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Source: Journal of Vertebrate Biology, 69(2)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/jvb.20064

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Journal of Vertebrate Biology

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J. Vertebr. Biol. 2020, 69(2): 20064

DOI: 10.25225/jvb.20064

SPECIAL ISSUE: AFRICAN SMALL MAMMALS

Two new species of *Crocidura* (Mammalia: Soricidae) from Ethiopia and updates on the Ethiopian shrew fauna

Adam KONEČNÝ[1*], Rainer HUTTERER[2], Yonas MEHERETU[3] and Josef BRYJA[1,4]

[1] *Vertebrate Research Group, Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic; e-mail: akonecny@sci.muni.cz*

[2] *Zoological Research Museum Alexander Koenig, Bonn, Germany; e-mail: r.hutterer@leibniz-zfmk.de*

[3] *Department of Biology and Institute of Mountain Research & Development, Mekelle University, Mekelle, Ethiopia; e-mail: meheretu.yonas@mu.edu.et*

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

▸ Received 28 June 2020; Accepted 4 September 2020; Published online 13 November 2020

Abstract. We describe two new species of white-toothed shrews from south-western and central Ethiopia, based on recent collections and an application of morphological and genetic methods, *Crocidura similiturba* sp. nov. and *Crocidura makeda* sp. nov. Comparisons are provided with other *Crocidura* species known to occur in the country. Both new species are currently known only from the Ethiopian Highlands. Furthermore, we provide new geographical records and discuss biogeographical patterns in the country. New molecular data, even if based primarily on mitochondrial cytochrome *b*, suggests substantial divergence within afrotropical *Suncus megalura*, suggesting that the East African lineage might be considered separated at the species level – *Suncus sorella* (Thomas, 1897), stat. nov. Molecular data support a monophyly of the clade, grouping most *Crocidura* species endemic to Ethiopia (the East African subclade of the Old World clade), but also indicates additional colonisations of Ethiopian Plateau from East and Central Africa in the past. The remarkable number of endemics shows that Ethiopia is an important centre for the *Crocidura* radiation, as is the case for other groups of non-flying terrestrial vertebrates.

Key words: shrews, Crocidurinae, East Africa, taxonomy, phylogeny, diversity, new records

Introduction

The extraordinarily diverse fauna of Ethiopia is associated with the varied topographical features of the country. The Ethiopian relief covers a wide range of altitudes from below sea level to 4,620 m a.s.l. and 40% of the country consists of highlands over 2,500 m a.s.l. These extensive plateaus are bisected centrally by the Rift Valley, which is the major zoogeographical barrier for organisms living in the highlands. In accordance with this geomorphological diversity and separation from other mountain blocks in East Africa, the Ethiopian fauna is characterized by a high level of endemism. At present, more than 50 mammalian species are considered to be endemic to Ethiopia (Yalden & Largen 1992, Yalden et al. 1996, Lavrenchenko 2003, Monadjem et al. 2015, Lavrenchenko et al. 2016, Wilson & Mittermeier 2018, Bryja et al. 2019a).

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* *Corresponding Author*

The Ethiopian fauna of small mammals is particularly diverse. For example, the recent annotated check-list of rodents includes 108 species (some still requiring formal description), 43 of which are endemic to the Ethiopian Highlands (Bryja et al. 2019a). The family Soricidae is represented in Ethiopia by at least 28 species, 10 of which are endemic (Lavrenchenko et al. 2016). In view of the rapid habitat destruction in Ethiopia, knowledge of the geographical distribution of evolutionary diversity is critical for the identification of regions and habitats worthy of urgent conservation action. Therefore, taxonomic and evolutionary studies on Ethiopian fauna are very important and small mammals are particularly suitable models for assessing patterns of diversity.

During trapping sessions of small mammals in southwest and central Ethiopia from 2012 to 2019, we collected a series of shrews that were barcoded by genotyping mitochondrial cytochrome *b* gene (cyt*b*). We also analysed their external and skull morphology and this integrative approach revealed two new species which are described here. We further provide updated distributional information for some species and indicate the groups requiring further taxonomic work.

Material and Methods

A total of more than 250 shrews were collected in Ethiopia from 2012 to 2019 by members of Ethio-Czech research programme, led by the Institute of Vertebrate Biology (IVB) of the Czech Academy of Sciences (Czech Republic) and Mekelle University (Ethiopia). Specimens (mostly preserved in alcohol with skulls extracted) were deposited in Research Facility of IVB in Studenec (field labels starting with ETH) and selected representatives (e.g. types) in the National Museum (Natural History) in Prague (NMP). Comparative material was examined in the Natural History Museum, London (NHM), Field Museum of Natural History, Chicago (FMNH), the Liverpool Museum (LIV), Zoological Research Museum Alexander Koenig, Bonn (ZFMK) and Staatliches Museum für Naturkunde, Stuttgart (SMNS).

For the present study 124 specimens were analysed genetically (79 for the first time) and about 150 specimens were measured and studied anatomically (Table S1). External body measurements (HB – head-body length, T – tail length, HF (–n) – hind foot length without claws, E – ear length) were recorded in the field. Skulls were measured using an electronic calliper and a field microscope. The following measurements were taken: CI – condylo-incisive length, PL – hard palatine length, UTR – tip of the first upper incisor to upper posterior margin of the third molar, P4-M3 – upper P4-M3 length, PGL – post-glenoid width (measured between lateral parts of the ento-glenoid processes), GW – greatest width (maximum transverse diameter of the braincase), MB – width across maxillaries, IO – interorbital width (level of ethmoidal foramina), HCC – height of cranial capsule, COR – height of mandibular coronoid process, ML – length of mandible, LTR – length of lower tooth row, m1-m3 – length of lower molar row, CH – height of coronoid process, CW – width of coronoid process.

Material from each species analysed includes voucher specimens identified using morphological and molecular methods. Cranial and dental nomenclature follows Meester (1963), Repenning (1967), Butler & Greenwood (1979), Butler et al. (1989), Dannelid (1998), Lopatin (2006), Wible (2008) and Jenkins et al. (2009). The terminology of the three upper unicuspid teeth of *Crocidura* is still not settled, Hutterer (2005) called them I2, I3 and C. For the purpose of this paper, we apply the term antemolars A1, 2 and 3.

We performed multivariate Principal Component Analysis (PCA) based on 13 cranial and mandibular measurements (all those defined above, except CH and CW) in Past v4.03 (Hammer et al. 2001). All variables were measured in the same unit (mm) and the principal components were extracted from the variance-covariance matrix.

To confirm species identification and investigate the phylogenetic relationships of new Ethiopian shrew samples, we performed a cyt*b*–based barcoding and a maximum likelihood phylogenetic analysis. We studied sequences from 62 shrew samples from Ethiopia and 15 *Crocidura turba* and two *Suncus* individuals from neighbouring countries (Table S1). Additionally, 49 shrew sequences were selected from the GenBank database (NCBI) to represent all related species by two or three sequences (Table S1). DNA was extracted from spleen samples and kept in 96% ethanol after dissection in the field. All the sequences were generated according to the protocol of Bryja et al. (2014) and deposited in GenBank under accession numbers MT990644-MT990721 (Table S1).

We used mitochondrial cyt*b* sequences for generating maximum likelihood trees using the PHYML algorithm (Guindon et al. 2010). GTR + Gamma substitution model was chosen using AIC (Posada & Buckley 2004) and implemented in Geneious v1.9.8 platform (©2005-2017 Biomatters Ltd.), branch support was estimated using 1000 bootstrap iterations. The phylogenetic trees were visualized using FigTree v1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/). Maps showing the geographical position of samples analysed were created using QGIS v3.4.4-Madeira (https://qgis.org/en/site/).

Results

Two new species of *Crocidura* from Ethiopia

The combination of external and skull morphology with the molecular phylogenetic approach revealed two species not yet described in the scientific literature. Here we provide their formal description and additional details about their distribution and ecology.

Crocidura similiturba sp. nov.

Holotype: NMP 96961 (field number ETH2068), male, preserved in alcohol, skull extracted, collected by A. Konečný, D. Mizerovská and J. Šklíba on 8 December 2018 (Fig. 1).

Type locality: Ethiopia, Kafa zone, Medabo village (7.56294 N, 36.04964 E), 1,563 m a.s.l., dried periodic wetland and shrubby edge (Fig. 2).

Paratypes: NMP 97132 (ETH2067, male); NMP 97133 (ETH2112, female); same locality and altitude.

