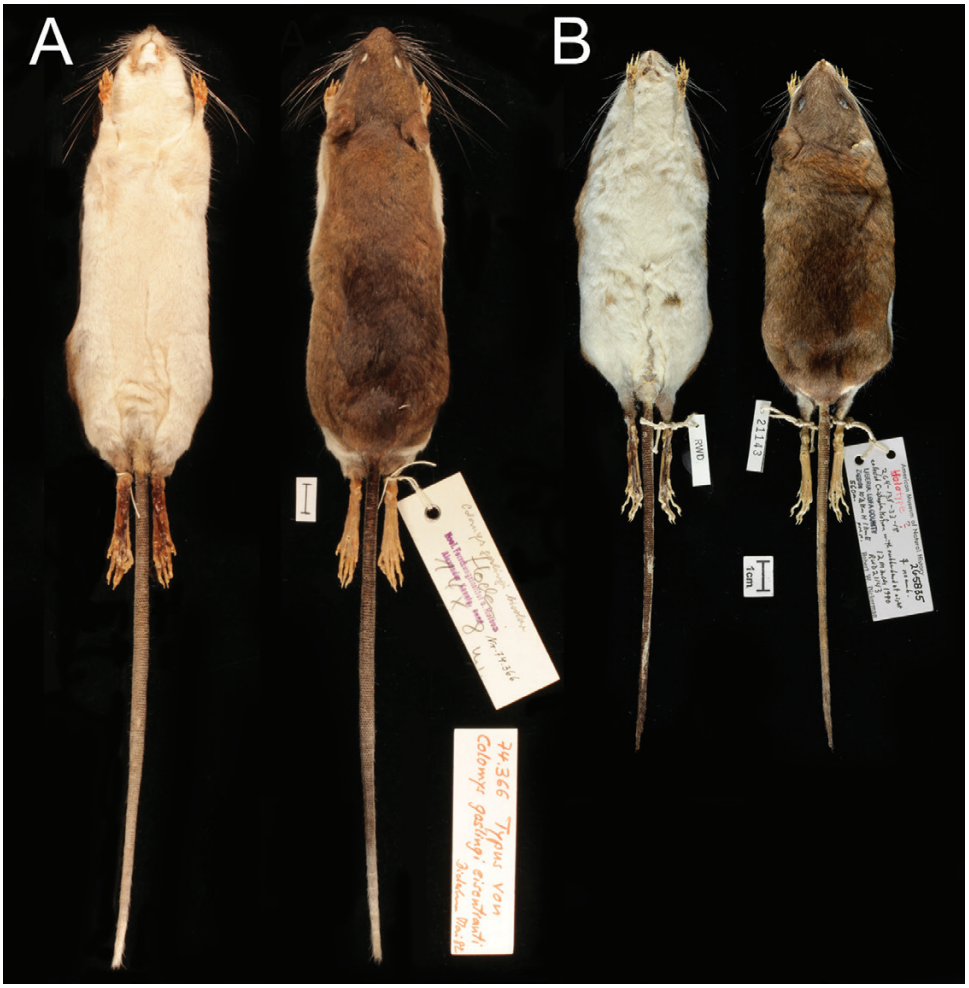

Figure 10. Dorsal and ventral aspects of the holotype skins of (A) *Colomys eisentrauti* (ZFMK 1974.0366) and of (B) *Colomys wologizi* (AMNH 265835).

Figure 11. Stream habitat near Lisco, Liberia where *Colomys wologizi* (ZWW 78) was captured.

Africa until 2019, when MLM collected a second specimen in Liberia and a third specimen from the Ziama Man and Biosphere Reserve in neighbouring Guinea, which is the first record of *Colomys* from that country (photograph of habitat shown in Fig. 11). Despite extensive surveys in nearby uplands in the Liberia–Guinea border area (such as Mount Nimba and the Simandou Mountain Range), this species has not been recorded anywhere else.

Liberia is located almost entirely within the tropical lowland rainforest belt (Curry-Lindahl, 1969). The vast majority of the country was originally forested with Upper Guinea lowland rainforest (Voorhoeve, 1965). However, most of the lowland rainforest in Liberia today is old and climax secondary (Voorhoeve, 1965; Curry-Lindahl, 1969), with FAO (2014) estimating less than 2% of the country (1750 km^2) is now covered with primary forest. Nonetheless, with 41 710 km^2

of lowland rainforest, Liberia has the largest area of Upper Guinean lowland rainforest remaining, and it covers 37% of the country. The Upper Guinea lowland rainforest extends into southern Guinea, including the Ziama Massif. Kofron & Chapman (1995) discussed deforestation in Liberia with reference to the Wonegizi Mountains. The Upper Guinea rainforest was reported to be the richest area in Africa for endemic mammals (Bibby *et al.*, 1992), and it is one of five 'hotspots' in Africa (Myers *et al*., 2000) – areas with exceptional concentrations of endemic species undergoing exceptional loss of habitat. The Upper and Lower Guinea rainforests are rated as a critical/endangered ecoregion in the World Wildlife Fund's Global 200, which is a priority list for global conservation of outstanding and representative habitats of biodiversity (Olson & Dinerstein, 2002) and they are the most fragmented tropical rainforests in the world (Minnemeyer, 2002). The ecoregion is not well protected and it is endangered due to slash-and-burn shifting agriculture, bushmeat hunting, logging, civil war and mining (Lebbie, 2020).

The paratype from Guinea was collected 12.8 km north-east of the holotype location in Liberia. The Wonegizi Range in Liberia is contiguous with the Ziama Massif and its biosphere reserve in south-eastern Guinea. In effect, the Wonegizi Range is a southern spur of the Guinea Highlands (BirdLife International, 2020b). Within Guinea, the paratype location is 5.4 km north of Kpoda (alternate spelling Gboda) and just south of the Ziama Massif. The location is near its southern base and in headwaters of the St. Paul River (also called Nianda River or Diani River in Guinea) that flows south-west into Liberia to drain into the Atlantic Ocean near Monrovia.

