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RESEARCH PAPER

Integrative taxonomic revision of endemic dwarf shrews from the Ethiopian Highlands

Evan W. CRAIG[1,2*], Anna BRYJOVÁ[3], Josef BRYJA[3,4], Yonas MEHERETU[5,6], Leonid A. LAVRENCHENKO[7] and Julian C. KERBIS PETERHANS[8,9]

[1] *University of Massachusetts Boston, School for the Environment, Boston, USA; e-mail: evan.craig001@umb.edu*

[2] *Field Museum of Natural History, Science and Education, Chicago, USA; e-mail: ecraig@fieldmuseum.org*

[3] *Institute of Vertebrate Biology of the Czech Academy of Sciences, Brno, Czech Republic; e-mail: bryjova@ivb.cz, bryja@ivb.cz*

[4] *Masaryk University, Faculty of Science, Department of Botany and Zoology, Brno, Czech Republic*

[5] *Swedish University of Agricultural Sciences, Department of Wildlife, Fish & Environmental Studies, Umeå, Sweden; e-mail: yonas.meheretu@slu.se*

[6] *Mekelle University, Department of Biology and Institute of Mountain Research and Development, Mekelle, Ethiopia*

[7] *A. N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Moscow, Russia; e-mail: llavrenchenko@gmail.com*

[8] *Roosevelt University, College of Arts & Sciences, Chicago, USA; e-mail: jkerbis@yahoo.com*

[9] *National Museum of Kenya, Nairobi, Kenya*

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Abstract. The biodiversity of the Ethiopian Highlands features a significant level of endemism. Among its diverse fauna, the genus *Crocidura* (Soricidae), with many cryptic species, remains poorly documented, particularly for species of minute size. This study describes a newly discovered minute shrew – one of the smallest mammals worldwide – and addresses the taxonomy of the so-called 'Afromontane clade' of *Crocidura* in Ethiopia. We combined extensive field sampling of recent and historical specimens with advanced genetic analyses (genome skimming, Illumina sequencing, and cyt*b* phylogenetics) and morphological examination (external and craniodental) to delineate the new species and address taxonomic affinities among other minute *Crocidura* from Ethiopia. One of our newly collected forms represents a distinct genetic lineage, corresponding with unique physical characteristics such as tail length and cranial features. Its discovery highlights the rich, yet still incompletely understood, mammalian diversity in the Ethiopian Highlands and underscores the importance of integrating morphological and molecular data in taxonomic studies.

Key words: cryptic species, minute shrews, biodiversity, taxonomy, museomics, morphometrics

Introduction

The identification of species is pivotal in understanding biodiversity, particularly in regions with high levels of endemism and unique evolutionary histories. The Ethiopian Highlands, divided by the Great Rift Valley (GRV), is a part of the Eastern Afromontane biodiversity hotspot, exemplified by the highest

* *Corresponding Author*

continental mammalian endemism (17.7%) in the eastern hemisphere (Lavrenchenko & Bekele 2017).

This rich endemism reflects the highlands' unique environmental conditions, complex topography, and significant climatic fluctuations during the Pleistocene. For instance, out of 104 Ethiopian rodent species, 43 are endemic to the Ethiopian Highlands (Bryja et al. 2019b). Similarly, the Ethiopian shrew list currently stands at 30 species, with 12 endemics (Konečný et al. 2020). This high degree of endemism and diversity underscores the need for detailed taxonomic research, particularly for small, often overlooked mammals like shrews that risk extinction before they are even formally recognized.

Shrews have been underrepresented in biodiversity research due to taxonomic biases and the challenges of identifying small, cryptic species (Patterson 2001). Although *Crocidura* is the most speciose mammalian genus in Africa, where it is widely distributed across the continent, its taxonomy remains poorly understood (Happold 2013). This study focuses on minute shrews within the Ethiopian Afromontane clade (*sensu* Bannikova et al. 2021, Dianat et al. 2024), one of two major evolutionary clades of *Crocidura* in Africa. The so-called 'Afrotropical clade' (*sensu* Dubey et al. 2008) exhibits a broad distribution across various ecosystems throughout sub-Saharan Africa. In contrast, the so-called 'Afromontane clade' (*sensu* Dianat et al. 2024), closely linked to the montane habitats within the Eastern Afromontane Biodiversity Hotspot, traces its origins to the highlands of Ethiopia (Bannikova et al. 2021, Dianat et al. 2024). Building on the comprehensive phylogenomic and biogeographical analysis conducted by Dianat et al. (2024), which highlighted significant genetic divergence within the Afromontane clade, our study seeks to resolve further the taxonomy of these shrews, particularly those of the *C. bottegi* species complex (i.e. the *C. bottegi* and *C.* cf. *bottegi* clades in Dianat et al. 2024).

In 2015, we collected minute shrews (< 5 g) from the Simien Mountains National Park, which preliminary genetic analysis suggested formed a sister lineage to what we thought represented *C. bottegi*, but its novelty could not be confirmed without additional integrative taxonomic analysis. Other minute specimens collected from different localities in Ethiopia, resembling *C. bottegi* in size, were also not satisfactorily resolved (Konečný et al. 2020). The primary reasons for this are their rarity in collections, small size (not captured in standard rodent traps; Thorn & Kerbis Peterhans 2009), and cryptic nature (Happold 2013).

This study aims to address significant information gaps in the taxonomy and evolutionary diversity of minute members of the genus *Crocidura* in Ethiopia, particularly within the Afromontane clade. We employ multiple approaches to address these challenges, utilizing our collection of genomic data sampled from various localities in Ethiopia and Eastern Africa. We adopt advanced techniques in genetic analysis, specifically genome skimming and Illumina sequencing, to obtain DNA from historic specimens referred to as *C. bottegi* (Hutterer & Yalden 1990). Additionally, we used Bayesian Inference for mitochondrial phylogeny reconstruction using cyt*b* sequences, integrating extensive datasets from both recently collected and historical specimens. This comprehensive phylogenetic reconstruction, coupled with between-group principal component analysis (bgPCA) and standard PCA for craniodental characters in our morphological analysis, offers a comprehensive perspective on species delimitation and taxonomy, building on Dianat et al. (2024). We provide morphological support for the presence of two divergent lineages in Ethiopia, one of which we describe as a new species. Finally, we provide a brief overview of the minute members of the genus *Crocidura* from Ethiopia and identify directions for future research.

Material and Methods

Sampling

This study examined 106 specimens of small members of the genus *Crocidura* found in Eastern Africa (Table S1). The sample set comprised 48 specimens from the Afromontane clade, specifically collected from various locations in Ethiopia, which were the primary focus of our research. Additionally, we included 58 specimens belonging to the Afrotropical clade, classified according to their designated names in museum collections or GenBank entries. The majority of the genetic and morphological data for the Afromontane specimens were obtained through our field collections. This subset encompasses individuals previously reported in literature as *C. bottegi* and *C.* cf. *bottegi* (e.g. Dianat et al. 2024), *C.* sp. nov. indet. (Craig et al. 2020), and *C. bottegoides*. Due to the previous taxonomic uncertainty associated with these small Afromontane *Crocidura*, we categorized the specimens into two groups based on the relative length of their tails, distinguishing them as either 'short tail' (TV/HB < 70%) or 'long tail' (TV/HB > 75%). This characteristic not only provided a clear morphological distinction but also aligned with their geographical distribution and phylogenetic topology