Diagnosis: A large, overall blackish *Crocidura* (n = 3) with a long and narrow skull, similar to *C. turba*, but with a longer tail (T 57.5-67.5 mm *vs.* 50-65 mm in *C. turba*, n = 19) with lower pilosity (48% *vs.* 76% in *C. turba*, n = 2) and longer hindfeet (HF 15.2-17.9 mm *vs.* 13.7-17.1 mm in *C. turba*, n = 18). Skulls of females smaller than of males. Rostrum long and narrow. Genetically (at cyt*b*) it represents a lineage close to *C. turba* of Zambia, Malawi, Tanzania, and DR Congo (Fig. 2C). Both species belong to the so-called *Crocidura poensis* complex (sensu Nicolas et al. 2019), distributed primarily in the Guineo-Congolian forests.

Description: Relatively large-sized (head and body length 86-102 mm, weight 13-21 g) with a moderately long tail, ranging between 66 and 69% of head and body length, basal 48% of tail covered

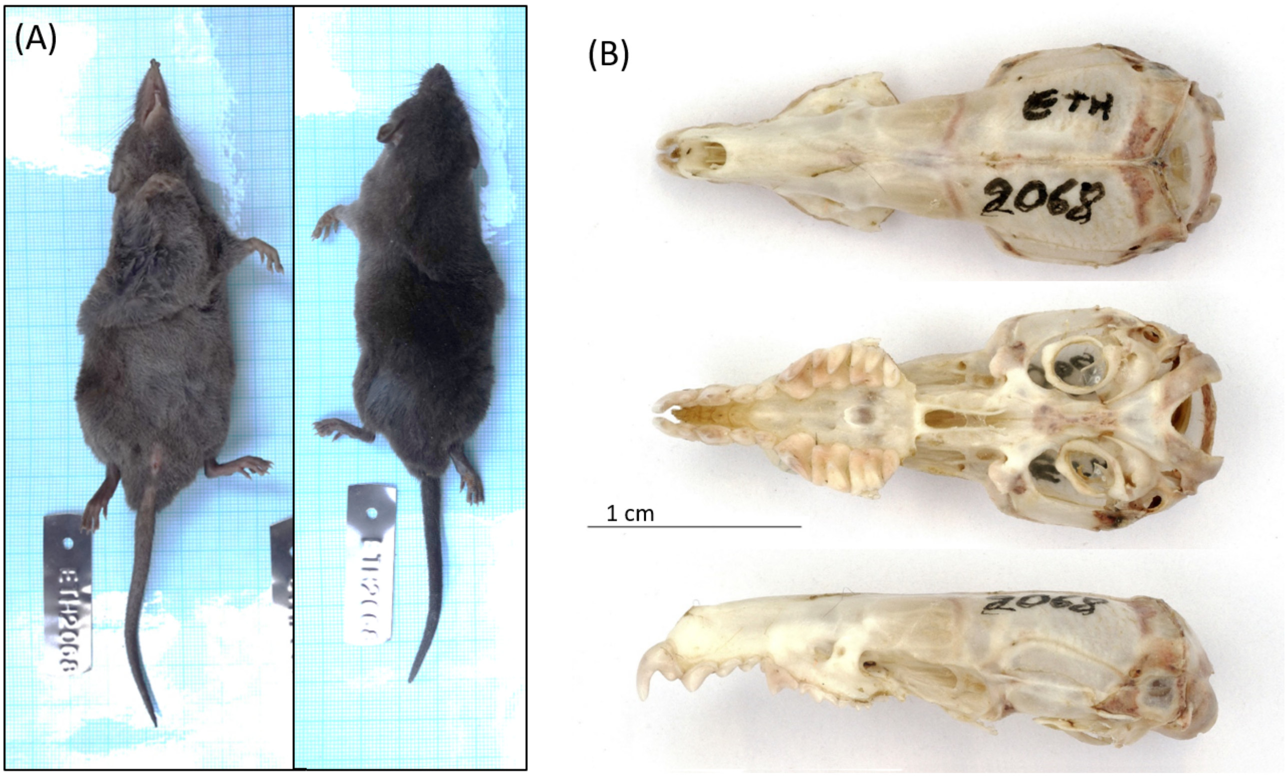

Fig. 1. (A) Ventral (left) and dorsal (right) appearance of *Crocidura similiturba* sp. nov. (specimen ETH2068, holotype). (B) Dorsal (top), ventral (middle) and lateral (bottom) view of the skull of *C. similiturba* sp. nov. (specimen ETH2068, holotype).

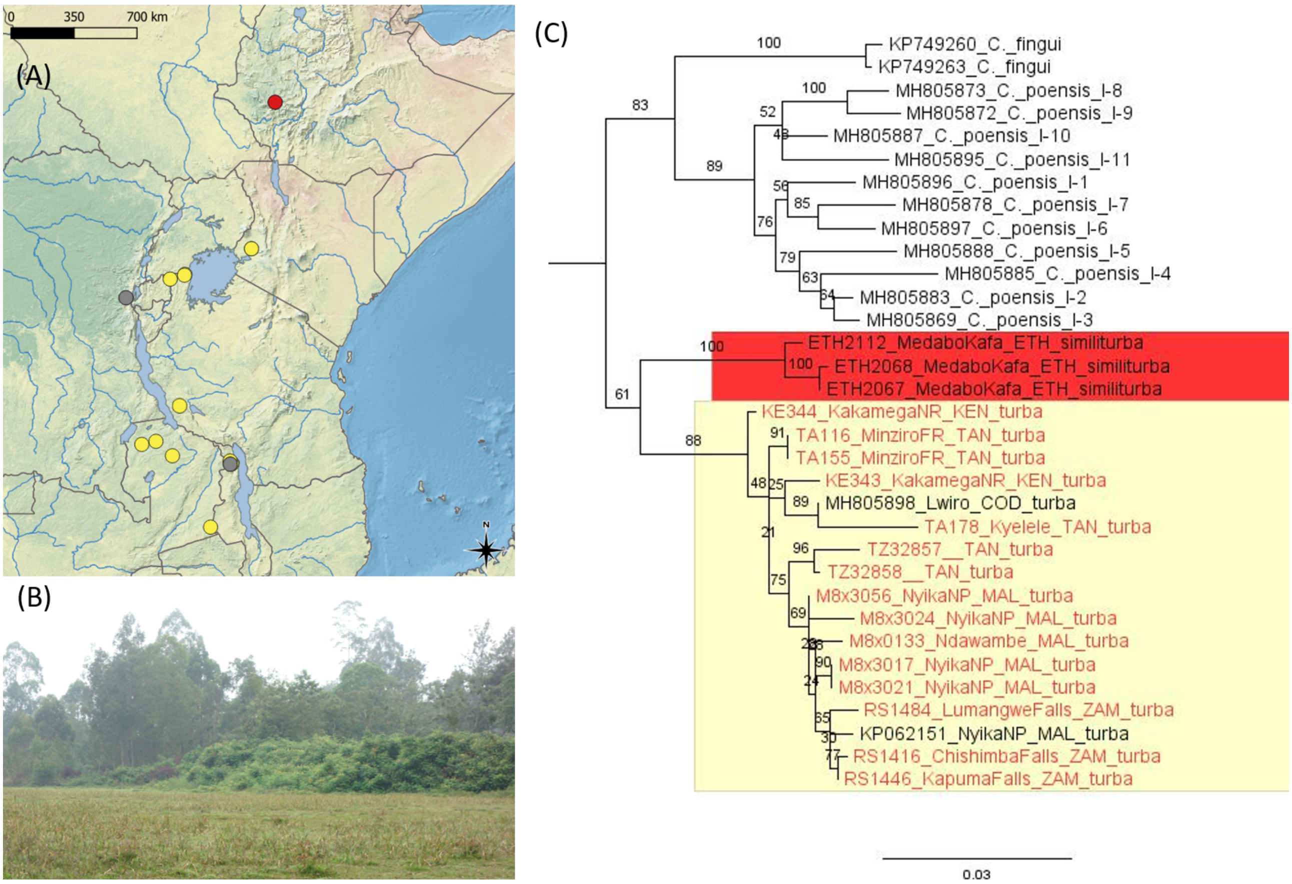

Fig. 2. (A) Distribution of *Crocidura similiturba* sp. nov. (red point) and *Crocidura turba* (yellow points – new localities of specimens genetically confirmed in this study; grey points – localities previously reported by Nicolas et al. 2019). (B) Habitat of *C. similiturba* sp. nov., close to Medabo village (Kafa zone, south-western Ethiopia). Currently this represents the only known locality of the species. (C) Phylogenetic tree of the Central and East African part of the *Crocidura poensis* species complex (sensu Nicolas et al. 2019) estimated by maximum likelihood analysis of cyt*b* sequences. Sequences of *C. similiturba* sp. nov. are highlighted in red, and those of its sister species *C. turba* in yellow background. New sequences of *C. turba* are shown in red, GenBank sequences are in black. The West African species of the complex (lineages IV-IX sensu Nicolas et al. 2019) and more distant outgroups are not shown.

by long bristle hairs. Dorsal pelage blackish-brown (Fig. 1A), hairs grey at base, blackish-brown on most of its length at tip. Length of dorsal hair 6 mm. Ventral hairs blackish, hairs dark grey at base, blackish-brown at tip. Dorsal surface of forefeet pale grey, hindfeet moderately long (15.2-17.9 mm). Tail blackish-brown above and brownish-grey below, not appearing as bicoloured.