The paratype from near Lisco (full name Lisco Camp, from Liberian Iron and Steel Corporation; also known as Alabama Camp), Lofa County, northern Liberia, was collected along a tributary of the Lofa River near the western base of the Wologizi Range (22 km length), 6.7 km south of Lisco. This location is 53 km west of the holotype location. The Wologizi Mountains are an isolated range in northern Liberia that includes Mount Wuteve (1447 m a.s.l.), which is the country's highest peak. The area is rich in iron ore (BirdLife International, 2020a), and mining is a competing interest.

The holotype and paratypes were collected between 500 to 600 m a.s.l. and are associated with the bases of the Ziama Massif, Wonegizi Range, and Wologizi Range. The three collecting locations are in the upper watersheds of the St. Paul River and the Lofa River, and the uppermost headwaters of both originate on the Ziama Massif: uppermost headwaters of the St. Paul River originating on the eastern and southern slopes, and uppermost headwaters of the Lofa River originating on the western slopes. In Liberia, the two rivers flow nearly parallel to each other, with the two mouths separated by 36 km distance. Liberia has at least 13 species of endemic freshwater fish, and six of these are restricted to the St. Paul River and its tributary the Via River (Paugy *et al.*, 1990; Stiassny, 1991; Fricke *et al*. 2020; Living National Treasures, 2020). This new species of semi-aquatic *Colomys* may be endemic to the lowland rainforests (500–600 m a.s.l.) of the Ziama–Wonegizi–Wologizi landscape drained by the St. Paul River and the Lofa River.

Etymology: The specific epithet refers to the Wologizi Mountains, Liberia, at the foothills of which the second Liberian specimen was collected in 2019. It is used as a noun in apposition. The Wologizi Mountains, together with an expanse of lowland rainforest that connects them to the Wonegizi Mountains (the type locality for this species), have not yet gained any form of protected status, an omission we strongly suggest remedying. The area still has good coverage of rainforest and is remarkably diverse, with a number of endemic species. It is, therefore, of critical conservation concern.

COLOMYS LUMUMBAI KERBIS PETERHANS, GIARLA & DEMOS, SP. NOV.

ZooBank Life Science Identifier (LSID): urn:lsid:zoobank.org:act:E5249D3E-4F68-4EAA-92F2-7EACC2895D34.

1923 *Colomys bicolor*, Kershaw, *Revue Zoologique Africaines* 11(4): 367. (part)

1926 *Colomys goslingi*, Cabrera & Ruxton, *Annals and Magazine of Natural History* 9(17): 599.

1940 *Colomys goslingi*, Hatt, *Bulletin of the American Museum of Natural History* 76: 505–507.

1952 *Colomys goslingi*, Sanborn, *Publicações Culturais da Companhia de Diamantes de Angola* 14: 107–118.

1971 *Colomys goslingi*, Misonne, Rodentia. In: Meester & Setzer, eds. *Mammals of Africa, an identification manual, Part 6*. Washington: Smithsonian Institution Press, 19. (part)

1983 *Colomys goslingi goslingi*, Dieterlen, *Bonner Zoologische Beiträge* 34 (1–3): 93. (part)

1995 *Colomys goslingi*, Kerbis Peterhans & Patterson, *Zoological Journal of the Linnean Society* 113: 333.

2005 *Colomys goslingi*, Musser & Carleton. In: Wilson & Reeder, eds. *Mammal species of the world: a taxonomic and geographic reference (3rd edn)*, Baltimore: Johns Hopkins University Press, 1307–1308. (part)

2013 *Colomys goslingi*, Dieterlen. In: Happold, ed. *Mammals of Africa, Vol. III: rodents, hares and rabbits*, London: Bloomsbury, 390–393. (part)

2017. *Colomys goslingi*, Denys, Taylor & Aplin. In: Wilson, Lacher Jr & Mittermeier, eds. *Handbook of the mammals of the world, Vol 7. Rodents II*. Barcelona: Lynx Edicions 801–802,

Holotype: AMNH 55219, a young adult female, collected by Reverend R. W. Callewaert on 20 June 1923, in 'St. Joseph de Luluabourg' (now known as Kananga, 5.89° S, 22 42° E), *c*. 640 m a.s.l., Democratic Republic of the Congo. The specimen consists of a museum study skin with accompanying cranium and mandible; skin poorly prepared (understuffed, belly partially open), skull well prepared (with dried tissue attached, allowing for antique DNA extraction). Total length 285 mm, tail 162 mm (Tail 132% HB), hindfoot 40 mm, ear length (na), weight (na). Skull measurements in Table 2.

Paratypes (11): AMNH 55209, 55211, 55213, 55215–55218, 55220; BMNH 26.7.6.284, 26.7.6.287, 26.7.6.294.

Diagnosis: A medium-sized *Colomys* characterized by a broad zygomatic plate (2.4–2.9 mm) with bulging convex anterior margin (Fig. 12B). Available data indicate that the rostral breadth (BR, mean of 6.6 mm) is also larger than in *C. goslingi* (mean BR 6.1 mm) as is the length (oblique) of the auditory bullae.

Description: Colomys lumumbai is a species comparable in size to *C. goslingi* and was previously known by that name for over a century (Fig. 13). As such, it is intermediate in size between the smallest species in the genus, *C. wologizi*, and the larger *C. eisentrauti*. Typically bicoloured: rusty grey-brown above contrasting with ventral surface that displays pure white pelage to roots. Forelimbs all white distal to elbows. Hindlimbs bicoloured to ankle, dark brown above, white below. Feet sparsely clothed in white hairs. Vibrissae long (> 40 mm), black hairs in colour above and white hairs toward lip. Ears conspicuous and projecting. White, subauricular spot weakly