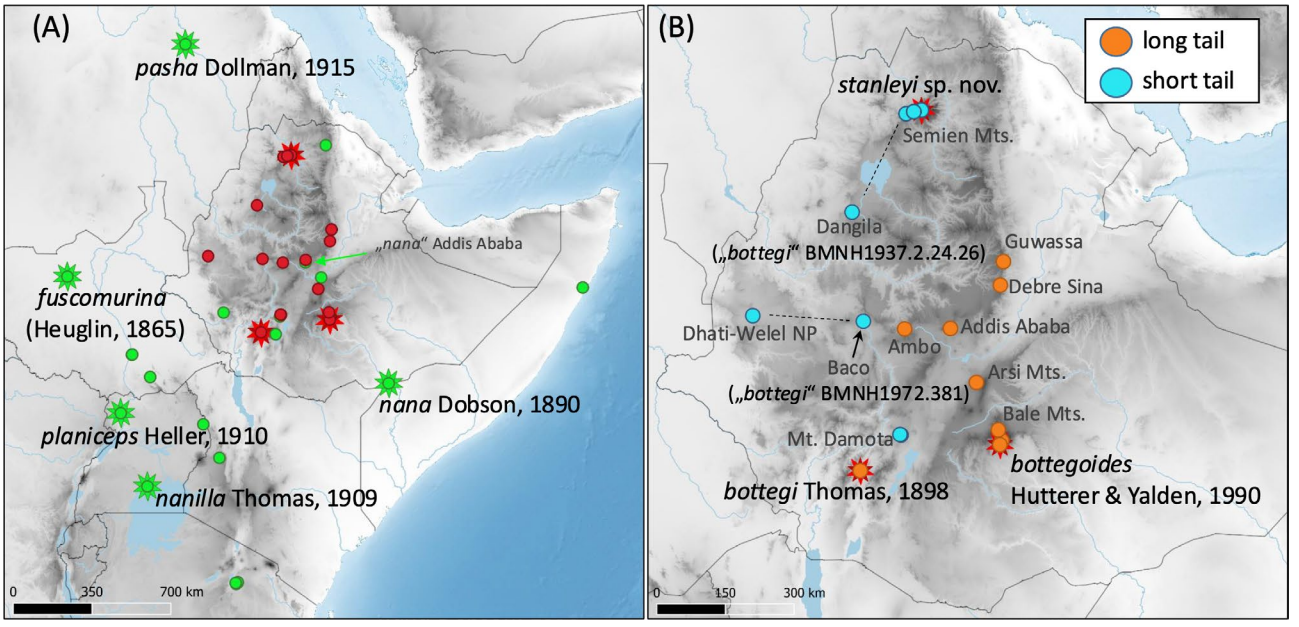

Fig. 1. Distribution of studied material and taxonomic summary. Stars show type localities with species names and authors of description. A) Localities of minute shrews from the Eastern Afromontane clade (= 'Old-World clade' *sensu* Dubey et al. 2008) are in red, while those of the *fuscomurina* group (*sensu* Hutterer & Yalden 1990) from the Afrotropical clade (*sensu* Dubey et al. 2008) are in green. B) Details of the Ethiopian Highlands with localities of minute shrews from the Eastern Afromontane clade (see more details on its phylogeny in Dianat et al. 2024). Orange and blue colours distinguish the two major morphological and phylogenetic groups. Note that both museum specimens of *C. bottegi* in BMNH are morphologically distinct from the holotype and their cyt*b* sequence clusters with *C. stanleyi*, sp. nov. Dashed lines link the populations of *C. stanleyi*, sp. nov. that cluster together in the phylogenetic analysis of cyt*b*.

(Figs. 1, 2). The 'short tail' group is introduced as *Crocidura stanleyi* sp. nov. within this study, and we will refer to it by this name for clarity moving forward. Similarly, we align two 'species' with the 'long tail' group: *C. bottegi* and *C. bottegoides*. We have no typical or topotypical genetic samples from true *C. bottegoides*, so we refer to possible specimens of this taxon as *Crocidura* cf. *bottegoides*.

Molecular methods

Sequencing of mitochondrial DNA

The analysis of genetic diversity and phylogenetic relationships was primarily based on the mitochondrial gene for cyt*b*, which is a simple genetic marker illustrating the phylogeny of African *Crocidura* shrews assessed by genomic approaches (e.g. Dianat et al. 2024). We obtained new cyt*b* sequences from 22 recently collected samples, two historical samples of *C. bottegi* from the NHM collection in London (catalogue numbers ZD 1937.2.24.26 and ZD 1972.381; Hutterer & Yalden 1990), and downloaded 14 additional sequences from GenBank. This dataset included 16 sequences of minute Ethiopian shrews from the Afromontane clade (*sensu* Bannikova et al. 2021, Dianat et al. 2024) and 22 sequences from other shrews belonging to the so-called Afrotropical clade (*sensu* Dubey et al. 2008). They represent shrews with minute body size from the '*fuscomurina* group' (*sensu* Hutterer & Yalden 1990, i.e. *C. nana*, *C. nanilla*, *C. fuscomurina* and *C. planiceps*), but we also included sequences of the *C. crossei/jouvenetae* complex that clustered with *C. fuscomurina* in the study of Dubey et al. (2008). For the list of sequenced individuals and the GenBank accession numbers, see Table S1.

From the recently collected tissues, mostly the spleen, we extracted DNA using the DNeasy Tissue kit (Qiagen). The amplification of the cyt*b* gene was performed by the polymerase chain reaction (PCR) using primers L14723 and H15915 and the protocol described in Bryja et al. (2014). PCR products were commercially sequenced by the Sanger method. To get the cyt*b* sequences from the old museum samples of the two specimens of *C. bottegi*, we used the genome skimming approach (Dodsworth 2015). The DNA was extracted from samples of ca. 1 mm^2 of dry skin tissues by the innuPREP Forensic Kit (Analytik Jena, Germany) and eluted to 35 µl of 10 mM TRIS solution. The quality of extracted DNA was checked on the Agilent 2100 Bioanalyzer by the High Sensitivity DNA kit (Agilent, US). Because DNA was already fragmented into 50-200 bp fragments, we did not use DNA restriction in the next step. The two samples differed by their concentration: ZD1937.2.24.26 (collected in the field in 1928) had 0.5 ng/µl and ZD1972.381 (collected in 1969) had 4,2 ng/µl. The genomic libraries were prepared by two different protocols to get higher coverage and multiple sets

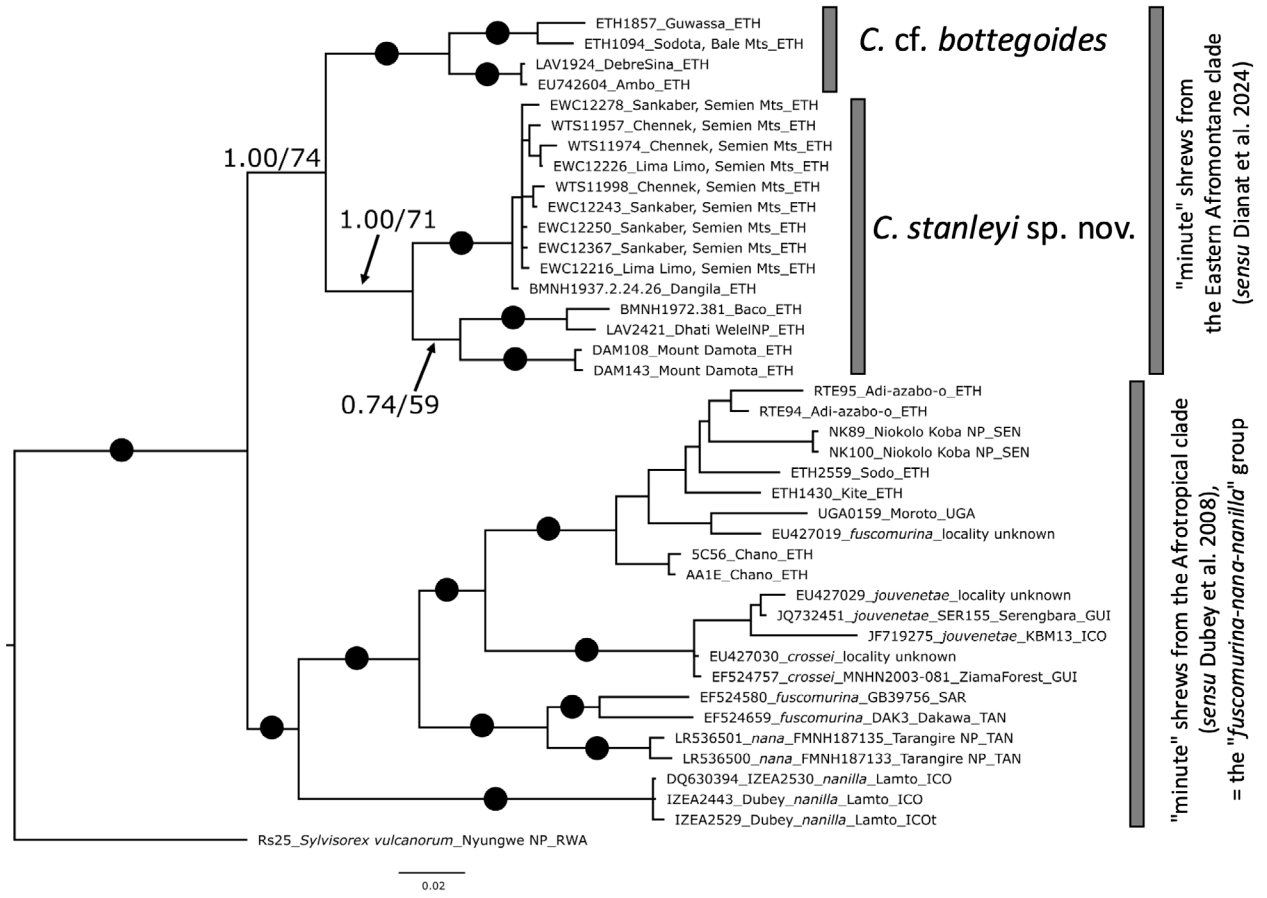

Fig. 2. Phylogenetic reconstruction of minute *Crocidura* specimens based on the available mitochondrial cyt*b* sequences. Note that we also added sequences of *C. crossei* and *C. jouvenetae* that clustered with *C. fuscomurina* in the study of Dubey et al. (2008). The sequences of *C. bottegoides* and *C. stanleyi* sp. nov. belong to the Eastern Afromontane clade of the genus (*sensu* Bannikova et al. 2021 and Dianat et al. 2024), while the others are members of the speciose Afrotropical clade (*sensu* Dubey et al. 2008), where the taxa with minute body size require integrative taxonomic revision. We used the species names as indicated in GenBank. We show the topology from the BI analysis, but the ML inference had a similar topology. Black dots indicate PPs PP > 0.95 (from MrBayes) and bootstrap support BS > 0.75 (from IQ-TREE), lower support is shown by numbers above branches.

of raw reads from each specimen. First, we prepared two independent dsDNA libraries for each sample by using the protocol of the KAPA HyperPrep Kit (Roche). Second, we used the same DNA extracts and prepared two independent ssDNA libraries using the xGen™ ssDNA & Low-Input DNA Library Preparation Kit (IDT, Inc., US). The libraries (four for each DNA extract) were checked on the Agilent 2100 Bioanalyzer by the High Sensitivity DNA kit, pooled equimolarly, and sequenced by the Illumina technology in Novogene, UK (on average five million 150 bp PE reads per library).