Skull long (CI 26.3 mm in the male holotype; 23.6 mm in the female ETH2112; see also Table 1) with a long and narrow rostrum (similar to *C. turba*), and relatively narrow maxillary, interorbital and braincase (Fig. 1B). Dorsal profile of skull almost straight. Nasals long and straight. Anterior opening of infraorbital canal small but visible in dorsal view. First upper incisor (I1) relatively small in size, talon reduced. Its lateral cingulum weak and extending down as a thin ridge to the base. First upper antemolar (A1) twice as large as the following two antemolars, in occlusal view, the tooth is about twice as long as wide. The second and third upper antemolars (A2, A3) are about 1/3 of the height of A1 (lateral view) and about half the size in occlusal view, their buccal cingula are very thin. The third upper antemolar (A3) almost in contact with the parastyle of P4. The parastyle of the fourth upper premolar (P4) is weak and barely visible in side view. M1 and M2 are much wider than long and M3 is relatively short and narrow. Mandible weak, with a long and narrow angular process and a small coronoid process. The first lower incisor (i1) has no denticulation of the cutting ridge and an indistinct postero-buccal cingulum. The second incisor (i2) is long and narrow (occlusal view), about half of the tooth in contact with i1, and about 1/3 of its posterior border overlapping with p4. The second incisor has a broad cingulum. The lower p4 is small, but has the typical V – shape of its cutting blade. The molars m1 to m3 are of normal shape, all have a prominent cingulum. The posterior part of the third molar has a deep basin.

Table 1. Comparison of body mass (g) and external and cranial measurements (mm) of *Crocidura similiturba* sp. nov. and *Crocidura turba*. These data were used to perform the PCA multivariate analysis (Fig. 3A).

Voucher	ID	Species	Type	Sex, age	BM (g)	HB	T	HF (−n)	E	CI	PL	UTR	P4-M3	PGL	GW	MB	IO	HCC	COR	ML	LTR	m1-3	CH	CW
NMP 96961	ETH2068	*C. similiturba*	Holotype	M, ad.	21	102	67.5	17.9	10.4	26.31	11.18	11.63	6.03	6.55	10.43	7.51	4.79	5.75	5.87	16.30	10.63	4.91	2.68	2.46
NMP 97132	ETH2067	*C. similiturba*	Paratype	M, ad.	18	90	62	16.1	10.3	-	-	10.70	5.63	-	10.40	6.96	-	6.32	5.54	15.39	10.05	4.81	2.11	1.82
NMP 97133	ETH2112	*C. similiturba*	Paratype	F, ad.	13	86	57.5	15.2	10.1	23.60	10.29	10.26	5.36	6.30	9.79	6.52	4.46	5.58	4.94	14.31	9.60	4.41	1.78	1.61
	mean for *C. similiturba*				17.3	92.7	62.3	16.4	10.3	24.96	10.74	10.86	5.67	6.43	10.21	7.00	4.63	5.88	5.45	15.33	10.09	4.71	2.19	1.96
	SD for *C. similiturba*				4.04	8.33	5.01	1.37	0.15	1.92	0.63	0.70	0.34	0.18	0.36	0.50	0.23	0.39	0.47	1.00	0.52	0.26	0.46	0.44
	TA116	*C. turba*		M, ad.	19.5	87	65	17.7	11.2	25.02	10.68	10.93	6.18	7.11	10.31	7.98	4.93	6.17	5.95	14.97	10.02	5.11	-	-
	TA155	*C. turba*		M, ad.	17	-	52	14.7	10.4	23.07	9.64	10.12	5.67	6.44	9.83	7.04	4.51	5.26	5.22	14.01	9.46	4.62	-	-
ZFMK1999.0891		*C. turba*		M, ad.	-	90	45	14	8	22.60	9.39	9.84	5.47	6.44	9.57	6.94	4.44	5.88	5.15	13.94	8.80	4.60	2.25	1.74
	mean for *C. turba*				18.3	88.5	54	15.5	9.9	23.56	9.90	10.30	5.77	6.66	9.90	7.32	4.63	5.77	5.44	14.31	9.43	4.78	-	-
	SD for *C. turba*				1.77	2.12	10.15	1.97	1.67	1.28	0.68	0.57	0.37	0.39	0.38	0.57	0.27	0.46	0.44	0.58	0.61	0.29	-	-

Paratype ETH2067 is another male, but with a broken skull. In the remaining measurements (Table 1), it is as large as the holotype. It seems probable that this new species shows a case of sexual dimorphism in skull size, which is uncommon in shrews, although a few cases are known from Africa for *Crocidura fulvastra* Sundevall, 1843 (Hutterer 1984).

Comparisons: This is a large and dark shrew, comparable in general size to the Ethiopian taxon *Crocidura zaphiri* Dollman, 1915, which however is similar (if not identical) to *Crocidura olivieri* (Hutterer 1981). However, the skull of *C. zaphiri* and members of the *C. olivieri* group (sensu Jacquet et al. 2015) have a wide rostrum and maxillary while *C. similiturba* sp. nov. has a very narrow and slender rostrum. In this respect the new species is more similar to *Crocidura stenocephala* Heim de Balsac, 1979, a species endemic to the Kahuzi Mountains of Central Africa (Dieterlen & Heim de Balsac 1979) or to *C. turba* Dollman, 1915 from south-eastern Africa (Nicolas et al. 2019). The latter species, however, has relatively shorter tail and hindfeet (T 56 mm and HF 14.7 mm in average over 22 *C. turba* individuals *vs.* T 62.3 mm and 16.4 mm over three *C. similiturba* sp. nov.; Table 1, Table S1).

The PCA based on 13 linear measurements of *C. similiturba* sp. nov. and *C. turba* (skull measurements in Table 1) revealed non-overlapping separation along PC 2, that accounts for additional 7.50% (PC 1 for 88.13%) of the total variance (Fig. 3A). PC 2 is positively correlated with cranial widths (MB, r = 0.630 and basicranial PGL, r = 0.391), and with height of mandibular coronoid process (COR, r = 0.325). On the other hand, no differences were found along PC 1 which is positively correlated with lengths: CI, r = 0.663; ML, r = 0.421; PL, r = 0.311; UTR, r = 0.301; LTR, r = 0.283).

In general, *C. similiturba* sp. nov. can be distinguished from other large to medium-sized species of Ethiopian *Crocidura* by the following features: large body (mean HB 93 mm), dark, almost blackish colour, reduced (48%) pilosity of tail, long and narrow rostrum, long and slender skull (CI 26.3 mm in the male; 23.6 mm in the female).

Genetics: C. similiturba sp. nov. is placed genetically on a distinct branch sister to *C. turba* from south-eastern Africa (Fig. 2C). They form a monophyletic lineage within the *C. poensis* species complex, which further includes West-Central

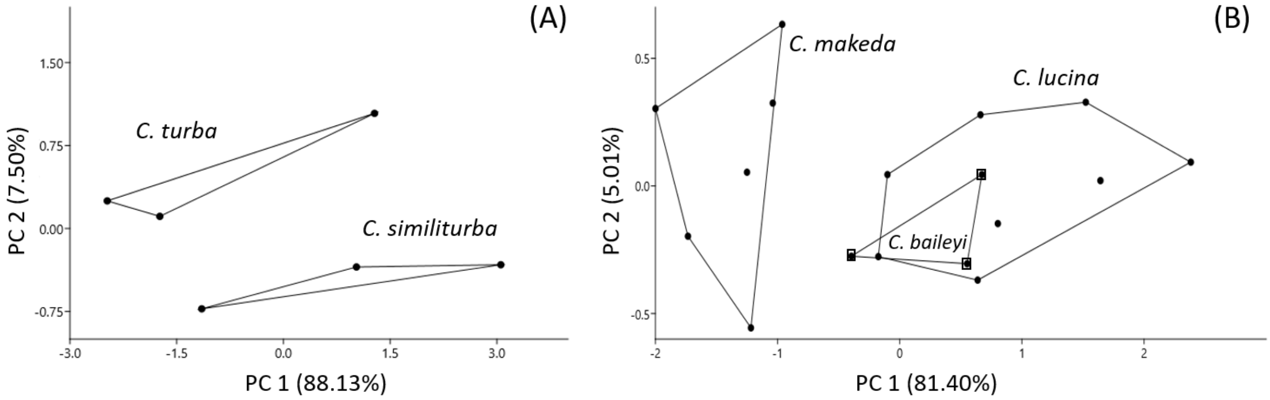

Fig. 3. Plots of the principal component analysis (PCA) on 13 cranial and mandibular linear measurements (first two PC axes shown). Comparison of *Crocidura similiturba* sp. nov. and *Crocidura turba* (A) and *Crocidura makeda* sp. nov., *Crocidura lucina* and *Crocidura baileyi* (B).