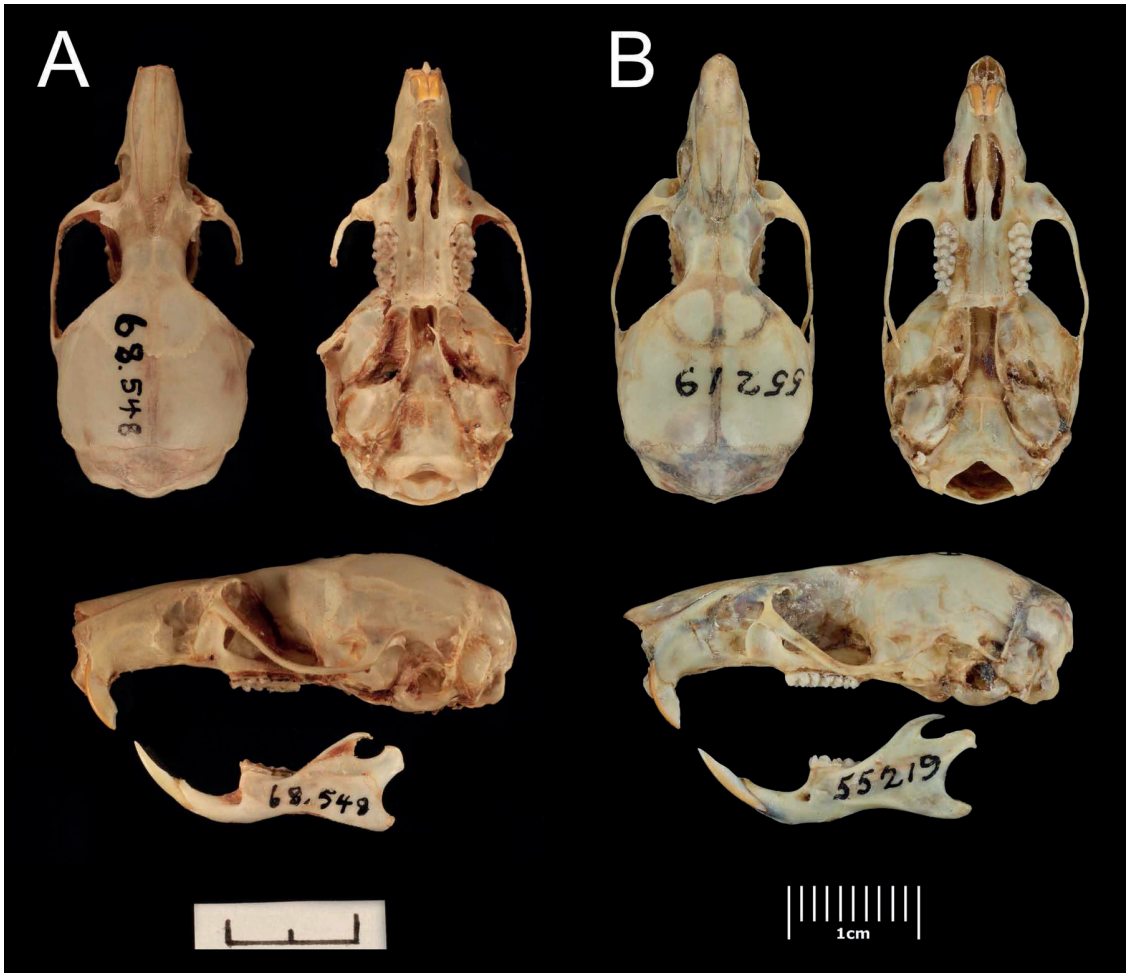

Figure 12. Skulls of (A) *Colomys goslingi* (ZFMK 1968.0548; holotype of *ruandensis*) and (B) of *Colomys lumumbai* (AMNH 55219; holotype).

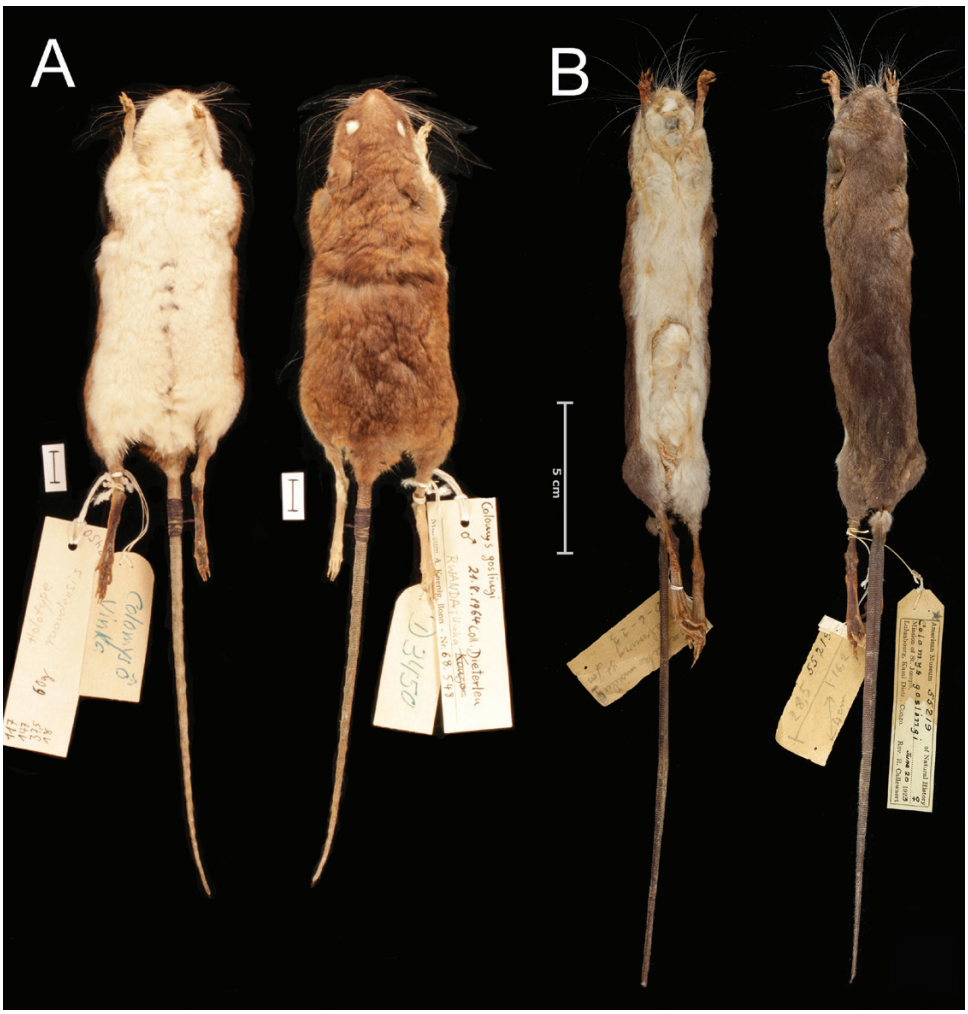

Figure 13. Ventral and dorsal aspects of the skins of (A) *Colomys goslingi* (ZFMK 1968.0548; holotype of *ruandensis*) and (B) *Colomys lumumbai* (AMNH 55219, holotype) skins.