Assembly of mitogenomes from the old museum samples

The obtained Illumina reads were mapped to the reference mitogenome of *C. russula* (GenBank accession number AY769264) in Geneious 9.0.5. The two dsDNA libraries from ZD1937.2.24.26 produced 1.2 and 6 million PE reads in total and 300 and 50 thousand mapped to the reference (with mean coverage 5.6 and 44, respectively). Two ssDNA libraries resulted in 1.5 and 6 million PE reads, 290 and 695 thousand mapped with a mean coverage of 34.5 and 72.4, respectively. For the second specimen (ZD1972.381), the values were as follows: dsDNA libraries: 7 and 12 million PE reads, 20 and 300 thousand of mapped reads, mean coverage 80 and 130, respectively; ssDNA libraries: 5 and 6 million PE reads, 300 and 5 thousand mapped reads, mean coverage 48.6 and 72, respectively. The consensus sequences from four different libraries per specimen were checked by eye for mismatches (they occurred only in the D-loop region that was not used in follow-up analyses) and merged into a final mitogenome sequence. Alternatively, all reads from four libraries were mapped to the reference, and this produced the same consensus sequence. The mitogenome sequences were uploaded to GenBank under accession numbers PV684676 and PV684687. Finally, we excised the sequences of cyt*b* and used them in phylogenetic reconstructions.

Reconstruction of mitochondrial phylogeny

The cyt*b* sequences were edited and aligned in Geneious 9.0.5 (Biomatters, Ltd.). The final alignment contained 40 sequences of African *Crocidura* shrews with minute body size (see above; GenBank accession numbers are in Table S1) and the sequence of *Sylvisorex vulcanorum* (GenBank accession number PV684687) used as outgroup (Table S1). In the first step, we reconstructed the mitochondrial phylogeny using Bayesian Inference (BI). The FindModel web application (http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html) was used to identify the most appropriate substitution model for the ingroup alignment. The Akaike information criterion (AIC), compared among 12 biologically relevant substitution models, revealed that the model best fitting the data was General Time Reversible plus Gamma (GTR + G). BI analysis was performed in MrBayes v. 3.2.6 (Ronquist & Huelsenbeck 2003). Three heated and one cold chain were employed, with the runs initiating from random trees. Two independent runs were conducted with five million generations each; the trees and parameters were sampled every 1,000 generations. Convergence was checked using TRACER 1.7 (Rambaut et al. 2018). For each run, the first 25% of sampled trees were discarded as burn-in. Bayesian posterior probabilities (PP) were used to assess the branch support of the MCMC tree. Alternatively, the phylogeny was reconstructed by a Maximum Likelihood (ML) approach, using the same alignment and outgroup. The inference was made in IQ-TREE v. 2.1.3 (Nguyen et al. 2015). The nucleotide substitution model was chosen within IQ-TREE with the ModelFinder tool (Kalyaanamoorthy et al. 2017), which considered all GTR-based models, possibly combined with discretized gamma (Yang 1994) or free model (Yang 1995) of substitution rate variation across sites. The sequences were partitioned according to the codon positions, and no molecular clock was specified, so the branch lengths are in substitution units. The node support was estimated by ultra-fast bootstrap (Hoang et al. 2018).

Morphological methods

A total of 90 specimens were involved in our morphological analyses. External measurements for nearly half were based on our data generated from fieldwork in various parts of Ethiopia over the last two decades, while all others were sourced from previously published data. The following external measurements were taken (mm): total length (TL), tail vertebrae length (TV), head and body length (HB, or a subtraction of TL – TV when HB not available), hind foot length, including claw (HF), ear length (EAR), and body mass (BM (in g)). In addition, we calculated the ratio of tail vertebrae length to head and body length (TV/HB) and percent tail pilosity (PIL), defined as the length of the bristled portion of the tail/TV * 100.

To support our morphological analyses of craniodental characters we examined 52 voucher specimens held at the Field Museum of Natural History, Chicago (FMNH), the Natural History Museum, London (NHM), the Zoological Museum of Moscow State University, Moscow (ZMMU), the World Museum, Liverpool (NML), and Institute of Vertebrate Biology of the Czech Academy of Sciences, Brno (IVB CAS). Measurements were taken to the nearest 0.01 mm using digital callipers and, with few exceptions, were performed by either J.C. Kerbis Peterhans or E.W. Craig, or both, to cross-validate and ensure consistent results. We selected measurements that are frequently reported for *Crocidura* in the published literature, allowing direct comparison with historical series, and were available for the majority of museum specimens examined. Specifically, we followed the linear craniodental protocol illustrated by (Hutterer et al. 2018), including: condylo-incisive length (CIL), maxillary breadth (MB), minimum interorbital breadth (IO), greatest width of skull (GWS), upper toothrow length (UTR), postglenoid width (PGL), height of cranial capsule (HCC), length of lower toothrow including incisor (LTR), and height of coronoid process (COR), length of anterior tip of upper P4 to posterior border of M3 (P4-M3), post palatal length (PPL), and mandible length (ML). For all morphological analyses presented in this study, only adult specimens with fused basi-occipital sutures were included. Small sample sizes precluded us from reliably testing for sexual dimorphism in each species; however, we did not find evidence of dimorphism upon visual inspection of the data and therefore did not consider the sex of individuals in subsequent analyses. The following morphological analyses were carried out in R (R Core Team 2019).

Species predictions using bgPCA

To test for morphological support for the species delimitations implicated by the mitochondrial phylogeny, we used a between-group principal component analysis (bgPCA). The bgPCA method is particularly useful for examining phenotypic variations across different populations or species and to identify the main axes of variation between them. Unlike standard PCA, which would use the covariance matrix of the original samples, bgPCA focuses on the variation between pre-defined groups by projecting

the original samples onto the covariance matrix derived from the group means. On this basis, we used bgPCA to predict group membership for the *C. bottegi* holotype and two additional museum specimens from NHM London (Hutterer & Yalden 1990). To avoid taxonomic confusion, for the bgPCA training dataset we made groupings of the Afromontane clade phylogeny following exploratory visualization – specifically, using violin plots to compare genetic lineages recovered in the mitochondrial phylogeny (excluding BMNH specimens 1898.2.5.6, 72.381, and 37.2.24.26; see discussion below and Figs. 1B and 2) based on relative tail length (group 1: Afromontane short tail (< 70%); group 2: Afromontane long tail (> 75%)). Unlike *C. nanilla*, which has been recorded exclusively in dry habitats and low elevations, three specimens allocated to *C. nana* are from higher elevations in the central Ethiopian Highlands (ca. 2,200 m). These individuals are also markedly larger than their counterparts found in lower, drier habitats (Osgood 1936). Accordingly, we separated '*C. nana*' into two groups for the training dataset: group 3: *C.* cf. *nana* highland plateau, large, CIL > 16; group 4: *C. nana*, lowland savannah, small, CIL < 16).

Considering these four groups comprise rarely collected taxa where preserved skull material is limited and in various states of condition (i.e. impracticable measurements of damaged skulls), we used an economy of data approach to prepare the dataset. Missing values comprised 28% of the raw craniodental dataset. Therefore, to retain as much information as possible while minimizing potential bias from missing values, we started by examining the data to identify any measurements associated with a high proportion of missing values across individuals. ML, P4-M3, and PPL were excluded on this basis, accounting for over half (52%) of the missing values. We then excluded any individuals contributing less than three measurement values (n = 2). Finally, any remaining missing values (15%) were imputed using Multiple Imputation Principal Component Analysis (MIPCA) as implemented in the missMDA package (Josse & Husson 2016). Prior to imputation, the optimal number of components to retain was estimated to capture the most significant axes of variance within the data, and all variables were scaled to unit variance. A regularized iterative algorithm was employed with the threshold of convergence set to 1×10^{-4}, at which point the change in imputed values between consecutive iterations fell below this threshold. To account for variability in imputed values, 100 bootstrap samples were generated. A Bayesian treatment of the model was applied for multiple imputations employing a Markov Chain Monte Carlo (MCMC) sampling approach with a burn-in period of 1,000 iterations and a chain length of 100 iterations. To assess the influence of missing values and visualize the uncertainty of imputed values, we plotted the 100 imputed datasets against the reference PCA dimensions (Fig. S1). We performed the bgPCA via linear discriminant analysis (LDA) on the training set only, using the MASS package (Venables & Ripley 2002) to model clade membership as a function of nine (of the 12; see list above) craniodental measurements. A jackknife (leave-one-out) estimate of classification error was computed on the training data to assess model performance. Finally, the fitted LDA model was used to predict PPs of clade membership for the three withheld specimens (BMNH specimens 1898.2.5.6, 72.381, and 37.2.24.26).