African *C. poensis* and *Crocidura fingui* (Fig. 2C, see also Nicolas et al. 2019). Being part of the so-called Afrotropical clade, subclade III (Dubey et al. 2008), this species complex is distributed mostly in western and central Africa with only two East-African representatives, *C. turba* (until now genetically confirmed from two localities by Nicolas et al. 2019; for new localities see Fig. 2A) and the Ethiopian endemic *C. similiturba* sp. nov.

Distribution: Only known from the type locality (Fig. 2), but may be more widespread in the understudied forest zone of south-western Ethiopia.

Habitat: All animals were captured near Medabo village in the Kafa zone, south-western Ethiopia. The habitat was an ecotone of dried wetland and forest with dense shrub and herb vegetation (Fig. 2B).

Etymology: The new species is similar (Latin: *similis*) to *C. turba*.

Comment: Osgood (1936) reported on two specimens in FMNH from "Njabara, Gojjam" in his paper on Ethiopian mammals, which he referred to *Crocidura turba nilotica* Heller, 1910. It is possible that he dealt with the new species described here, but Gojjam is in the northwest of Ethiopia, and not

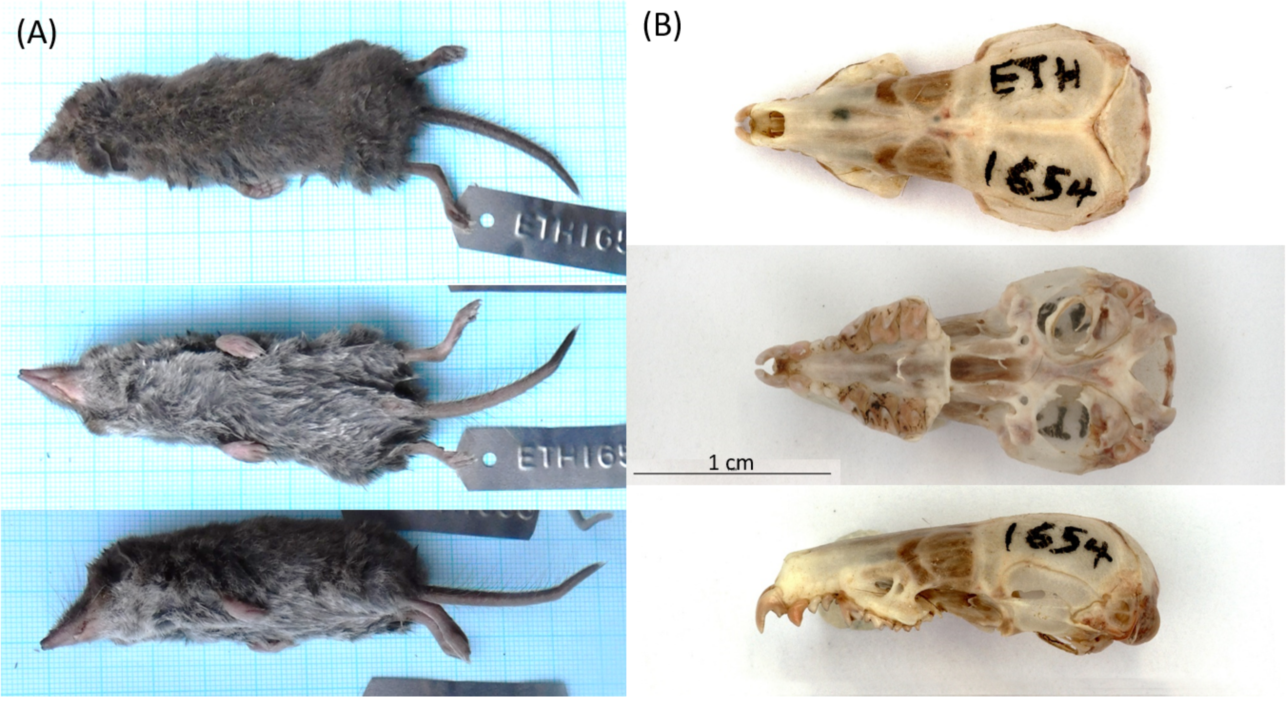

Fig. 4. (A) Dorsal (top), ventral (middle) and lateral (bottom) appearance of *Crocidura makeda* sp. nov. (specimen ETH1657, paratype). (B) Dorsal (top), ventral (middle) and lateral (bottom) view of the skull of *C. makeda* sp. nov. (specimen ETH1654, holotype).

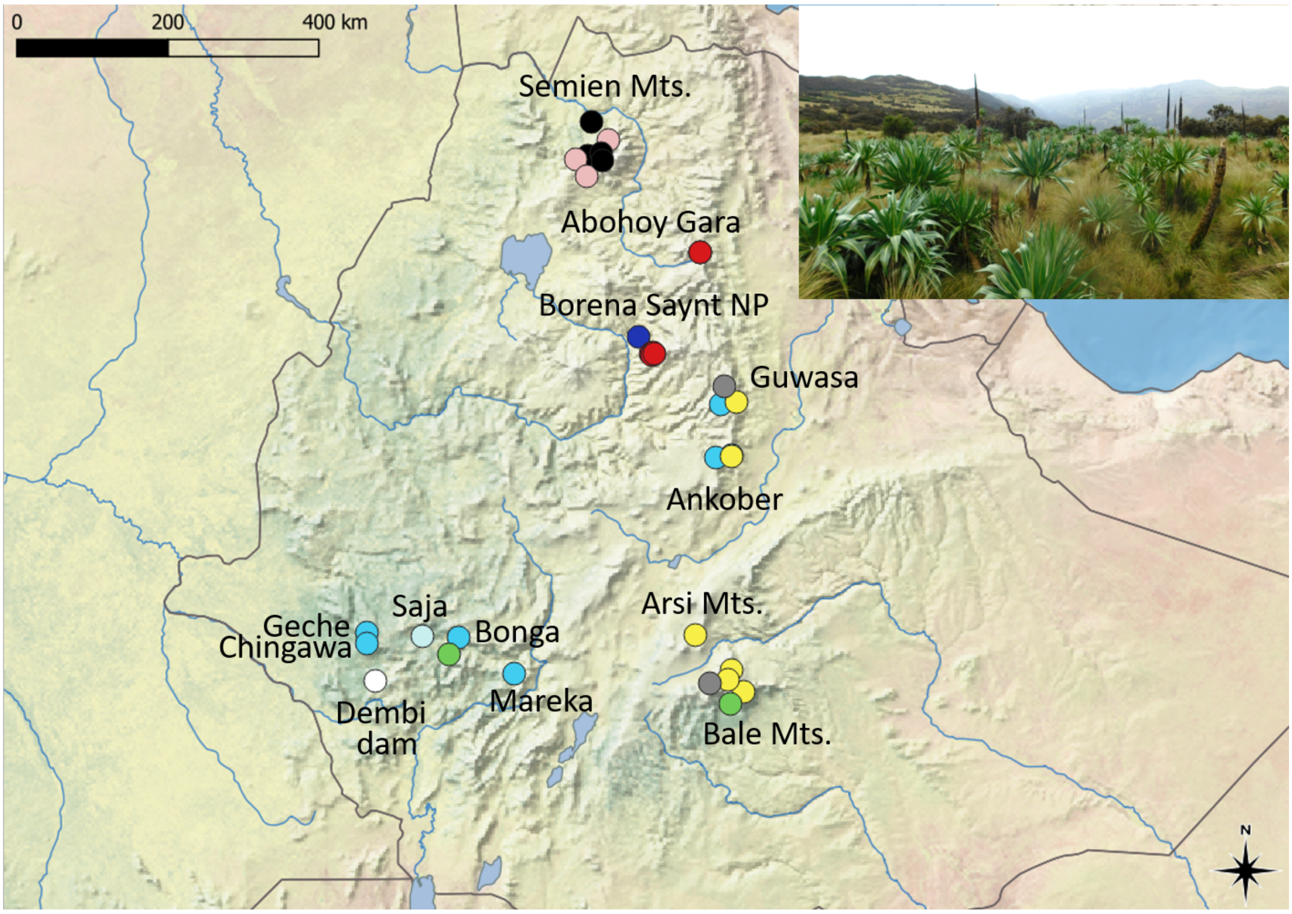

Fig. 5. Distribution map of selected *Crocidura* species from the so-called Old-World clade sensu Dubey et al. 2008, the East African subclade (all except *C.* cf. *bottegi*, are Ethiopian endemics): *C. makeda* sp. nov. (red points), *C. baileyi* (black), *Crocidura* sp. (sensu Craig et al. 2020, pink), *C.* cf. *bottegi* (grey), *C. lucina* (yellow), *C. harenna* (green), *C. macmillani* (white). Three shades of blue represent the three intraspecific lineages of mtDNA assigned to *C. yaldeni* (see Fig. 7); the populations in Ankober, Guwasa and Borena Saynt NP are morphologically and ecologically very different and likely represent cases of interspecific mtDNA replacement (see main text for detail). Inset figure: Afroalpine habitat of the type locality of *C. makeda* sp. nov. in the Borena Saynt National Park (ca. 3,500 m a.s.l.).

in the moist Kafa zone, which makes it less likely. The FMNH specimens still have to be re-studied.