developed or absent. Tail with 16–17 annulations per cm, sparse white hairs throughout. Both fluid-preserved specimens from Angola display five pads on their hindfeet and five on their manus (hypothenar pad below digit V exceptionally large). Vestigial thumb with tiny nail on manus, followed by small tuft of carpal vibrissae. Teats 4 + 4 (FMNH 80305). An artistic illustration of *C. lumumbai* is provided in Fig. 14.

Maxilla with lateral projections extending into the vacuities of the incisive foramina, as is typical for the genus. Maxillopalatal suture strongly V-shaped, passing across level of the posterior third of the M1 in younger adults and in the middle of the M1 in older adults. Posterior palatal foramina immediately follow this suture accordingly: at the rear of M1 in younger adults and between M1 and M2 in older adults. Sphenopalatine vacuity broad and parallel. Origin of nasals approaches the interorbital region, originating well proximal to the zygomatic arch. Rostral region swollen at base. Incisors opisthodont.

Comparisons: Easily distinguished from *Colomys wologizi* by its bulging, convex and broader zygomatic plate (≥ 2.4 mm) vs. a straight (orthogonal) anterior rim to more narrow zygomatic plate (≤ 2.2 mm). Bony palate longer (5.8–6.8 mm) vs. shorter (4.9–5.8 mm) in *C. wologizi*. Auditory bullae longer 4.5–5.0 vs. 4.2–4.3 mm in *C. wologizi*. Compared to *C. eisentrauti*, *C. lumumbai* is smaller in most dimensions, including CI (mean of 30.9 vs. 32.5 mm), zygomatic breadth (mean of 16.1 vs. 17.4 mm) and, especially, braincase breadth (13.7–15.3 vs. 15.6–15.9 mm). Its rostrum is also shorter, as reflected in shorter incisive foramina (5.9–7.3 vs. 7.4–7.9 mm). However, despite being smaller, its zygomatic plate is broader (2.4–2.9 mm) and convex vs. narrower (1.9–2.2 mm) and concave (at ventral intersection of maxilla; see Fig. 12). It is most similar to *C. goslingi*

Figure 14. Illustration of *Colomys lumumbai* by Velizar Simeonovski.

from the Congo Basin from which it differs in its broader rostrum (BR) and bulging, broad and convex zygomatic plate (2.4–2.9 mm) vs. a narrower zygomatic plate (1.95–2.5 mm) with a more orthogonal anterior margin (Fig. 12). It is more difficult to distinguish *C. lumumbai* from specimens from Kenya, eastern Uganda and South Sudan (formerly known as *C. g. denti*), as select individuals of these populations may also display a broad and bulging zygomatic plate. It should be noted that when we performed a PCA using the metrics presented by Hatt (1940: 584), populations of *Colomys* '*goslingi*' from Luluabourg were distinguished from more northern samples from the right bank of the Congo River, with greatest loadings on breadth of zygomatic plate (results not shown).

Distribution and habitat: The distributional limits of this species are not well characterized. We definitively assign a specimen to this species only if it has been included in the phylogenetic analysis, the morphometric analysis or if it is from the same locality as a specimen included in one of those analyses. Based on these criteria, the new species is definitively known from just five localities in Angola and the Democratic Republic of the Congo. Only one of these localities occurs east (right bank) of the Lualaba River – a headstream of the Congo River – at Batianoka, a site close to the Lualaba River near Kisangani, map number 73 in Figure 2. The other four definitive locales occur west (left bank) of the Lualaba River: (1) near Dundo, Angola, close to the border with the DRC, map number 1; (2) the type locality at Kananga (formerly Luluabourg), where the Lulua River empties into the Kasai River, map number 20; (3) close to the Lualaba River, near Kisangani, map number 71; and (4) close to the Luidjo River (Lomami River tributary), near Kindu, map number 26. Another specimen from virtually the same locality (2.668217° S, 25.27682° E) was picked up by J. and T. Hart and photographed (pers. comm.) but not retained as a voucher. This specimen was found on a footpath in grassy savannah some distance from a stream. We speculate it might have been dropped by a predator.

Based on the wide geographic range of the five definitive locales, it is likely that several unexamined *Colomys* specimens known from other sites in central and southern DRC, and perhaps east of the Lualaba River, could be assigned to this new species. This includes a number of specimens housed at RMCA from various sites in DRC that we were unable to include in our study. Another putative member of this species from north-west Zambia is catalogued as number '64.26:4' in the Medical Ecology Centre, Johannesburg, but we were not able to examine it. It is represented by a mandible recovered from an owl pellet. The locality is listed by Ansell (1965, 1978), Dieterlen (1983) and Bryja *et al.* (2012) as originating in the Mundwiji Plain (11° 44' S, 24° 43' E, *c.* 1400 m a.s.l.; map number 71 in Fig. 1). All undetermined *Colomys* specimens are listed as *Colomys* sp. *indet*. in Supporting Information, File S1, Table S1, and Figures 1 and 2. Further sampling and verification of RMCA materials from both banks of the Lualaba River is essential to mapping the distributional limits of this new species.

As noted by Callewaert on his original skin tags, habitats for this species include 'water's edge', 'in a brook' and 'in the forest' (Cabrera & Ruxton, 1926; Hatt, 1940). FMNH 226974 was also collected from along a slow, trickling stream. There are no records of this species above 800 m. In sum, the species has a riparian distribution as is typical for the genus.