Visualizing morphological variation

Based on the delimitations inferred by the reconstructed mitochondrial phylogeny and the results of the craniodental bgPCA predictions, we constructed violin plots and PCA plots (packages *ggplot2* and FactoMineR, respectively) to visualize the morphological variation among and between species (Lê et al. 2008, Wickham 2016). Violin plots were supplemented with boxplots to represent the interquartile range (IQR) and the median of the data. Following a thorough examination of the violin plots for each standard external measurement variable, we subjectively selected those that most vividly illustrated the differences between species. The selection was further supplemented by two violin plots derived from combinations of craniodental variables. The choice of these variables and the subsequent calculations were informed by our observations of distinctive skull characteristics to easily convey the relative shape characteristics of the skulls for each species. These included relative braincase height (calculated as the ratio of HCC to CIL) and relative braincase width (ratio of GWS to CIL). Using the same craniodental dataset as we used for the bgPCA (see bgPCA methods above), we applied a standard PCA to visualize the variation between species based on craniodental characters. We chose to apply a standard PCA for this task, as multivariate plots generated by the bgPCA method tend to display spuriously exaggerated separations between groups when (as in our case) the number of groups is outnumbered by variables (Cardini et al. 2019). Note, however, that the bgPCA method remains suitable for predictive assignment because classification relies on PPs computed in the full multivariate space, not on the visual scaling of a two-dimensional plot.

Fig. 3. Photographs of the skull of the holotype specimen (FMNH 229521) of *Crocidura stanleyi* sp. nov.

Results

Based on the results of our morphological and molecular phylogenetic analysis, we recognize a new species of shrew from Ethiopia.

A new species of *Crocidura* from the Ethiopian Highlands

Crocidura stanleyi, sp. nov.

Crocidura bottegi, part. (Yalden et al. 1976, Hutterer & Yalden 1990, Hutterer 2013)

Holotype: FMNH 229521, young adult male, field number WTS 11974, collected by the late William T. Stanley on September 27, 2015; museum voucher skin, skeleton, and skull in good condition (Fig. 3).

Type locality: Near Chennek Camp, Simien Mountains National Park, Debark Woreda, North Gondar Zone, Amhara State, Ethiopia (13.25952° N, 38.19140° E, 3,597 m a.s.l.) (Fig. 4).

Paratypes: 34 specimens (24 males, 10 females) were collected along the western slope of the Simien Mountains between September 21 and November 28, 2015. Seven specimens FMNH 229512-13, 229526, 229528, 229533, 229538, 229763 were collected from the type locality (Chennek camp) vicinity (13.262° N,

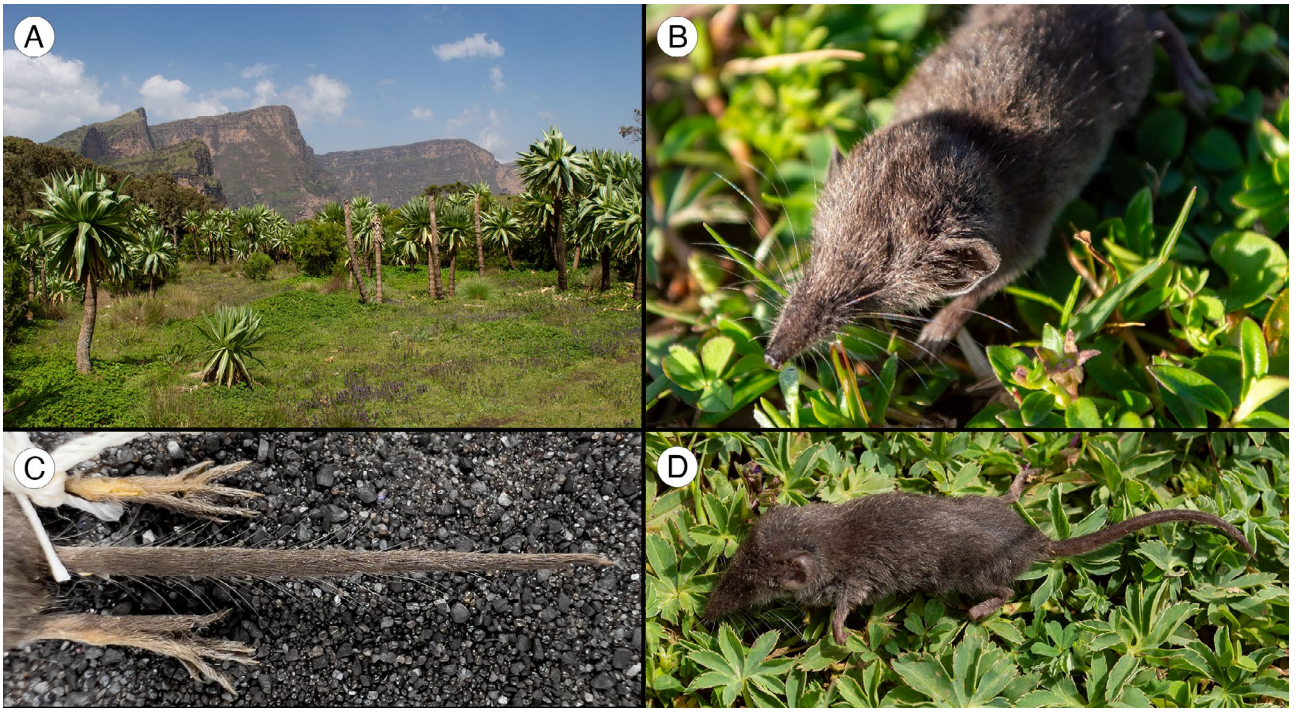

Fig. 4. Photographs showing the type locality habitat (A) and external characteristics of the head, tail, and body of *Crocidura stanleyi* sp. nov. (B-D).

38.193° E, 3,600 m), eight specimens FMNH 229561-62, 229770-74, 230013 from the Lima Limo camp vicinity (13.192° N, 37.892° E, 2,900 m), and 18 FMNH 229565-67, 229775-83, 229785-89, 229791 from the Sankaber camp vicinity (13.232° N, 38.038° E, 3,250 m). All specimens were prepared at the Field Museum of Natural History before a portion was returned to Mekelle University in Ethiopia (see Table S1).

Etymology: The species name, *stanleyi*, is chosen in honour of William (Bill) T. Stanley, a dedicated mammologist and collections manager at the Field Museum of Natural History, whose passion for African mammals was unparalleled. Bill Stanley's contributions were pivotal to the success of the multi-elevational survey in the Simien Mountains NP and transformative for many of the people involved. His unexpected and untimely passing in the very mountains where this new species was discovered casts a solemn light on this designation. The name *C. stanleyi* not only commemorates his last fieldwork but also celebrates his enduring legacy and the indelible mark he left on mammalogy, conservation, and the many lives he touched with his mentorship and collaborative spirit. His efforts in educational outreach, including the creation of the Tanzania Mammal Key (Stanley et al. 2011), an innovative web-based tool available in both English and Kiswahili, and various educational materials for local communities, personify his commitment to sharing knowledge and fostering appreciation for the local fauna. His foresight and enthusiasm for the biodiversity of the Ethiopian Highlands live on through this tiny shrew that thrives in the high, cold mountains – a fitting tribute to a man who held a deep respect for the intricacies of nature and the wonders it holds.

Diagnosis: A tiny bicoloured shrew exhibiting a dark brownish gray pelage above, lighter grey below (due to lighter tips). Braincase somewhat flat. Tail short and well-bristled. Parastyle of P^4 prominent and projecting forward. Unicuspids 2 and 3 sub-equal in size, but U3 often slightly larger. M3 well-developed.

Description: A very small shrew (Fig. 4) with the following mean external measurements: weight 3.0 g, head and body length 50.4 mm, tail length 32.6 mm, and hind foot length 10.1 mm. Overall appearance of dorsal pelage is a ticked brownish-gray, roots slate gray, tips brown. The ventral pelage is slate gray with lighter tips, giving it a bicoloured appearance. The colour transition about the flanks is abrupt and in line with the lateral plane of the tail and limbs, which exhibit the same bicolouration. The colour of the dorsal and ventral hairs on the tail matches those of the body, while the dorsal and distal, and ventral and proximal surfaces of the limbs match the dorsal and ventral colouration of the body, respectively. The tail length is two-thirds (66%) that of the body and is densely bristled about 73% of its length by long, light gray hairs (Fig. 4). White hairs to feet, paws and ears. Dark lateral streak on pes. The skull of *C. stanleyi* sp. nov. has a non-geometric aesthetic with smoothed rather than sharp transitions between cranial features. The rostrum is slightly convex, as is the braincase. The braincase is overall slender in its proportions and ovate. The sagittal crest extends above the braincase, forming a small ridge. The interorbital region is cambered. The occipital condyle is well developed, and its posterior projection is prominent. The coronoid process and angular process are long but slender. The lower incisor features an indentation, or crease, along its posterior ridge but is not denticulated. Three unicuspids; U2 is reduced in size, approximately 80% that of U3, while U1 is much larger than both. We found one specimen with an extra incisor on only one side. The first incisor has a very slight recurve, pointing just barely to the posterior instead of straight down.