Crocidura makeda sp. nov.

Holotype: NMP 96962 (field number ETH1654), male, collected by J. Bryja, M. Uhrová, D. Mizerovská and Y. Meheretu on 10 November 2018 (specimen in alcohol, skull extracted).

Type locality: Ethiopia, Amhara, Borena Saynt National Park, camp of the guards (10.8499 N, 38.7937 E). Bank of a small stream, *Erica* and grassland mosaic, 3,198 m a.s.l.

Paratypes: NMP 97134 (ETH1657, female; Fig. 4A), NMP 97135 (ETH1681, female), NMP 97136 (ETH1687, male), NMP 97137 (ETH1691, female), same locality as the holotype, but the latter three specimens from the altitude 3,514 m a.s.l. (Afroalpine grasslands with giant lobelia; Fig. 5).

Other specimens: Including the holotype and paratypes, 38 specimens were collected from Borena Saynt NP (3,121-3,514 m a.s.l.; November 2014 and November 2018) and 32 specimens from Abohoy Gara Community Conservation Area (CCA; 3,533-3,783 m a.s.l.; November 2014 and September 2019; Table S1). It was the most abundant shrew species at these localities.

Diagnosis: A small-sized, pale greyish-brown *Crocidura* with a whitish belly, similar in external measurements (HB 73.5, T 36-42 mm) to *Crocidura baileyi* Osgood, 1936 but smaller in cranial size (CI 21.0-21.6 mm).

Description: Small-sized *Crocidura* (HB 68-83 mm, weight 8.5-15 g) with a short tail (31-50 mm), 57% of head and body length. Dorsal hairs long (9 mm), dorsal pelage light greyish-brown, single hairs dark grey at base, light brown at tip. Ventral pelage whitish, hairs dark grey at base, pale–yellowish

Table 2. Comparison of body mass (g) and external and cranial measurements (mm) of the holotype and paratypes of *Crocidura makeda* sp. nov. from the type locality, and its related species *Crocidura lucina* and *Crocidura baileyi*. These data were used to perform the PCA multivariate analysis (Fig. 3B).

Voucher	ID	Species	Type	Sex, age	BM (g)	HB	T	HF (–n)	E	CI	PL	UTR	P4-M3	PGL	GW	MB	IO	HCC	COR	ML	LTR	m1-3	CH	CW
NMP 96962	ETH1654	*C. makeda*	Holotype	M, ad.	10.5	73	46	14.3	10	21.01	8.85	9.21	5.11	6.73	9.49	6.65	4.64	5.51	4.67	12.66	8.58	4.45	1.71	2.14
NMP 97134	ETH1657	*C. makeda*	Paratype	F, ad.	9.7	72	42	14.6	9.4	20.99	9.18	9.51	5.22	6.77	9.27	6.30	4.49	5.38	4.86	13.13	8.85	4.48	1.53	2.10
NMP 97135	ETH1681	*C. makeda*	Paratype	F, ad.	11	81	40	14.4	10.3	21.37	9.40	9.62	5.25	6.90	9.89	6.73	4.81	5.72	4.87	13.17	8.74	4.31	1.87	2.06
NMP 97136	ETH1687	*C. makeda*	Paratype	M, ad.	10	72.6	43.3	14.2	-	21.60	8.83	9.78	5.31	6.59	9.41	6.49	4.57	5.29	4.57	13.50	8.96	4.47	1.46	1.90
NMP 97137	ETH1691	*C. makeda*	Paratype	F, ad.	11.3	72	44.2	14.2	8.6	21.29	9.16	9.53	5.10	6.92	9.85	6.81	4.81	6.36	4.88	13.38	8.97	4.31	-	-
	ETH1183	*C. makeda*		-	11	75	34	14.8	7.3	20.99	9.00	9.60	5.59	6.58	9.80	6.55	4.90	5.69	5.17	13.37	8.89	4.44	-	-
mean for *C. makeda*				-	10.6	74.3	41.6	14.4	9.1	21.21	9.07	9.54	5.26	6.75	9.62	6.59	4.70	5.66	4.84	13.20	8.83	4.41	1.64	2.05
SD for *C. makeda*				-	0.63	3.48	4.16	0.24	1.21	0.25	0.22	0.19	0.18	0.15	0.26	0.18	0.16	0.38	0.21	0.30	0.15	0.08	0.18	0.11
	ETH0161	*C. lucina*		M, ad.	13.5	83	42	15.7	10	23.46	9.99	10.41	6.07	7.49	10.75	7.54	5.44	6.20	5.46	14.47	9.78	5.03	-	-
	ETH0943	*C. lucina*		M, ad.	16	-	-	-	-	22.91	9.64	10.26	5.82	7.62	10.66	7.35	4.68	6.06	5.36	14.21	9.55	4.91	-	-
	ETH0944	*C. lucina*		F, subad.	13	-	-	-	-	22.26	9.98	10.19	5.77	6.77	10.02	6.89	5.22	6.05	4.91	14.11	9.46	4.83	-	-
	ETH1776	*C. lucina*		M, ad.	14	85	47	16.6	-	22.58	9.68	10.12	5.76	6.73	10.32	7.19	4.96	5.87	5.28	14.00	9.27	4.76	-	-
	ETH1781	*C. lucina*		M, ad.	13	80	50	15.3	9.5	22.04	9.37	9.91	5.78	6.78	9.74	6.86	4.81	5.69	5.08	13.48	9.23	4.82	-	-
	ETH1864	*C. lucina*		M, ad.	13	85	44	15.8	12	22.53	9.39	9.98	5.74	7.10	10.37	7.30	5.11	5.86	5.46	13.65	9.09	4.81	-	-
	ETH1913	*C. lucina*		M, ad.	13	87	49	15.9	11.1	22.94	10.06	10.30	5.74	7.57	10.26	7.37	5.01	5.93	-	14.58	9.43	4.68	-	-
	ETH1914	*C. lucina*		M, ad.	13	83	47	15.8	9.6	21.98	9.17	9.87	5.62	7.10	9.62	7.06	5.01	5.87	5.28	13.74	9.12	4.55	-	-
mean for *C. lucina*				-	13.6	83.8	46.5	15.9	10.4	22.59	9.66	10.13	5.79	7.15	10.22	7.20	5.03	5.94	5.26	14.03	9.37	4.80	-	-
SD for *C. lucina*				-	1.05	2.40	3.02	0.42	1.08	0.50	0.33	0.20	0.13	0.37	0.40	0.24	0.24	0.16	0.20	0.39	0.23	0.14	-	-
	ETH0580	*C. baileyi*		M, ad.	11.2	87	45	15.6	9.5	22.61	9.31	9.90	5.63	7.03	10.23	6.90	4.85	5.95	5.61	14.15	9.17	4.56	-	-
	ETH0592	*C. baileyi*		-	10.3	72	48	14.8	11.1	22.63	9.60	10.04	5.57	6.81	10.00	6.83	5.04	5.81	5.31	13.89	9.32	4.67	-	-
	ETH0593	*C. baileyi*		-	9.9	78	43	14.4	10.4	21.92	9.11	9.89	5.60	6.69	9.74	6.76	5.00	5.62	5.12	13.68	9.01	4.48	-	-
mean for *C. baileyi*				-	10.5	79	45.3	14.9	10.3	22.39	9.34	9.94	5.60	6.84	9.99	6.83	4.96	5.79	5.35	13.91	9.17	4.57	-	-
SD for *C. baileyi*				-	0.67	7.55	2.52	0.61	0.80	0.40	0.25	0.08	0.03	0.17	0.25	0.07	0.10	0.17	0.25	0.24	0.16	0.10	-	-

white at tip (Fig. 4A). Dorsal surface of fore- and hindfeet whitish. The tail is dark grey-brown above and paler below. Bristle hairs are long, dark-grey at base, pale-grey at tip and present along almost the full length (80%) of the tail. External ears visible, but embedded in long pelage. Dorsal surface of fore- and hindfeet whitish, hindfoot short (14.2-14.8 mm; Table 2, Table S1).