Etymology: The specific epithet refers to Patrice Émery Lumumba, who was born on 2 July 1925 in Katako-Kombe, in the middle of the range of the new species. He was a Congolese politician and independence leader who served as the first Prime Minister of the newly independent Democratic Republic of the Congo from June until September 1960. He was one of the principle individuals involved in the independence of

the DRC and he led the Congolese National Movement party from its founding in 1958. This movement was inclusive and not based on ethnic lines. On 17 January, 1961, he was assassinated by Katangan and Belgian forces following an independence effort by the former group.

COLOMYS GOSLINGI THOMAS & WROUGHTON, 1907

1907 *Colomys goslingi* Thomas & Wroughton, *Annals & Magazine of Natural History* 19: 380.

1912 *Colomys bicolor* Thomas, *Annals & Magazine of Natural History* 10: 42–43.

1930 *Colomys goslingi* denti St. Leger, *Annals & Magazine of Natural History* 6: 527–528.

1983 *Colomys goslingi* ruandensis Dieterlen, *Bonner Zoologische Beiträge* 34 (1–3): 89.

2017. *Colomys goslingi*, Denys, Taylor & Aplin. In: Wilson, Lacher Jr. & Mittermeier (eds). *Handbook of the mammals of the world, Vol. 7. Rodents II*. Barcelona: Lynx Edicions, 801–802.

Holotype: BMNH 12.10.25.14. Adult male skin and skull from Gambi, Welle River, DRC (*c*. 3.46° N, 24.52° E, *c*. 560 m). Collected 31 January 1906 by G. B. Gosling.

Topotypes: None.

Diagnosis: A member of *Colomys* from the eastern and northern (right bank) side of the Congo River drainage system, distinct from two species to the west: a larger one (*C. eisentrauti*) just within the Niger River drainage and a smaller one (*C. wologizi*) from small rivers directly flowing into the Atlantic. It is distinguished from its closest relative and co-occupant of the Congo Basin, *C. lumumbai*, by its narrower zygomatic plate (mean of 2.2 vs. 2.6 mm) with a range of 1.95–2.5 mm compared with 2.4–2.9 mm. Anterior rim of zygomatic plate less convex and less bulging (Fig. 12A). Rostrum (BR) narrower (mean of 6.1 vs. 6.6 mm) than other taxa, except for *C. wologizi* (mean 5.9 mm).

Description: A medium-sized member of *Colomys* (means in mm: CI 30.6, ZB 15.9, CLM 5.3), larger than *C. wologizi* (means in mm: CI 29, ZB 15.3, CLM 4.9) and smaller than *C. eisentrauti* (means in mm: CI 32.5, ZB 17.4, CLM 5.5). Rostrum narrow (BR 6.1 mm). Thomas & Wroughton (1907 380–381) provided a thorough description for the species, which we quote here: 'Fur short, crisp and velvety in texture. Hairs of back 7–8 mm. General colour above wood brown and cinnamon on posterior dorsal area more blackened. Undersurface pure sharply defined white, hairs white to bases; line of demarcation high on cheeks and sides, fully half way up the body, the whole arc taking the whole of the forelimbs, which are white throughout, but the hind limbs have a narrow darker line running down behind them to the ankles. Ears fairly large, practically naked, grey; a prominent white spot on the side of the head below the ear notch. Upper surface of hands white, of feet flesh-colour. Tail finely scaled, 12 scales to the centimetre, practically naked, the few hairs at the end about a millimetre in length, uniformly grey above and below.'

Distribution and habitat: Its range is now restricted to three broad areas: (1) the headwaters of the White Nile and the Albertine Rift, including montane sites in the DRC, Kenya, South Sudan, Uganda, Rwanda and Burundi; (2) areas north and east of the Congo River and its main tributary, the Lualaba River, within DRC; and (3) lowland Cameroon. Within the Albertine Rift, Imatong Mountains and Kenyan Highlands, it has been documented only at elevations between 1200 and 2740 m, whereas in the Congo Basin it is found at localities between 470 and 750 m. This species might occur close to the right bank of the Lualaba River (i.e. map numbers 33, 36, and 37–41 in Fig. 2 and Supporting Information, File S1, Table S1), but specimens from those localities were not available for this study and cannot be confidently assigned to either this species or *C. lumumbai*. Like other members of this genus, *C. goslingi* occupies riparian and swampy habitats.

COLOMYS EISENTRAUTI (DIETERLEN, 1983) COMB. ET STAT. NOV.

1983 *Colomys goslingi eisentrauti* Dieterlen, *Bonner Zoologische Beiträge* 34 (1–3): 89.

2005 *Colomys goslingi eisentrauti*, Musser & Carleton. In: Wilson & Reeder, eds. *Mammal species of the world: a taxonomic and geographic reference (3rd edn)*, Baltimore: Johns Hopkins University Press, 1307–1308. (part)

2013 *Colomys goslingi eisentrauti*, Dieterlen. In: Happold, ed. *Mammals of Africa, Vol. III: rodents, hares and rabbits*, London: Bloomsbury, 390–393. (part)

2017 *Colomys goslingi*, Denys, Taylor & Aplin. In: Wilson, Lacher Jr. & Mittermeier, eds. *Handbook of the mammals of the world, Vol. 7. Rodents II*. Barcelona: Lynx Edicions, 801–802.

Holotype: ZFMK 1974.0366, adult male, skin and skull, collected by W. Böhme and W. Hartwig on 6 March 1974 at the edge of a creek in montane forest of the Bafut-Ngemba Forest Reserve, Mt. Lefo, SE Bamenda, Cameroon, at 1800–1900 m a.s.l. [05°49'–05°53' N,

10°13'–10°12' E; following Takem-Mbi (2013): fig. 1, and Ghislain *et al.* (2014)], field no. 88.

Paratypes: ZFMK 1974.0365 (female) and SMNS-Z-MAM 32300 (male), skins and skulls, same locality as holotype.