Comparisons: Compared to *C. nana* and *C.* cf. *nana*, the pelage of *C. stanleyi* sp. nov. is much darker above and below and more modestly bicoloured. It has a much more inflated and broadened braincase compared with both (Fig. 5). *Crocidura stanleyi* resembles *C. bottegi* but differs in its shorter tail (TV = 33 mm *vs.* 41 mm), presence of abundant tail bristles (70% *vs.* 0-10%), and a dark grey *vs.* brown pelage. Although similar in size, *C. bottegoides* is quite different from *C. stanleyi* sp. nov. externally, with a tri-coloured pelage with a dark brown dorsal stripe and a much longer tail 43-44 mm) void of long-bristle hairs. In describing *C. bottegoides*, Hutterer & Yalden (1990; Fig. 4) inadvertently compared it to *C. stanleyi* sp. nov. (i.e. BMNH1937.2.24.26 and BMNH1972.381). *Crocidura stanleyi* sp. nov. has a heavier first incisor, larger 3^{rd} and 4^{th} unicuspids, and larger M^3. It differs from *C. bottegoides* and *C.* cf. *bottegoides* in its braincase proportions, being narrower and flatter than both. Notable is the ear length (EAR), where *C. stanleyi* sp. nov. has an average ear length of 5.4 mm, compared to *C. bottegoides* (7.3 mm) and *C. bottegi* (7 mm).

Distribution: *Crocidura stanleyi* sp. nov. is known from the Ethiopian Highlands northwest of the rift valley, specifically within Simien Mountains NP and Dangila (2,150 m). Other populations forming separate

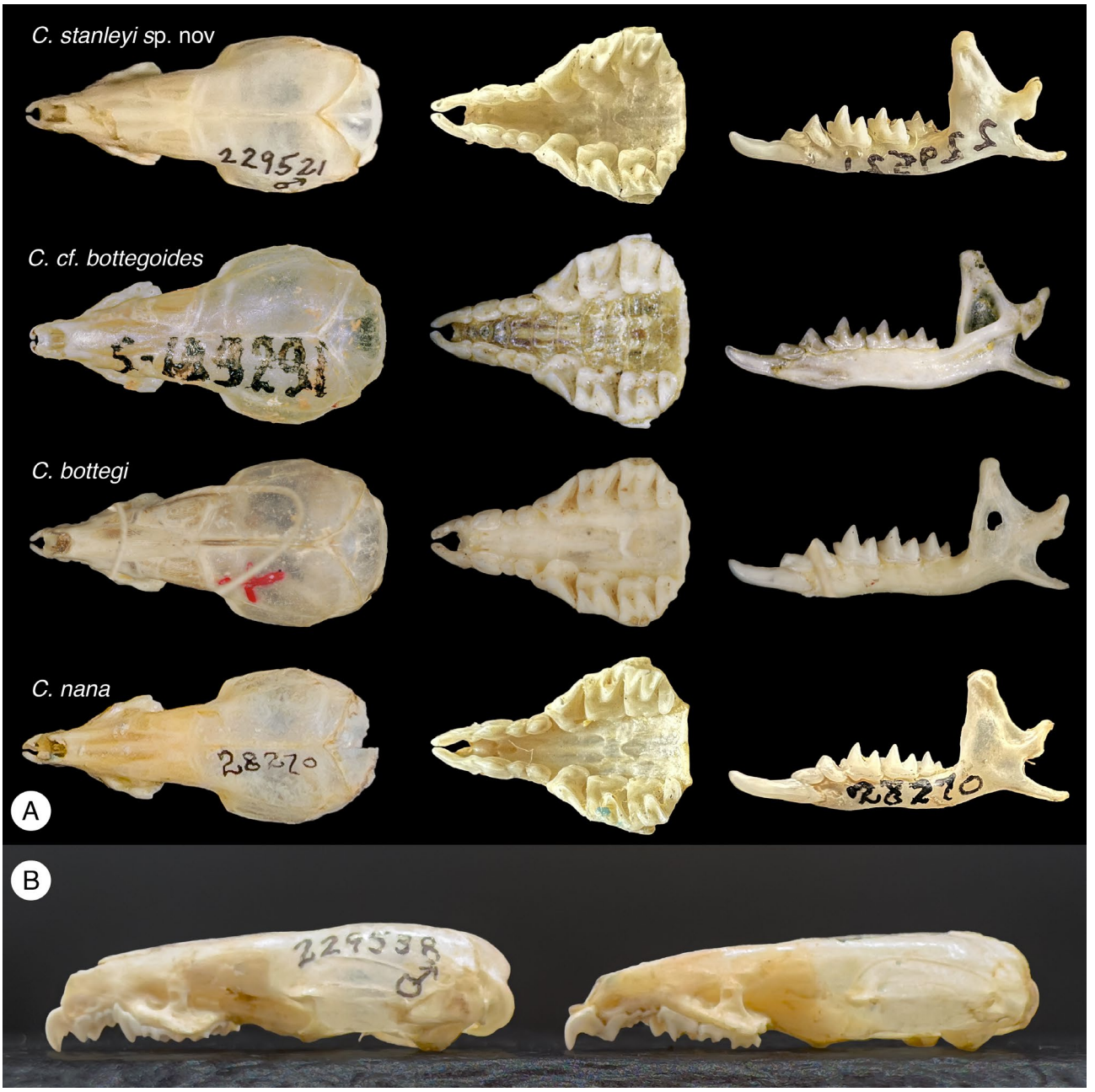

Fig. 5. A) Comparison of skull and craniodental features of four minute species of *Crocidura* recorded in Ethiopia (ordered top to bottom: FMNH 229521 (holotype), ZMMU s-189291, BMNH 1898.2.5.6 (holotype), FMNH 28270); B) comparison of skulls of *C. stanleyi* sp. nov. (left, FMNH 229521) and *C. nana* (right) in lateral view depicting 'flatness' of dorsal profile. The *C. nana* presented here is a lowland specimen (FMNH 28270) from Ethiopia that was collected in a habitat characteristic of this species.

intraspecific mtDNA lineages include those known to the south with records from Dhati-Welel (1,420 m) and Baco (1,700 m), and Mt. Damota (ca. 2,600 m).

Ecology: *Crocidura stanleyi* sp. nov. exhibits a broad ecological range within the Simien Mountains, where it has been found in diverse habitats from Afromontane forests to ericaceous heathlands (Craig et al. 2020). Known sympatric rodents, include *Lophuromys simensis*, *Stenocephalemys albipes*, *Arvicanthis abyssinicus*, *Dendromus lovati*, *Dendromus pseudomystacalis*, *Desmomys harringtoni*, *Mus mahomet*, *Mus imberbis*, *Otomys simiensis*, *Stenocephalemys zimai*, and its congener *Crocidura baileyi*, all of them being endemic to the Ethiopian Highlands. The habitats of *C. stanleyi* sp. nov. from the Simien Mountains are characterized by a rich mosaic of plant species, including *Juniperus procera*, *Olea europaea*, *Rapanea simensis*, *Hagenia abyssinica*, *Erica arborea*, and *Lobelia rhynchopetalum*, occupying both forested and open heathland environments. Microhabitats range from tall grasses in a patchwork of *Hypericum revolutum* and *Acacia* sp. to wetter regions shaded by dense *Erica arborea* foliage.

Mitochondrial phylogeny and distribution of mitochondrial variability

Both BI and ML phylogenetic reconstruction revealed two major groups of minute African *Crocidura* (Fig. 2). The first one belongs to the Eastern Afromontane clade (*sensu* Bannikova et al. 2021, Dianat et al. 2024), and this group is the main subject of our taxonomic revision. All these sequences originate from the Ethiopian Highlands (Fig. 1), documenting high endemicity of this area.

The second group harbours taxa from the Afrotropical clade (*sensu* Dubey et al. 2008) and is highly heterogeneous. All of this later group live in relatively arid open habitats in lower elevations, at least in eastern Africa (Fig. 1A), and were named (both in museum collections and GenBank) as *C. fuscomurina*, *C. nana*, or *C. nanilla*. Other species belonging to this morphological group (called '*fuscomurina* group' by Hutterer & Yalden 1990) are *C. pasha* and *C. planiceps* (Fig. 1A), but their sequences were not available. *Crocidura pasha* is much smaller (CI < 14.6) than specimens considered here and is confined to semi-arid savannahs, while *C. planiceps* is not known east of the River Nile (Churchfield & Jenkins 2013). We will not discuss these two further.