Skull short (CI 21.0-21.6 mm) with a short and narrow rostrum, maxillary wide, almost as wide as braincase, interorbital wide (Fig. 4B). Dorsal profile of skull elevated at braincase. Nasals short. Anterior opening of infraorbital canal barely visible in dorsal view. First upper incisor (I1) relatively long for the skull size, talon small. Its lateral cingulum weak and extending down as a thin ridge to the base. First upper antemolar (A1) twice as large as the following two antemolars, in occlusal view, the tooth is about twice as long as wide. The second and third upper antemolars, (A2, A3) are about 1/3 of the height of A1 (lateral view) and about half the size in occlusal view, their buccal cingula are very thin. The third upper antemolar (A3) overlaps slightly with the parastyle of P4. The parastyle of the fourth upper premolar (P4) is small but prominent in side view. M1 and M2 are much wider than long, and M3 is relatively robust. Mandible short and with a high coronoid process, and a medium-sized angular process. The first lower incisor (i1) has no denticulation of the cutting ridge and a narrow postero-buccal cingulum. The second incisor (i2) is small but long and narrow (occlusal view), about two thirds of the tooth are in contact with i1, and about 1/3 of its posterior border is overlapping with p4. The second incisor has a narrow cingulum. The lower p4 is small, but has the typical V – shape of its cutting blade. The molars m1 to m3 are of normal shape; all have narrow cingula. The posterior part of the third molar has a deep basin.

Variation: Specimens from the type series are uniformly coloured. All qualitative characters are relatively homogeneous, and no sexual dimorphism was observed. Specimens from Abohoy Gara (CCA) have shorter tails (35-36 mm).

Comparisons: This is a small shrew, comparable in external size (HB 68-83 mm, T 31-50 mm) to *C. baileyi* Osgood, 1936 (HB 72-93 mm, T 43-48 mm; Osgood 1936; Table 2), but smaller in average cranial size than the latter (*C. makeda* sp. nov., CI 21.0-21.6 mm; *C. baileyi*, CI 21.9-22.7 mm; Osgood 1936; Table 2). Larger than the following Ethiopian Afromontane-Afroalpine species: *Crocidura bottegoides* Hutterer & Yalden, 1990; *Crocidura bottegi* Thomas, 1898; *Crocidura* cf. *hildegardeae* Thomas, 1904; *Crocidura harenna* Hutterer & Yalden, 1990; *Crocidura phaeura* Osgood, 1936; but smaller than *Crocidura afeworkbekelei* Lavrenchenko et al., 2016; *Crocidura lucina* Dippenaar, 1980; *Crocidura macmillani* Dollman, 1915; *Crocidura glassi* Heim de Balsac, 1966 and *Crocidura yaldeni* Lavrenchenko et al., 2016. The values of CI for the first group of species range between 14.3 and 20.6 mm and for the second group between 21.8 and 27.2 mm (Dippenaar 1980, Hutterer 1981, Hutterer & Yalden 1990). The values for *C. makeda* sp. nov. lie between the two groups.

The PCA based on 13 linear measurements of *C. makeda* sp. nov. and similar *C. lucina* and *C. baileyi* (skull measurements in Table 2) revealed a clear non-overlapping separation of the new species from the others along the most explanatory PC 1, that accounts for 81.40% (PC 2 for 5.01%) of the total variance (Fig. 3B). This first component is positively correlated with skull lengths: condylo-incisive length (CI, r = 0.595) and mandible length (ML, r = 0.380). Therefore, *C. makeda* sp. nov. can be distinguished from its sister and similar *C. lucina* and *C. baileyi* by its significantly shorter skull (CI mean ± SE: 21.21 ± 0.10 mm *vs.* 22.59 ± 0.18 and 22.37 ± 0.23 mm; ML: 13.20 ± 0.12 mm *vs.* 14.03 ± 0.14 and 13.91 ± 0.14 mm, respectively). For comparison of the cranium and mandible morphology between *C. makeda* sp. nov. and its sister species on the mtDNA tree, *C. lucina,* see Fig. 6.

Genetics: In a cyt*b*-based phylogenetic tree (Fig. 7), the new species forms a monophyletic clade, sister to *C. lucina* known uniquely from Ethiopia on both sides of the Great Rift Valley (Bale + Arsi Mountains on the east and Ankober + Guwasa on the west; Fig. 5). Both species are part of the so-called Old World clade (Dubey et al. 2008), specifically its Afrotropical lineage that includes most of other *Crocidura* species endemic to the Ethiopian Highlands (Fig. 7, see also Lavrenchenko et al. 2009). Furthermore, this lineage includes an East African *C. bottegi* (known from Ethiopia as well) and a widely distributed East African lineage, composed of *Crocidura monax*, *Crocidura fumosa*, *Crocidura munissii*, *Crocidura mdumai*, *Crocidura newmarki*, *Crocidura usambarae*, *Crocidura tansaniana*, *Crocidura montis* and the only Ethiopian species *C. macmillani* (Fig. 7). Shrews of this clade

Fig. 6. Dorsal, ventral and lateral view of the cranium and dorsal and lateral view of the mandible of *Crocidura makeda* sp. nov. (specimen ETH1654, holotype) and *Crocidura lucina* (specimen ETH0943).

differ from the other sub-Saharan species (i.e. from the Afrotropical clade sensu Dubey et al. 2008) not only by mitochondrial genetics, but also by chromosomal numbers: Old World clade representatives having 2n = 28-36 *vs.* about 50 chromosomes in species of the Afrotropical clade (Lavrenchenko et al. 2016).

Distribution: Currently known only from Borena Saynt NP (3,121-3,514 m a.s.l.) and from Abohoy Gara CCA (3,533-3,783 m a.s.l., part of Mount Abuna Yosef; Fig. 5). In both mountain ranges it represents the most abundant shrew species, regularly captured in various Afromontane habitats.

Habitat: Mosaic of Afromontane grasslands with volcanic rocks, small shrubs (*Erica*, *Hypericum*) and *Lobelia* sp. (Fig. 5). These habitats, although declared as conservation areas, are threatened by overpopulation (Tsegaw 2016).

Etymology: Species named for Makeda, the Ethiopian Queen of Sheba. The specific name is a noun in apposition.

Other interesting records of Ethiopian shrews

Crocidura cf. *bottegi* Thomas, 1898

Four specimens from two localities: three from Guwasa C.C.A. (10.29385 N, 39.80034 E) at an elevation of 3,320 m a.s.l. in a mosaic of Afroalpine habitats and *Erica* shrubs and one (ETH1094) from Sodota (Bale Mountains, 6.9904 N, 39.7015 E) at 3,507 m a.s.l. (Fig. 5). The species seems to be a typical Afroalpine specialist, with exactly the same distribution as an Afroalpine rodent *Stenocephalemys albocaudatus* (Mizerovská et al. 2020). In body measurements (Table S1) and cranial size (ETH1857 – male: CI 14.91, UTR 6.44, MB 4.48, IO 3.19, GW 7.02, PGL 4.83, HCC 4.17, LTR 5.66, COR 3.53; ETH1859 – female: CI 14.94, UTR 6.39, MB 4.56, IO 3.27, GW 6.76, PGL 5.05, HCC 3.9, LTR 5.98, COR 3.44), the specimens are similar to *C. bottegi*. However, older specimens of these tiny shrews in the Natural History Museum London (NHM 1972.381 from near Baco, 1937.2.24.26 from Dangila, 40 mi S Lake Tana and 1898.2.5.6 from Lake Margharita) measured by Hutterer & Yalden (1990) have significantly shorter tails (29-30 mm) than the present specimens (40-42 mm). There are no sequences available for NHM specimens, and therefore the problem of their conspecificity with the new Ethiopian specimens cannot be solved at present.