New Specimens: CB ZV2780, CB VM_CMR.2007.2, CB VM_CMR.2009.17 and CB VM_CMR.2009.26, Mendongbuo, sites 1–4.

Diagnosis: Largest species of the genus with large body size (HB 116–137 mm), long hindfeet (HF 38.5–42 mm) and tail 128–145% of head and body length (Fig. 10A). Skull broad (BBC) and long (CI, GSL); rostrum elongate as reflected in high values for LD and LIF (Fig. 9A). Zygomatic plate narrow and with concave anterior margin toward its root at the maxilla (Figs 8, 9A; Table 7). White ear patch indistinct, dark lip patch, grey transition zone between dorsum and venter, anal opening surrounded by dark hairs, ten scale rows per cm near base of tail, tip of tail with whitish hair brush.

Description: A large representative of *Colomys* with a long tail; ten scale rows per cm, tail tip covered by long whitish hairs. Dark-brown dorsum contrasted against white venter; grey zone between brown and white body sides. Small white ear patch and dark lip patch. Fore- and hindfeet brownish; hindfeet long. Skull long and wide (Table 2); length of bony palate, length of diastema and breadth and shape of zygomatic plate (Fig. 9A) are diagnostic. Length of maxillary toothrow high (5.3–5.8 mm) but overlapping with *C. goslingi* and *C. lumumbai* (Table 2).

Distribution and habitat: Known only from south-western part of the Bamenda Highlands, North-West Province, Cameroon. The localities of Mt. Lefo and Mendongbuo lie approximately 30 km apart. The species is possibly absent from Mt. Oku, a local biodiversity hotspot located in the north-eastern portion of the range (Denys *et al.*, 2014). Whereas the type locality is situated within the Bafut-Ngemba Forest Reserve, the new specimens originate from an area that lacks any legal protection and thus could be harmed by human activities. At Mendongbuo, the mice were caught using snap-traps placed on stones or sandy places along or within small streams. On one occasion it was outside of a closed forest, near a stream running through pastures and *Pteridium* Gleditsch fern thickets, with only sparse trees and shrubs accompanying it. All specimens were collected during the dry season.

DISCUSSION

By integrating molecular phylogenetics and morphological analyses, we revise the taxonomy of *Colomys* and *Nilopegamys* and can now consider the evolutionary and biogeographic history of this poorly understood clade. The results presented here are the most recent revision in this group since Dieterlen (1983) and Kerbis Peterhans & Patterson (1995), and the only analysis to date to include both molecular and morphological data. The concatenated molecular phylogeny (Fig. 3; Supporting Information, File S2) demonstrates that *Nilopegamys plumbeus* is sister to *Colomys* and evolutionarily distinct from other murine rodents. Within *Colomys*, we have evidence for four species supported by both molecular and morphological data (Figs 3, 5, 6; Tables 2, 6; Key to species in the Appendix).

Our results indicate that *Colomys goslingi* (*s.s.*) has a more restricted range than previously appreciated. The four subspecies currently assigned to *C. goslingi* (*bicolor*, *denti*, *goslingi* and *ruandensis*) overlap in morphospace (Fig. 5). However, *bicolor* (lowland Cameroon) and *denti* (Kenya, South Sudan and eastern Uganda) are each reciprocally monophyletic relative to other branches in the tree (Fig. 3). *Colomys eisentrauti* was formerly recognized as a subspecies of *C. goslingi*, but it occupies its own clade in the phylogeny and does not overlap in morphospace with any other taxon in our analysis (Fig. 5). *Colomys eisentrauti* is known only from two adjacent montane sites in the Bamenda Highlands of north-western Cameroon. Terrestrial small mammals occurring in the highlands of the Cameroon Volcanic Line are often endemic to this region (Hutterer *et al.*, 1992; Denys *et al.*, 2014). Since a small area of Nigeria is included in the Cameroon Volcanic Line, this species may also occur in that country, but it is not likely to be widespread and is not likely to occur in lowland Nigeria.

Colomys wologizi is known from three specimens collected in the Upper Guinea lowland rainforest (500–600 m a.s.l.) of the Ziama–Wonegizi–Wologizi landscape drained by the St. Paul River and the Lofa River (both flowing south-west through Liberia), near the border of Liberia and Guinea. Molecular and morphometric evidence highlights its distinctiveness. It overlaps slightly with *C. goslingi* from north-eastern DRC in morphospace (Fig. 5), but is not closely related to that taxon in our phylogeny. Despite widespread rodent surveys in the lowland rainforests of south-eastern Guinea, eastern Sierra Leone and Liberia, *C. wologizi* has not been recorded elsewhere in the region (Coe, 1975; Gautun *et al.*, 1986; Denys *et al.*, 2009; Mamba *et al.*, Accepted) or anywhere else in the Upper Guinea rainforest zone (Monadjem *et al.*, 2015).

Colomys lumumbai is distinct both phylogenetically and morphometrically from *C. goslingi*, but its distribution relative to that species is uncertain. Four of the five definitive locales occur west (left bank) of the Lualaba River (a headwater stream of the Congo River) in Angola and the DRC, but the fifth site is just to its east. As such, these mice must be able to cross the Lualaba and could occur more broadly on its eastern (right bank) side. A series of specimens from just east of the Lualaba River, near Kisangani, housed at the Royal Museum for Central Africa (Tervuren, Belgium), were not examined in this study; DNA sequence data from those animals would help clarify the distributional limits of both *C. goslingi* and *C. lumumbai*. Gallery forests of northern Angola support populations of *Colomys* (Sanborn, 1952; Hayman, 1963) and one specimen from that region nested within the PCA cluster for *C. lumumbai* (Fig. 5). One additional partial specimen is known from north-western Zambia (Ansell, 1965, 1978). However, genetic material to confirm these affinities is not available. It is possible that *C. lumumbai* might occur more broadly along the riverine corridors of northern Angola and Zambia.