Within the Afrotropical clade, the sequences of *C. nanilla* from Ivory Coast are genetically very distant (see also Dubey et al. 2008). The sequences reported as *C. fuscomurina* in GenBank very likely represent two different species (Fig. 2), and eleven names have been proposed under *C. fuscomurina* (Hutterer 2005). The first one (EU427019) from an unknown locality included in the study of Willows-Munro & Matthee (2011) clusters with the sequences from the GRV in Ethiopia, Uganda, and Senegal, and might represent a widely distributed taxon in the Sudanian savannah. The second group of '*fuscomurina*' sequences (EF524580 and EF524659 from South Africa and Tanzania, respectively) forms a monophyletic group with *C. nana* from the Tarangire NP in Tanzania. This whole Afrotropical clade requires integrative taxonomic revision, which is beyond the scope of this study.

The minute Afromontane Ethiopian shrews are split into two major clades (Fig. 2; see also Dianat et al. 2024 for phylogeny based on thousands of nuclear SNPs), differing also by the relative length of the tail and its pilosity. The long-tailed shrews occur in the Bale (the type locality of *C. bottegoides*) and Arsi Mts. in the southeast part of the Ethiopian Highlands (i.e. Harar plateau), but also the eastern part of the northwest part of highlands (i.e. Abyssinian plateau) (Fig. 1B). The shrews with shorter tails and higher pilosity were recorded at five regions in the Ethiopian plateau, all of them in its north-western (Abyssinian) part. Interestingly, the sequences from two BMNH specimens referred to as *C. bottegi* (Hutterer & Yalden 1990) belong to this group, which agrees with their morphology (see below). It is possible to recognize three sub-lineages of short-tailed shrews (Fig. 2). The first one occurs in the Simien Mts. and clusters with '*C. bottegi*' from Dangila (BMNH 1937.2.24.26). The second was captured in Dhati-Welel NP and clusters with '*C. bottegi*' from Baco (BMNH 1972.381; Fig. 1B), and its sister third sub-lineage was recently (2023) captured on Mt. Damota. Unfortunately, we were not able to obtain the sequence from the holotype of *C. bottegi*, but it differs morphologically from the two referred BMNH specimens mainly by its long tail void of bristle hairs and its unicoloured dark brown pelage (J.C. Kerbis Peterhans, pers. observ.).

Phenotypic variability

We used bgPCA to predict group-membership probabilities for the *C. bottegi* holotype (BMNH 1898.2.5.6) and the two museum specimens from Baco and Dangila (BMNH 72.381 and BMNH 37.2.24.26; see Fig. 1 and Fig. S2), based on nine craniodental measurements. The jackknife (leave-one-out) misclassification error on the training set was 6.98%. Under this model, the holotype was assigned to

Table 1. Posterior probabilities of group membership for three withheld specimens (*Crocidura bottegi* holotype and two museum specimens), as estimated by the LDA based bgPCA model fitted on nine craniodental measurements. Probabilities are rounded to three decimal places.

Specimen	Afromontane long-tail	Afromontane short-tail	*C.* cf. *nana* (highland)	*C. nana* (lowland)
Holotype (BMNH 1898.2.5.6)	1.000	0.000	0.000	0.000
Baco (BMNH 72.381)	0.108	0.824	0.000	0.069
Dangila (BMNH 37.2.24.26)	0.011	0.278	0.000	0.711

Table 2. External and craniodental measurements of *C. stanleyi* sp. nov., *C. bottegoides*, *C.* cf. *bottegoides*, and *C. bottegi* are presented as the mean, standard error, standard deviation, range, and specimen count. All measurements are in mm except for body mass (g) and tail pilosity (%). Values presented for *C. bottegi* refer to measurements of the holotype.

	C. stanleyi sp.nov.	*C. bottegoides*	*C.* cf. *bottegoides*	*C. bottegi*
TL	83.0 ± 1.0/6.3/101-68/40	97.8 ± 2.4/4.8/104-91/4	94.8 ± 0.7/1.5/97-93/4	85
HB	50.4 ± 0.7/4.4/61-42/40	54.0 ± 1.8/3.7/57-48/4	52.3 ± 0.4/0.8/53-51/4	44
TV	32.6 ± 0.5/3.3/40-25/40	43.8 ± 1.0/1.9/47-42/4	42.5 ± 1.1/2.2/46-40/4	41
HF	10.1 ± 0.1/0.9/12-7/40	10.9 ± 0.3/0.6/12-10/4	11.4 ± 0.5/0.9/13-11/4	11
EAR	5.4 ± 0.2/1.2/8-4/39	7.2 ± 0.4/0.8/8-6/4	7.2 ± 0.4/0.8/8-6/4	7
BM (g)	3.0 ± 0.1/0.6/4.2-2.0/39	3.3 ± 0.2/0.5/3.8-2.5/4	3.1 ± 0.1/0.2/3-3/4	-
PIL (%)	75.7 ± 2.3/6.1/90-71/7	22.8 ± 0.0/0.0/0-0/4	45.6 ± 6.9/13.7/57-22/4	0*
CIL	15.4 ± 0.1/0.3/16.2-14.9/12	14.8 ± 0.1/0.3/15.1-14.3/4	15.0 ± 0.1/0.2/15-15/4	15.2
MB	4.5 ± 0.0/0.2/4.9-4.2/19	4.5 ± 0.1/0.1/4.5-4.2/4	4.6 ± 0.0/0.1/5-4/4	4.2
IO	3.2 ± 0.0/0.1/3.4-3.0/12	3.4 ± 0.1/0.1/3.5-3.2/4	3.4 ± 0.1/0.2/4-3/4	3.4
GWS	6.7 ± 0.1/0.3/7.1-6.3/11	7.1 ± 0.0/0.1/7.1-7.0/4	7.2 ± 0.1/0.3/7-7/4	7.2
UTR	6.3 ± 0.0/0.1/6.5-6.1/14	6.2 ± 0.0/0.1/6.0-5.9/4	6.4 ± 0.1/0.2/7-6/4	6.2
PGL	4.8 ± 0.1/0.2/5.1-4.3/12	4.8 ± 0.1/0.2/5.0-4.5/4	4.9 ± 0.0/0.1/5-5/4	4.8
HCC	3.6 ± 0.0/0.1/3.8-3.3/10	4.1 ± 0.0/0.1/4.1-4.0/4	4.1 ± 0.1/0.1/4-4/4	4.0
ML	9.0 ± 0.0/0.1/9.0-8.9/7	8.6 ± 0.0/0.0/8.4-8.4/1	8.6 ± 0.3/0.5/9-8/2	-
LTR	5.8 ± 0.0/0.1/5.9-5.7/8	5.5 ± 0.0/0.0/5.5-5.4/4	5.6 ± 0.2/0.4/6-5/4	5.7
COR	3.5 ± 0.0/0.1/3.8-3.3/11	3.3 ± 0.0/0.1/3.3-3.1/4	3.4 ± 0.0/0.1/4-3/4	3.1
P4.M3	3.6 ± 0.0/0.1/3.7-3.5/9	3.6 ± 0.0/0.0/3.5-3.5/1	3.6 ± 0.1/0.2/4-3/2	-
PPL	7.3 ± 0.1/0.1/7.5-7.2/3	7.0 ± 0.0/0.0/7.0-7.0/1	7.1 ± 0.0/0.0/7-7/1	-

* '(…) scarcely any elongate hairs' per Thomas' description of the holotype (1898).

the Afromontane long-tail group with a PP of 1.000 (100%), while the Baco specimen was assigned to the Afromontane short-tail group with a PP of 0.824 (82.4%). In contrast, the Dangila specimen was assigned to *C. nana* (lowland) with a PP of 0.711 (71.1%), followed by Afromontane short-tail (27.8%; Table 1).

Our comparisons of phenotypically similar Afromontane and Afrotropical species of *Crocidura* revealed some distinct morphological differences (Figs. 5, 6). Table 2 provides descriptive statistics of the external and craniodental characters analysed in this study for the focal Afromontane clade species *C. stanleyi* sp. nov., *C. bottegoides*, *C.* cf. *bottegoides*, and *C. bottegi*. External measurements demonstrated little size distinction between the clades (Fig. 6). Although there was considerable overlap in the ranges of head and body length (HB, referred to as body size hereafter), the Afrotropical species had somewhat higher mean values and IQRs, indicating it is the marginally larger clade. Within this clade, there was no discernible difference in body size between *C. nana* and *C. nanilla*. The most noticeable difference in external measurements was the longer tail of *C. nanilla*. However, this distinction, too, is evident only in the divergent mean values, as the range of tail lengths between the species overlapped significantly.