Crocidura harenna Hutterer & Yalden, 1990

Since the species description by Hutterer & Yalden (1990), only an additional eight specimens (three of which are cytogenetically characterized) have

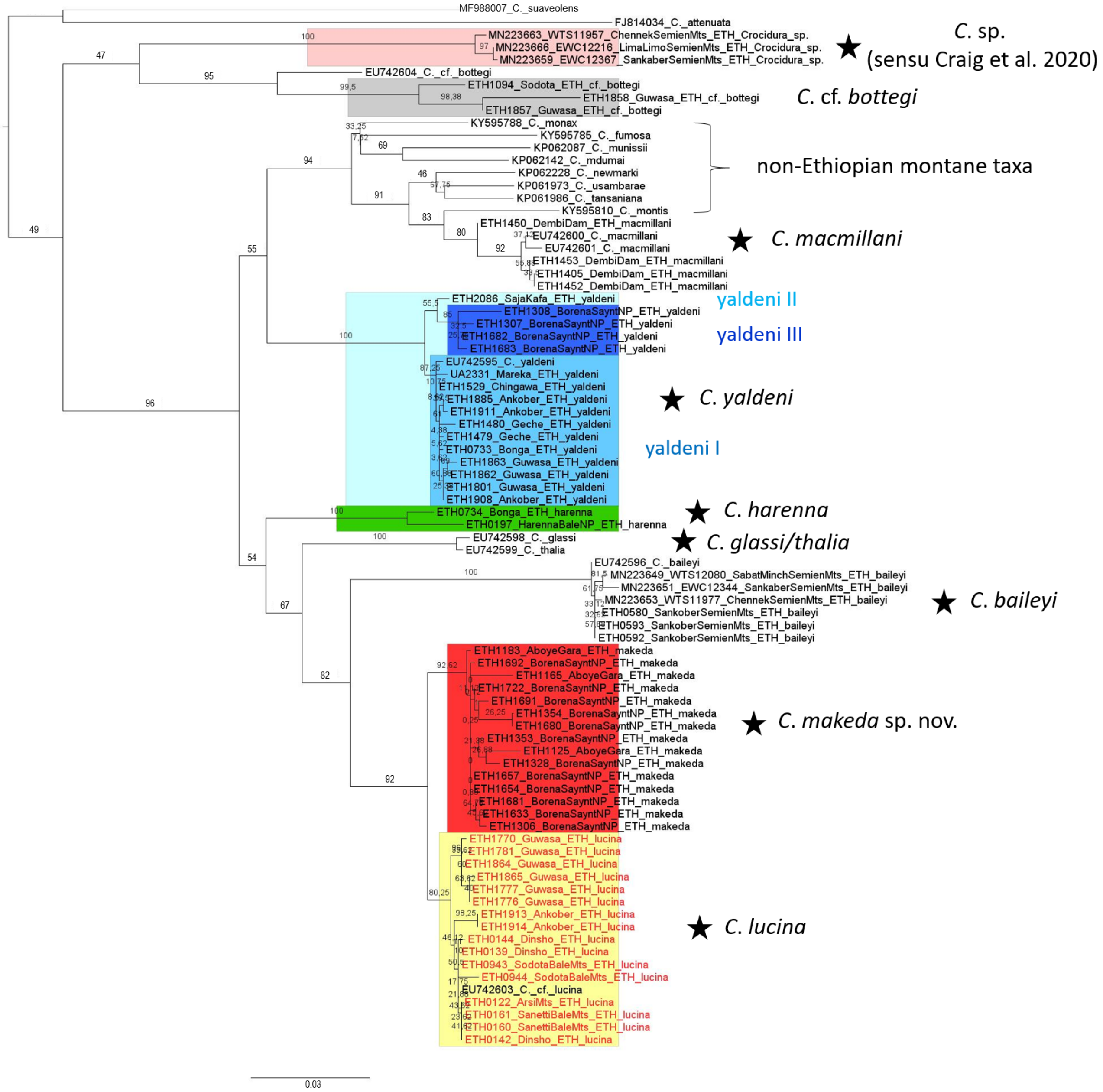

Fig. 7. Phylogenetic tree of *Crocidura* species from the Old World clade, the East African subclade (sensu Dubey et al. 2008), that comprises most of the Ethiopian endemics (marked with black stars; except the nearly endemic *C.* cf. *bottegi*). The phylogeny was reconstructed by maximum likelihood analysis of cyt*b* sequences. Background colours of Ethiopian species correspond to the distribution points shown in Fig. 5. Note that three shades of blue represent the three intraspecific lineages of mtDNA assigned to *C. yaldeni;* however, the populations in Ankober, Guwasa and Borena Saynt NP are morphologically and ecologically very different and likely represent cases of interspecific mtDNA replacement (see main text for detail). *C. suaveolens* and *C. attenuata* sequences were used as outgroups.

been collected in the Harenna forest in 1995 (Lavrenchenko et al. 1997). Here we present two specimens collected in the Harenna forest (Bale Mountains) on 7 November 2012 (ETH0197) and at Chara, 5 km west of Bonga, at 2,407 m, on 27 November 2012 (ETH0734). Both have a hairy tail covered with long bristles over 80% of its length. The new records show that the species is not confined to the Harenna forest but also occurs on the western side of the Rift Valley (Fig. 5).

Crocidura macmillani Dollman, 1915

Dembi Dam, Kite, Fanika Village (6.9796 N, 35.4958 E), 1,254 m (ETH1405, ETH1450, ETH1452, ETH1453). On the cyt*b* tree they cluster together with *C. macmillani* sequences from Lavrenchenko et al. (2009; Fig. 7), suggesting that the distribution of the species is limited to the forest zone of south-western Ethiopia (Fig. 5). It forms the only Ethiopian species in the *C. monax* species complex (see also Sabuni et al. 2018). Tails are very hairy (71% mean pilosity, 66-75%, n = 4).

Crocidura yaldeni Lavrenchenko et al., 2016

This large species was recently described on the basis of four specimens collected in the Beletta forest at 1,900 m a.s.l. (Lavrenchenko et al. 2016). Here we record new specimens with mtDNA of *C. yaldeni* from several localities of two different regions, elevations and habitat types. Six specimens morphologically very similar to the type series were collected in forests in south-western Ethiopia (near the type locality) at altitudes 2,010-2,407 m a.s.l. (localities Saja, Bonga, Chingawa, Geche and Mareka). An additional 25 specimens with almost identical mtDNA come from Afromontane habitats (*Erica* forest and grasslands with *Lobelia*) in central-northern Ethiopia at 3,121-3,514 m a.s.l. (7 specimens from Ankober, 7 from Guwasa and 11 from Borena Saynt NP; Fig. 5). They are smaller and resemble *Crocidura thalia* morphologically. However, a substantial level of intraspecific mitochondrial genetic variation has been recovered that does not correspond to these two geographical and morphological groups. Three main lineages separate i) an individual from Saja village (Kafa zone) from south-western forests (ETH2086, lineage "yaldeni II"); ii) individuals from an Afroalpine habitat in the Borena Saynt NP (lineage "yaldeni III"); and iii) all other localities from both south-western forests and Afroalpine localities in Ankober and Guwasa (lineage "yaldeni I"; Figs. 5, 7). This pattern might be explained by historical mitochondrial introgression of mtDNA of *C. yaldeni* from lower-elevation forests to the Afroalpine regions and the existence of a distinct hybridogenic taxon in mountains of central Ethiopia (Borena Saynt, Ankober, Guwasa), as has been recently documented for multiple rodent genera (*Arvicanthis* – Bryja et al. 2019b, *Stenocephalemys* – Bryja et al. 2018, Mizerovská et al. 2020). Understanding the evolutionary history of this complex will require further analyses based on genome-level data, as well as a comparison with a genetically and morphologically similar species, especially *C. thalia* (Dippenaar 1980, Hutterer 1981, Lavrenchenko et al. 2016).

Suncus sorella Thomas, 1897, stat. nov.

A single new specimen was obtained from south-western Ethiopia (ETH2097, Medabo village in