Fossil record

There is only one mention of fossil *Colomys* in the literature. Dietrich (1942) identified two skull fragments from Quaternary sediments of Garussi, southern Serengeti, as *Colomys* sp. This Tanzanian record, which was included in Kingdon (1974), would be significant if correct, because it would document the former occurrence of a semi-aquatic forest rodent in a part of Africa now dominated by savanna. Furthermore, Dietrich (1942) concluded from the condition of the bone that the specimens were of 'recent' origin rather than part of the fossil assemblage. We have examined the voucher specimens in the Palaeontological Institute of the Berlin Natural History Museum. There are two calvaria labelled as *Colomys* sp. (MB. R. 42497.1-2) from 'Garussi, Serengeti-South, Tanzania', collected by Kohl-Larsen in 1939. Both specimens represent the genus *Arvicanthis*. After our re-examination of the Tanzanian material, there remains no fossil record of *Colomys*.

Historical biogeography

Rivers have likely played an important role in the distribution and evolution of Africa's semi-aquatic rodents. Ancestors of *Nilopegamys plumbeus* may have reached montane Ethiopia from farther south via the White Nile and then the Blue Nile. *Colomys* and *Nilopegamys* diverged between 1.8 and 3.0 Mya (Fig. 4), toward the end of the Pliocene or start of the Pleistocene. Subsequent intensification of glacial–interglacial climatic cycles during the Mid-to-Late Pleistocene enhanced aridification of the Sahara and may have cut off gene flow from populations in the vicinity of the White Nile (Cowling *et al.*, 2008; Potts & Faith, 2015).

The Congo River (including its headstream, the Lualaba) is a formidable biogeographic barrier for many organisms (Nicolas *et al.*, 2011). The strong currents of the lower Congo River isolate fish populations on opposite banks (Markert *et al.*, 2010) and related clades of various mammals occur on either side of the Congo (e.g. *Pan* Oken, 1816: Ericksson *et al.*, 2004; *Cricetomys* Waterhouse, 1840: Olayemi *et al.*, 2012; *Malacomys*: Bohoussou *et al.*, 2015; *Hylomyscus*: Kerbis Peterhans *et al.*, 2020; Nicolas *et al.*, 2020). However, other mammals occur on both banks of the Congo/Lualaba, including two monkey species [*Allenopithecus nigroviridis* (Pocock, 1907): Maisels *et al.* (2020) and *Cercopithecus neglectus* Schlegel, 1876: Mwenja *et al.* (2019)] and at least three rodent lineages [*Praomys mutoni* Van der Straeten & Dudu, 1990: Kennis *et al.* (2011); *P. jacksoni* (de Winton, 1897) ('clade IV' per Mizerovská *et al.*, 2019) and *Colomys lumumbai*]. *Colomys lumumbai* is widely distributed south and west (left bank) of the Congo/Lualaba, with only one definitive right bank *C. lumumbai* locality (map number 73, Fig. 2; Supporting Information, File S1, Table S1). It diverged from *C. goslingi* between 0.4 and 0.8 Mya in the Late Pleistocene (Fig. 4), when glacial cycles affected the geographic extent of forests across Africa (Maley, 1989; Hamilton & Taylor, 1991). It is possible that these two species initially diverged allopatrically in different Pleistocene forest refugia, a phenomenon often implicated as a potential driver of diversification in lowland forest taxa (Nicolas *et al.*, 2011). Alternatively, an initial dispersal event across the Lualaba River, with concurrent cessation of gene flow, may have driven the initial speciation event between *C. lumumbai* and *C. goslingi*, with more recent re-expansion leading to the presence of *C. lumumbai* on the right bank. Without better sampling of these species in the Congo Basin, it is difficult to distinguish between either of these hypotheses.

In Cameroon, populations of *Colomys eisentrauti* and *C. goslingi* have been collected approximately 260 km apart. *Colomys goslingi* is found at lowland Bitye (650 m a.s.l.) along the Dja River, a distant westerly tributary of the Congo River drainage, as well as within the Sanaga River drainage (Yaoundé–Nkometou). The montane population of *C. eisentrauti* is found nearby on the opposite (western) side of the Cameroon Volcanic Line, but at much higher elevations (1850–2150 m a.s.l.). Streams of the western slopes of the Bamenda Highlands flow through the town of Babanki and continue under a series of names, including the Ntu River, the Menchum River and, ultimately, the Benue

River (a major tributary of the Niger River). *Colomys wologizi* is found over two thousand kilometres farther west in Liberia and Guinea in two small watersheds of rivers flowing south-west through Liberia and flowing directly to the Atlantic Ocean. We speculate that *Colomys* may have colonized this region by way of the Niger River whose headwaters are < 100 km to the north of the current known range of *C. wologizi*. The Niger River drainage meanders through arid zones in Mali and Niger, which became drier during the Pleistocene (Anhuf *et al.*, 2006). When gallery forest ecosystems desiccated, gene flow with populations farther to the east likely would have ceased, leading to the split between *C. eisentrauti* and *C. wologizi*, dated to *c*. 0.2–0.5 Mya (Fig. 4).

According to our time-calibrated species tree, the split between the two more western *Colomys* species and the two more eastern species occurred approximately 1.4 Mya (Fig. 4). It is possible that an ancestral *Colomys* lineage dispersed across the Cameroon Volcanic Line, because *C. eisentrauti* is only found at high elevations (all specimens were caught at 1850–2150 m a.s.l.). It would be useful to collect *Colomys* just to the east of known *C. eisentrauti* populations, on the Congo-side watersheds (e.g. the Sanaga and Congo Rivers), and determine to which species they are most closely related. It is also important to determine to what elevation *C. goslingi* ascends in the east, because genetically and morphologically the two species are distinct from one another.

CONCLUSIONS

In this paper we apply, for the first time, an integrative approach to address the systematics of a poorly studied genus of African wading mice, *Colomys*. We demonstrate that this genus is monophyletic and sister to *Nilopegamys*, one of the most enigmatic mammalian genera. Furthermore, we present evidence supporting: (1) the recognition of two new species, which we describe as *C. wologizi* and *C. lumumbai*; (2) the elevation of *C. eisentrauti* from subspecies; and (3) a more restricted range for *C. goslingi s.s.* Finally, we highlight the importance of additional small mammal sampling along (and within) the rivers and streams of African forests, an essential step in clarifying the distributions of semi-aquatic small mammals.