Overall, the Afrotropical clade exhibited a wide range of values across most external measurements. Notably, specimens of *C. nana* from higher elevations (FMNH 34233 and 34234) associated with the Ethiopian plateau were distinctly larger compared to those found in lower (FMNH 28270, the River Awash) drier habitats (Osgood 1936). In contrast, the external morphology of the Afromontane clade was generally less variable and therefore more indicative of the differences between species. There was no difference between species in terms of body size (disregarding *C. bottegi* (n = 1)). The tail provided the most pronounced separation in external morphology between the Afromontane species. Specifically, *C. stanleyi* sp. nov. had a significantly shorter tail in both absolute length (TV = 33.3 mm) and relative to the length of its body (66%) when compared to *C. bottegoides* (43.2 mm; 83%). Notably, the longest relative tail length of any individual examined in this study belonged to the holotype of *C. bottegi* (93%). The Afromontane species also differed in tail pilosity,

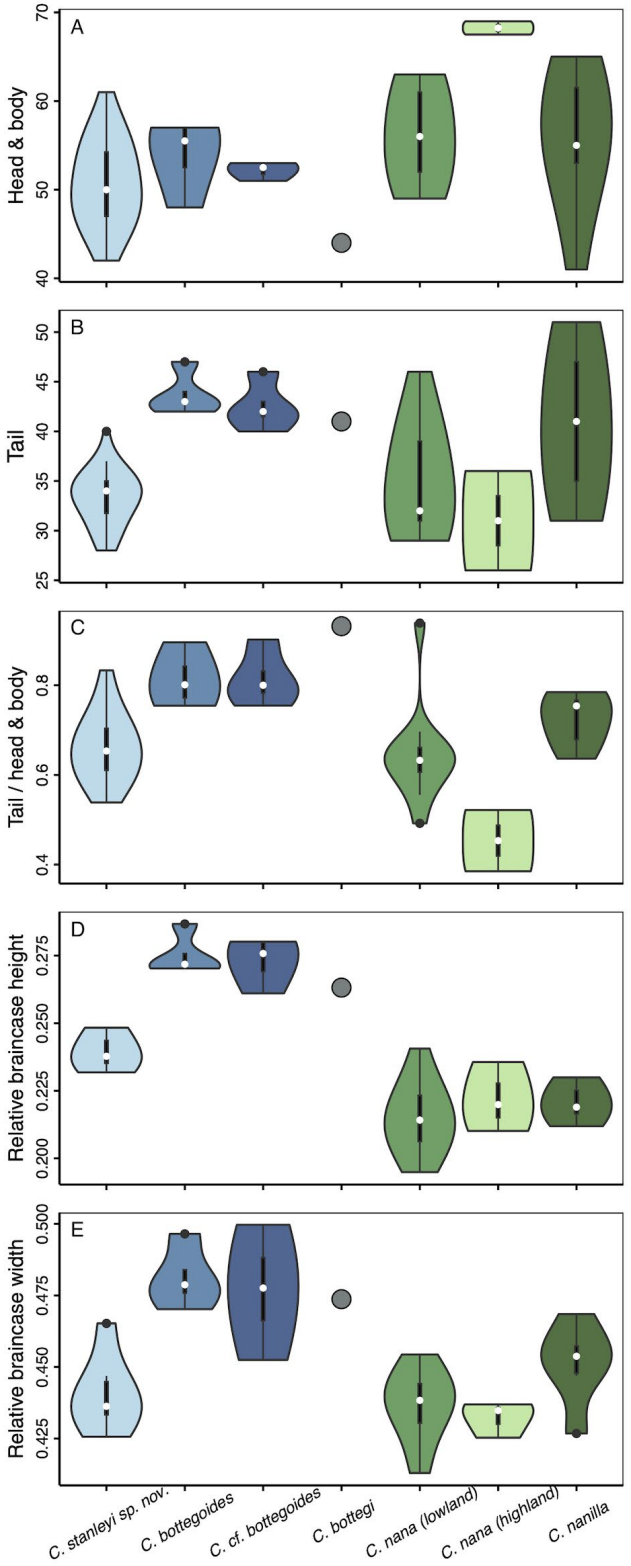

Fig. 6. Violin plots showing characteristics of external body forms (A-C) and skull shapes (D-E; calculations provided in methods) for species of minute *Crocidura* from the Afromontane clade (blues) and Afrotropical clade (greens). Note that *C. nana* recorded from highland localities (all three originating from the proximity of Addis Ababa in central Ethiopia) were plotted separately as they are clearly different. Values are plotted as points (n = 1) for the holotype of *C. bottegi*.

with the longer-tailed *C. bottegoides* and *C. bottegi* both bereft of bristles, to high pilosity for the shorter-tailed *C. stanleyi* sp. nov. ($\bar{x}$ = 70%). We remain perplexed by the high bristle count in *C.* cf. *bottegoides* (mean = 53%) as well as its uniformly grey pelage. Note that sample sizes were too small to test sexual dimorphism in most taxa; future work with larger series could clarify this present limitation.

Further, we found significant variation in craniodental morphology both between clades and within each clade (Fig. 6). The primary characteristic shared by these Afrotropical species (*C. nana* and *C. nanilla*) was a low braincase height relative to skull length. Within the Afromontane clade, skull morphology varied markedly between species. *Crocidura bottegoides* exhibited the tallest and widest braincase proportional to skull length (Hutterer & Yalden 1990; Fig. 6), similar to *C. bottegi*. In contrast, *C. stanleyi* sp. nov. shares more similarities with *C. nana* and *C. nanilla*, with all three species presenting narrower braincase proportions. While *C. stanleyi* sp. nov. also exhibits a low relative braincase height, it is not as pronounced as in the Afrotropical species *C. nana* and *C. nanilla*, which appear almost flat in profile (Fig. 5B).

We performed a PCA for the Afromontane clade based on nine linear craniodental measurements, but also included the similar *C. nana*, which shares an overlapping range (Fig. 7). The first two primary components explained 82.1% of the total variance. PC1, which accounts for 58.4% of the variance, does not show clear separation, and all species are broadly overlapping along this axis. This component is most strongly correlated with length proportions of the skull and dentition: condylo-incisive length (CIL, r = 0.94), upper tooth row (UTR, r = 0.89), maxillary breadth (MB, r = 0.87). Conversely, there is a distinct separation between *C. stanleyi* sp. nov. and its Afromontane congeners along PC2. This component accounts for 23.7% of the total variance and has high positive loadings for variables correlated with height and width proportions of the skull: height of cranial capsule (HCC, r = 0.89), interorbital breadth (IO, r = 0.72), and greatest width of skull (GWS, r = 0.57), and negative loadings for upper tooth row (UTR, r = –0.32) and lower tooth row (LTR, r = –0.52) suggesting and inverse relationship with these traits. Therefore, cranially, *C. bottegi*, *C.* cf. *bottegoides*, and *C. bottegoides* can be primarily distinguished from *C. stanleyi* sp. nov. and *C. nana* by their inflated braincases (higher braincases and broader skulls).

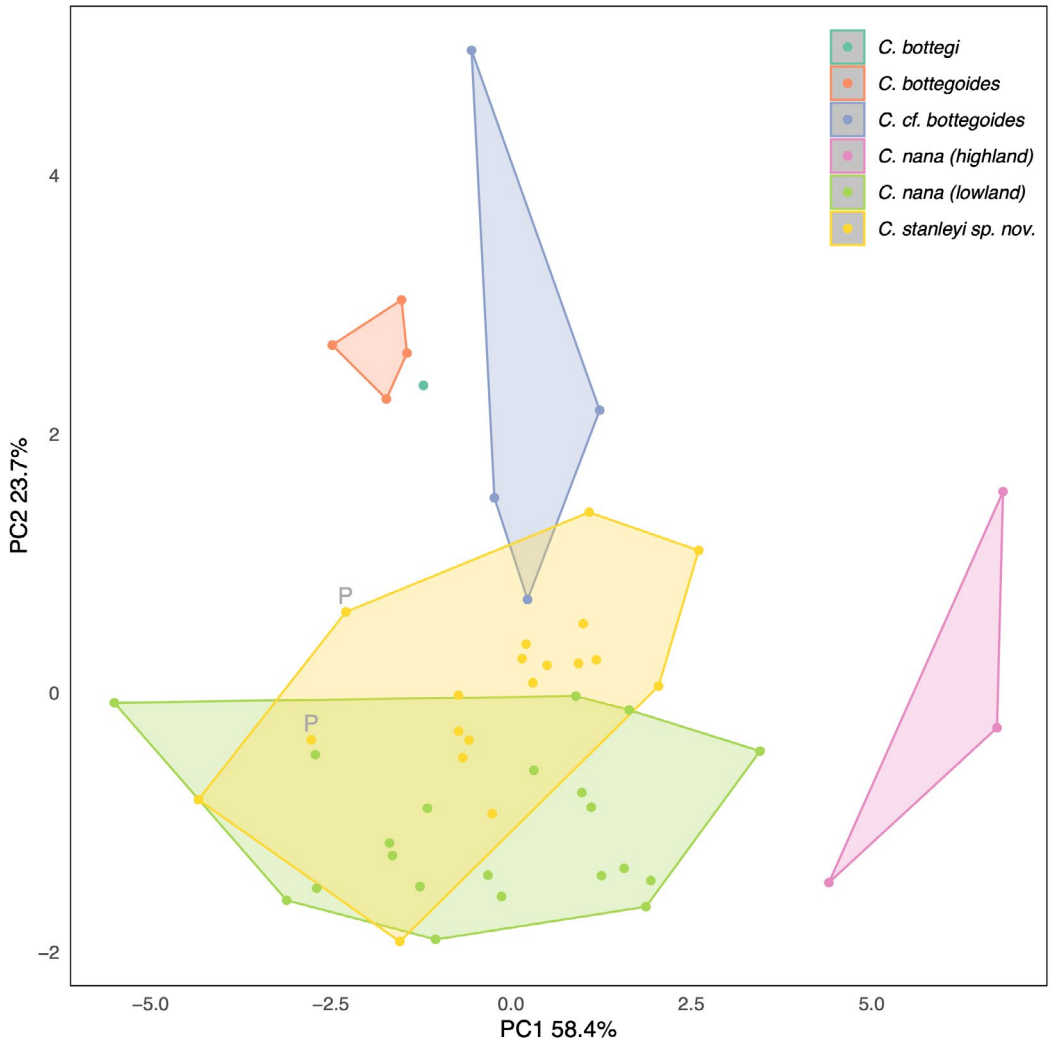

Fig. 7. Principal component analysis (PCA) on nine linear measurements of craniodental characters for species of minute *Crocidura* shrews of Ethiopia. The two points labelled with P denote the old museum specimens formerly considered paratypes of *C. bottegi*. Note that *C. nana* recorded from highland localities (all three originating from the proximity of Addis Ababa in central Ethiopia) were plotted separately as they are clearly different.