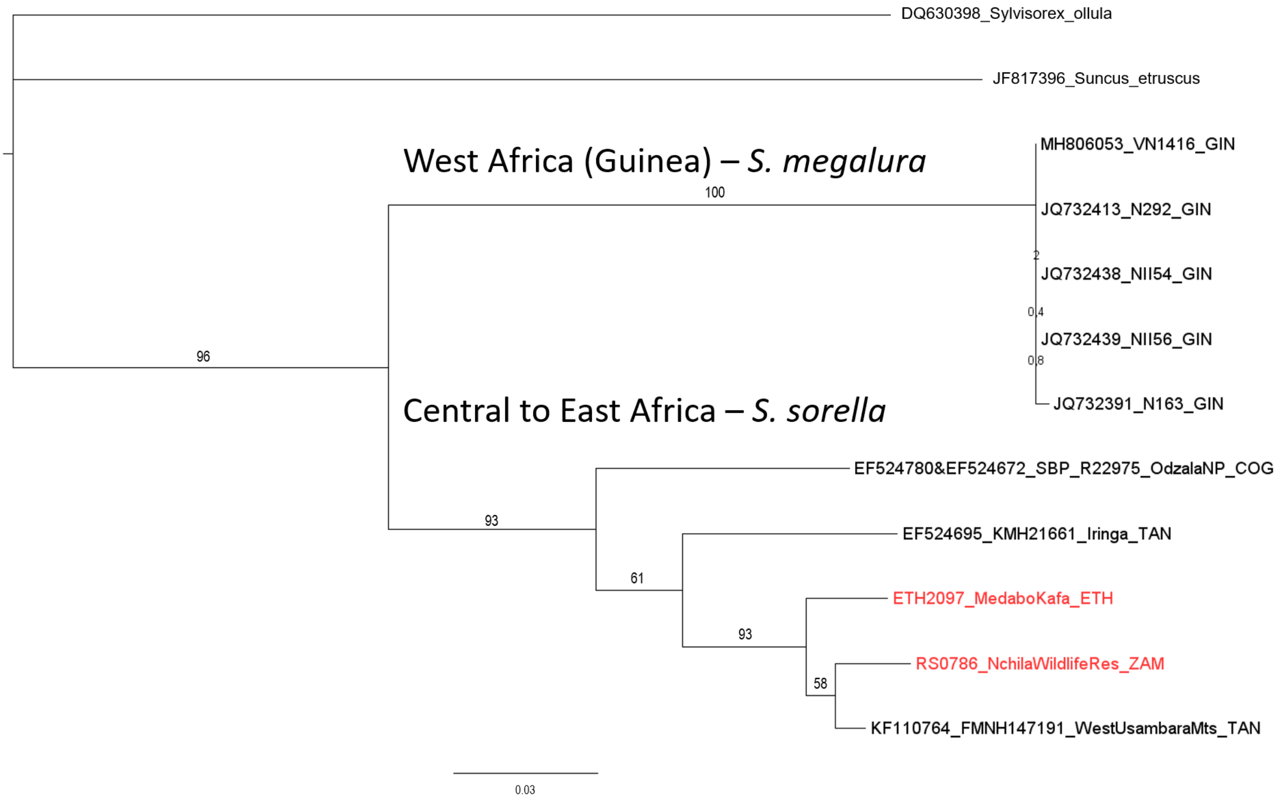

Fig. 8. Maximum likelihood phylogeny of *Suncus megalura* and *Suncus sorella* based on cytb sequences (new sequences in red and GenBank sequences in black). For each specimen the GenBank code is followed by specimen code, locality (if known) and country code. Country codes GIN = Guinea, COG = Republic of Congo, TAN = Tanzania, ETH = Ethiopia, and ZAM = Zambia. *Sylvisorex ollula* and *Suncus etruscus* sequences were used as outgroups.

the Kafa zone, December 2018) and from north-western Zambia (RS0786, Nchila Wildlife Reserve, April 2009; Table S1). A comparison of their sequences (Fig. 8) with those available in GenBank demonstrates that there are at least two taxa included in the clade that has been formerly called "*Sylvisorex megalura* Jentink, 1888" (Hutterer 1981, Yalden et al. 1996), confirming the previous results of Dubey et al. (2008). *Suncus megalura* occurs in West Africa, while *S. sorella* is known from the Congo Basin, Ethiopia, Tanzania and Zambia (Fig. 8). There are still not enough genetic data from Africa to draw the exact boundaries of their ranges, but it seems very likely that the forests in south-western Ethiopia have been colonized from the East African montane forest.

Diversity of shrews in Ethiopia

The most recent review of Ethiopian shrews by Lavrenchenko et al. (2016) lists two *Suncus* and 26 *Crocidura* species (including ten endemic species of the latter). Here, we add two newly described species (*C. similiturba* sp. nov. and *C. makeda* sp. nov.), known uniquely from Ethiopia. Together with a yet formally undescribed *Crocidura* sp. from the Simien Mountains (Craig et al. 2020), the updated Ethiopian shrew list consists of at least 31 species (two *Suncus* and 29 *Crocidura*) with 13 endemic *Crocidura* species. This checklist is certainly not final as there are indications for other taxonomically unresolved groups, including specimens that do not correspond to any recognized species (our unpublished data), suggesting a need for further sampling and comparative research (as also found in rodents (Bryja et al. 2019a); see also Ferguson et al. 2020). This high level of endemism is undoubtedly linked to the substantial heterogeneity of geomorphology and vegetation type in this mountainous African country (Lillesø et al. 2011, Bryja et al. 2019a), and also to the biogeographical position of the Ethiopian Highlands at the entrance to Africa from south-western Asia, notably the Arabian Peninsula. The phylogenetic relationships of *Crocidura* species show two major evolutionary clades that radiated in sub-Saharan Africa, the Afrotropical and the Old World clades (Dubey et al. 2008). Both comprise species currently distributed uniquely in Ethiopia. *C. similiturba* sp. nov. is the only endemic representative of the Afrotropical clade (subclade III sensu Dubey et al. 2008), whereas, remarkably, all the other Ethiopian endemics are members of the Old World clade (its East African subclade). They are all associated with mountain or forest habitats and characterized by a distinct karyological pattern (Lavrenchenko et al. 2009, 2016). Comparison with the Asian and Mediterranean members of the Old World clade suggests that a hypothesis of at least two independent colonisations of sub-Saharan Africa is likely (by the Afrotropical and the Old World clades, Dubey et al. 2008). The ancestors of one of the Old World subclades (the East African) moved to Africa through the Arabian Peninsula and entered the Ethiopian mountains, where they likely became isolated and adaptively radiated to establish the current endemic habitat specialists. Only a single sublineage of these Old World-East African species (the *C. monax* species complex) has continued southward to colonize other East African mountains (e.g. the Eastern Arc Mountains) and diversified in many Kenyan or Tanzanian montane endemics (e.g. *C. monax*, *C. usambarae*, *C. tansaniana*, *C. mdumai*, *C. munissii*, Stanley et al. 2015; Fig. 7). However, one member of this sublineage, *C. macmillani* (Sabuni et al. 2018, this study) is now known only from the moist habitats of south-western Ethiopia (including a new locality added in this study) and might represent the only species of this group returning to the north.

A similar biogeographical pattern to that documented for rodents appears to apply to shrews (Bryja et al. 2019a). For example, the forests of south-western Ethiopia are unique with a number of small mammals either endemic to this region or reaching the north-eastern edge of their distribution (*C. macmillani*, *C. phaeura*, *C. similiturba* sp. nov., *C. yaldeni*, *C. zaphiri*, *S. sorella* stat. nov. for shrews; *Otomys fortior*, *Aethomys hindei*, *Desmomys yaldeni*, *Lemniscomys macculus*, *Mylomys rex* or *Lophuromys brunneus* for rodents, Bryja et al. 2019a). Undoubtedly, a unique fauna is associated with the North-Ethiopian mountains (Simien Mountains, Abohoy Gara, Borena Saynt NP etc.) with endemic *C. baileyi*, *C. makeda* sp. nov., or *Crocidura* sp. (sensu Craig et al. 2020). Most of the montane localities (together with their fauna) are divided and isolated by the Great Rift Valley, which may not be as strong a barrier to migration as previously thought. A new record of *C. harenna* in forests of south-western Ethiopia (ETH0734 collected close to Bonga) shows a larger distribution of this species, previously known uniquely from the Harenna forest in the Bale Mountains (Fig. 5). A distribution on both sides of the Rift Valley is also reported here for *C. lucina* (Arsi and Bale Mountains *vs.* Guwasa and Ankober) and *C.* cf. *bottegi* (Bale Mountains *vs.* Guwasa) (see similar biogeographical patterns in Afromontane rodents and frogs, e.g. Freilich et al.

2014, Bryja et al. 2018, Bryja et al. 2019b, Mizerovská et al. 2020). The extraordinary Ethiopian diversity in geomorphology and vegetation types across an elevational gradient, and its unique position between the Arabian Peninsula, Nile river valley, south-eastern Sahara desert, Sudanian belt and Somalian deserts make this part of Africa an obvious biodiversity hotspot with all related consequences (Mittermeier et al. 2011). At the same time, the steeply increasing human population and overexploitation of natural resources make it one of the most endangered hotspots, requiring urgent science-based conservation action.

Acknowledgements

This study was supported by the Czech Science Foundation (projects no. 18-17398S and 20-07091J). The help of many people involved in the fieldwork is acknowledged, we thank especially D. Mizerovská, J. Šklíba, M. Uhrová, R. Šumbera, T. Aghová, E.W. Craig, J. Krásová, H. Konvičková, L.A. Lavrenchenko, M. Lövy, V. Mazoch, A. Ribas, W.T. Stanley, S. Šafarčíková, T. Zewdneh and J. Zima. All fieldwork complied with legal regulations in Ethiopia and sampling was carried out with the permission of the Ethiopian Wildlife Conservation Authority. D. Rohwedder (Bonn) helped to generate photos of shrew skulls. We thank A. Bryjová, D. Mizerovská, A. Hánová, M. Dianat and T. Aghová for the help with sequencing. Author contributions: A. Konečný and J. Bryja conceived the study, A. Konečný, Y. Meheretu and J. Bryja collected new material in the field, A. Konečný analysed genetic data, R. Hutterer and A. Konečný produced morphometric data and performed formal taxonomic descriptions, A. Konečný, R. Hutterer 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 specimens used for molecular (cyt*b* phylogeny), morphological and geographical analyses (https://www.ivb.cz/wp-content/uploads/JVB-vol.-69-2-2020-KonecnyA.-et-al.-Table_S1-1.xlsx).