ACKNOWLEDGEMENTS

We dedicate this paper to the memory of Dr Fritz Dieterlen (1929–2017), whose studies in the ecology and taxonomy of African small mammals are a model for all. We thank the following museums and their curators and collection managers for loan of materials or access to specimens for this study: Zoological Research Museum Alexander Koenig (Jan Decher), American Museum of Natural History (Rob Voss and Neil Duncan), The Natural History Museum, London (Roberto Portela Miguez), Carnegie Museum of Natural History (Sue McLaren), Eswatini National Museum (Themb'alilahlwa A. M. Mahlaba), Field Museum of Natural History (John Phelps and Adam Ferguson), Louisiana State University Museum of Natural Science (Jake Esselstyn, Donna Dittmann and Steve Cardiff) and State Museum of Natural History Stuttgart (Fritz Dieterlen† and Stefan Merker).

This study involved countless hours of fieldwork and help from many individuals and funding agencies. JCKP is grateful to Leif Davenport (USAID, Peace Corps, Burundi), who, in 1990, caught the first *Colomys* specimen he had seen by placing a trap inside a shallow stream in Kibira NP, Burundi. CPK was in Liberia under a Fulbright award, and the views expressed in this paper are his and not those of the United States Fish and Wildlife Service. We thank Ernest Vunan Amohlon and the entire Big Babanki (Kedjom Keku) community for their kind support during the field work in Cameroon. Fieldwork in West Africa was carried out under the auspices of the Conserving and Connecting the Ziama–Wonegizi–Wologizi Transboundary Forest Landscape between Guinea and Liberia of Fauna & Flora International (FFI) and in partnership with West Africa Biodiversity and Climate Change Programme (WA BiCC) of USAID, Forest Development Authority, Liberia and Centre Forestière N'Zérékoré (N'Zérékoré Forestry Centre), Guinea with funding from the USAID West Africa Biodiversity and Climate Change Program (USAID WA BiCC). For assistance with photographs and fieldwork in TL2 and the Ituri Forest (DRC), we thank John and Theresa Hart. We are also grateful to Gerhard Nikolaus, whose recent expedition to the Imatong Mts of South Sudan provided important records from that country.

Fieldwork in eastern and central Africa was funded by various agencies in cooperation with the Field Museum. The Field Museum's Council on Africa, Ellen Thorne Smith Fund, Marshall Field III Fund and Barbara E. Brown Fund for Mammal Research were critical to fieldwork and analyses. The John D. and Catherine T. MacArthur Foundation, Fulbright Program of the US Department of State, Wildlife Conservation Society, US Peace Corps/United States Agency International Development and the Centers for Disease Control and Prevention sponsored and/or assisted in providing samples from Burundi, DRC, Rwanda, Kenya, and Uganda. Permits were obtained thanks to the support of the Uganda Wildlife Authority, National Museums of Kenya, Centre de Recherche de Scientifique Nacional (DRC), Institut Nacional

pour l'Environment at la Conservacion de la Nature (Burundi: A. Nyokindi, L. Ntahuga) and MINIRENA & Rwanda Development Board (Rwanda: T. Mudakikwa).

Field collaborators included: B. Agwanda and F. Awuor (Kenya); R. Kityo, S. Waswa, S. Sebuliba, B. Nalika, S. Akoth, P. Austin, S. Jennings and E. Tibenda (Uganda); P. Kaleme, J. Mwanga and N. Ruziga (DRC); L. Davenport, J. Udelhoven and A. Fisher (Burundi); and N. Ntare, N. Chao, M. Masozera, M. Mayjambere, D. Mvunabandi and W. Ndayisaba (Rwanda).

Finally, we are grateful to several people for help with generating and analysing data. For help with morphometric data analysis, we thank Gaston Celesia. For help with laboratory work, database management and data processing, we are grateful to many Siena College students over the past five years, including Daniel Biljanoski, Naisla Defran, Mathew Dolinar, Francesca Gallo, Ashley Herkert, Nimra Komal, Samerna Masih, Margot Pavlik and Maria Valdez.

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APPENDIX

KEY TO *NILOPEGAMYS* AND *COLOMYS* SPECIES BASED ON CRANIAL MEASUREMENTS

These two genera are medium-sized (40–110 g) semi-aquatic, stream-edge mice with long feet (34–42 mm; HF/HB ≥ 25%) and striking bicoloured fur, with belly hairs pure white to the roots. Abbreviations explained in the text.

1. BZP > 3.0 mm, Ear/HF < 40%..... *Nilopegamys plumbeus*
2. BZP < 3.0 mm, Ear/HF > 40%..... *Colomys*, 3
3. BZP < 2.0 mm, CLM ≤ 5.0 mm..... *Colomys wologizi*
4. BZP 2.0–2.9 mm, CLM > 5.0 mm..... 5
5. CI > 32.0 mm, LIF ≥ 7.4 mm..... *Colomys eisentrauti*
6. CI < 32.0 mm, LIF ≤ 7.4 mm..... 7
7. BZP > 2.4 mm, ZP strongly convex..... *Colomys lumumbai*
8. BZP < 2.5 mm, ZP straight/slightly convex..... *Colomys goslingi*

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Supplementary File S1.
Table S1. Specimen information.
Table S2. Previously published primer sequences.
Table S3. Primers designed for amplification of antique DNA.
Table S4. GenBank sequences downloaded and used in phylogenetic analyses.
Table S5. GenBank accession numbers for newly generated sequences.
Table S6. Best-fitting nucleotide substitution models and partitioning schemes.
Figure S1. Maximum likelihood phylogeny based on concatenated mitochondrial loci.
Figure S2. Maximum likelihood phylogeny based on concatenated nuclear loci.
Supplementary File 2. Zip file containing complete DNA sequence alignments and Newick-formatted tree files for all phylogenetic analyses.
Supplementary File 3. Comparison of morphological characters of *Colomys* spp. and *Nilopegamys*, based on Kerbis Peterhans & Patterson (1995).