Discussion

Methodological notes

This study underscores the usefulness of museomics analysis in resolving the taxonomy of small cryptic species when morphological methods fail to support clear diagnoses. Our findings resonate with the growing consensus in the field of taxonomy that advocates for an integrative approach of morphological, ecological, genetic, and, importantly, genomic data to delineate species with greater accuracy (Vences et al. 2024). However, the incorporation of museomics comes with two main challenges. The first challenge is the availability of the museomics itself. To perform such analyses relies on obtaining tissue samples from target specimens typically held in museum collections. Although only a minuscule piece of tissue is typically required, museum collection managers may be hesitant to allow such 'destructive sampling' of very small type specimens. The second challenge relates to successfully extracting DNA from the tissues, which naturally degrade over time. Fortunately, new innovative approaches, such as the genome skimming technique and dual library preparation methods utilized in our study, coupled with high-throughput sequencing, offer promising solutions to these obstacles (Vences et al. 2024). These methods enable the efficient recovery and sequencing of highly degraded DNA from museum specimens.

The incorporation of museomics is likely necessary to resolve the taxonomy of small African *Crocidura* completely. For instance, besides the completely unresolved Afrotropical '*C. fuscomurina* group', which includes *C. nana*, we are confused by the status of *C. bottegoides* and *C.* cf. *bottegoides*. They are close in geography (southern and central domains, respectively – see discussion of domains in the next

section) and in craniodental metrics, but *C. bottegoides* has two major differences from *C.* cf. *bottegoides*: the tri-coloured pelage and the tail without elongate bristle hairs (photos available in Fig. S3). They share a bulbous braincase and a wide interorbital region. *Crocidura bottegoides* has no elongate bristle hairs. Especially pertinent is that the description of *C. bottegoides* was based on morphological comparison with *C. bottegi* (n = 3), which comprised the holotype and two referred specimens. Sequence data from the two referred specimens revealed that both represent *C. stanleyi* sp. nov. These species should be taxonomically re-evaluated using genetic markers. Doing so will rely on the availability of DNA material from type specimens.

The availability of DNA material from the holotype of *C. bottegi* is especially important. Though once thought to be widespread, the reallocation of populations in West Africa to *C. obscurior* (including *C. eburnea*) constrained the known distribution of *C. bottegi* to four localities prior to this work (Hutterer 2013). As of this taxonomic revision, there appears to remain a maximum of only three specimens from two localities representing the species: the holotype at NHM in London, a 'co-type' at the Natural History Museum Giacomo Doria (Genova), and possibly a single specimen record from Marsabit, Kenya (Heim de Balsac & Meester 1977) that has been called for re-evaluation (Hutterer 2013).

Evolutionary notes

The taxonomic confusion surrounding these minute shrews may be explained, at least in part, by convergent evolution between the Afromontane and Afrotropical clade. In particular, *C. nana* and *C. stanleyi* sp. nov. are morphologically very similar. Our analyses of the craniodental and external characters show considerable overlap for these species (Figs. 6, 7). Though little ecological information is known, the fact that they typically occupy different grassland/scrub habitats in the lowlands (= *C. nana*) *vs.* the highlands (= *C. stanleyi* sp. nov.) suggests that they may occupy the same niche space (Lavrenchenko et al. 2016). Despite *C. nana* generally being recognized as a species adapted to dry, low-elevation environments (Churchfield & Jenkins 2013), collection records include a few exceptional individuals from higher elevations associated with the Ethiopian plateau (ca. 2,200 m a.s.l.) that we believe represent an undescribed species. Specifically, these high-elevation individuals have 22.3% larger bodies (HB, $\bar{x}$ = 68.5 mm, range: 68-69 mm) and 10.3% larger skulls (CI, $\bar{x}$ = 17.08 mm, range: 16.56-17.40 mm) compared to their lowland counterparts (HB, $\bar{x}$ = 56 mm, range: 49-63 mm; CI, $\bar{x}$ = 15.49 mm, range: 13.84-16.64 mm). In contrast, these individuals have tails that are 11.4% shorter (TV, $\bar{x}$ = 31 mm, range: 26-36 mm) than lowland populations (TV, $\bar{x}$ = 35 mm, range: 29-46 mm). We anticipate that results from museomics work will elucidate their relationship with low-elevation *C. nana*. It is plausible that the highland *vs.* lowland *C. nana* represent different species.

The phylogeography of the Afromontane clade of minute shrews in Ethiopia aligns well with findings for other montane small mammal taxa in the region. The broadest pattern is the separation of north-western fauna (e.g. *C. stanleyi* sp. nov.) from south-eastern fauna (e.g. *C. bottegoides*). This finding is not surprising given the geographic context of the GRV, which is a significant barrier to dispersal for highland fauna (Evans et al. 2011). However, recent evidence suggests that the GRV is not necessarily impassable for montane rodents. Similar patterns to those seen in the distributions of *C. stanleyi* sp. nov., found exclusively northwest of the GRV, while *C. bottegoides* may span both sides, have been documented in Afroalpine rodent congeners in Ethiopia (Bryja et al. 2018, 2019a, Mizerovská et al. 2020, 2023). For instance, the high-elevation specialists of *Stenocephalemys* (*S. zimai* and *S. albocaudatus*) and *Arvicanthis* (*A. abyssinicus* and *A. blicki*) have distributions that remarkably match those of the Afromontane *Crocidura* (compare Fig. 1 with Fig. 1 in Mizerovská et al. 2020; and Fig. 3 in Bryja et al. 2019a). In each case, the south-eastern representatives also have disjunct populations found on mountains across the GRV to the north. Thus, the phylogeography of minute Afromontane *Crocidura* supports the existence of two distinct biogeographic montane domains northwest of the GRV, a 'northern' domain dominated by the Simien Mountains (and to a lesser extent Mt. Choqa) and a 'central' domain that comprises ranges broadly north of Addis Ababa (e.g. Debre Sina, Guwassa). Based on the close phylogenetic affinities found between the central domain and southern (Bale-Arsi Mts.) taxa, this central domain has been proposed to be a zone linking the northern domain and southern biota (Mizerovská et al. 2023), which suggests that entire ecosystems were shaped by the same climatic conditions, with the highest massifs of the northern domain serving as crucial refugia for endemic fauna.

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Author Contributions

E.W. Craig, J. Bryja, and J.C. Kerbis Peterhans conceived the study; E.W. Craig, J. Bryja, Y. Meheretu, and L.A. Lavrenchenko collected material; A. Bryjová, J. Bryja, and L.A. Lavrenchenko produced or analysed genetic data; E.W. Craig, J.C. Kerbis Peterhans analysed morphometric data; E.W. Craig and J. Bryja wrote the first version of the manuscript; all authors provided comments on the manuscript and agreed to publication.

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Supplementary online material

Table S1. List of all *Crocidura* specimens used in this study (https://www.ivb.cz/wp-content/uploads/JVB-74-2025-Evan-W.-Craig-et-al.-Table-S1.xlsx).

Fig. S1. Visualization of uncertainty in imputed missing values. This biplot depicts the uncertainty associated with imputed missing values in the craniodental dataset by plotting 1,000 iterations of imputation (blue) against the reference PCA dimensions. The spread along these dimensions reflects the degree of uncertainty, with axis values ranging from –1.0 to 1.0, indicating the relative uncertainty of the imputed values.

Fig. S2. Between-group PCA (via LDA) of nine craniodental measurements showing four morphogroups. Training specimens are plotted as coloured circles according to their assigned morphogroup. The three withheld specimens (holotype BMNH 1898.2.5.6, Baco BMNH 72.381, and Dangila BMNH 37.2.24.26) are overlaid as black triangles and labelled by catalogue number. LD1 and LD2 correspond to the first two linear discriminant axes from the LDA, which together capture the majority of between-group variance.

Fig. S3. Representative photographs of *Crocidura* cf. *bottegoides* specimens collected by the authors (L.A. Lavrenchenko top/middle, J. Bryja bottom) depicting pelage colouration.

(https://www.ivb.cz/wp-content/uploads/JVB-74-2025-Evan-W.-Craig-et-al.-Fig.-S1-S3.pdf)

NOMENCLATURAL ACTS REGISTRATION

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