



Diversity of shrews in Ethiopia, with the description of two new species of *Crocidura* (Mammalia: Lipotyphla: Soricidae)

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Abstract

Two new species of white-toothed shrews, *Crocidura afeworkbekelei* and *Crocidura yaldeni*, are described from southern Ethiopia. Comparisons are made with other species of *Crocidura* known to occur in Ethiopia. A list of 28 species of shrews known from Ethiopia is provided, 10 of which (including both newly described species) are currently considered to be endemic to Ethiopia. The endemic shrew fauna consists of forest and montane species known to occur within the altitudinal range of 1200–4050 m a.s.l. The remarkable number of endemic species of *Crocidura* shows that the Ethiopian Plateau is an important centre of diversity and adaptive radiation of the genus. Current cytogenetic and molecular data support the monophyly of most species of *Crocidura* endemic to Ethiopia.

Key words: biodiversity, taxonomy, morphometrics, endemism, Ethiopia, Afework Bekele, Derek Yalden

Introduction

The 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 4620 m a.s.l.; 40% of the country consists of highlands above 2500 m a.s.l. These extensive plateaus are bisected centrally by the Rift Valley, which is the major zoogeographical barrier within the country. In accordance with this geomorphological diversity, the Ethiopian fauna is characterised by a high level of endemism. At present, about 40 mammalian species are considered to be endemic to Ethiopia (Yalden & Largen, 1992; Yalden *et al.*, 1996; Lavrenchenko, 2003; Wilson & Mittermeier, 2011; Monadjem *et al.*, 2015), and we will add two further species to this list. The Ethiopian fauna of small mammals is particularly diverse. The family Soricidae is represented by 26 species known to occur in the country, 8 (28%) of which are endemic. Local endemism may be rather high: of the 6 species known from the Bale Massif, 4 are endemic (Hutterer & Yalden, 1990). In view of the fast habitat destruction in Ethiopia, taxonomic and evolutionary studies on Ethiopian small mammals are particularly urgent in order to target specific field conservation projects for endangered species. During extensive trapping sessions of small mammals in southern, western and south-eastern Ethiopia, the senior author collected an important series of shrews between 1986 and 2015. This collection includes undescribed species of shrews and also new records of species already known for Ethiopia. This paper presents descriptions of two new species and a brief review of the diversity of Ethiopian shrews.

Material and methods

Field work was carried out in the framework of the Joint Ethiopian-Russian Biological Expedition (JERBE). A

total of 275 shrews were collected in Ethiopia from 1986 to 2015. Specimens (mainly dry skins with skulls, some preserved in alcohol) were deposited in the Zoological Museum of the Moscow State University, Moscow (ZMMU). Comparative material and type specimens were examined in the Natural History Museum, London (BMNH), Field Museum, Chicago (FMNH), the Liverpool Museum (LIV), the Harrison Museum, Sevenoaks (HM), Zoological Research Museum Alexander Koenig, Bonn (ZFMK), Staatliches Museum für Naturkunde, Stuttgart (SMNS), and National Museum of Natural History, Paris (MNHN).

For the present study 39 newly collected skulls of 13 species were analysed (see Appendix 1). External body measurements (HB—head-body length, TI—tail length, HF (-n) and HF(+n)—hind foot length without and with claws, EL—ear length) were recorded in the field by the senior author. High-resolution images were employed for cranial and toothrow measurements. Our method based on digital photography and two-dimensional landmarks makes measurements on small objects easier and more gently than traditional tools such as calipers or binoculars (Hammer, 2002). All skulls and mandibles were scanned in ventral (skull) and lateral/medial (mandible) views using a flatbed scanner (Epson Perfection V300) with 2400 dpi resolution. The images were landmarked (Fig. 1) with tpsDig ver. 1.40 (Rohlf & Slice, 1990) three times for minimize of the "metering error". The analysis was performed on mean values of these replicates. IMP 7 (Sheets, 2001) was used to measuring by traditional frame: CI—condylo-incisive length, PL—hard palatine length, UAL—upper antemolar row length, P4L—P4 length (length of buccal side), M1L—M1 length (length of buccal side), M2L—M2 length (length of buccal side), M3W—M3 width (perpendicular to toothrow), M3L—M3 length (maximum transverse length of the tooth), UML—upper molar row length, P4s/d—inner distance between left and right P4 (level of the protoconus), ZYG—zygomatic process width, M3s/d—inner distance between left and right M3, PTL—postpalatine torus width, IO—interorbital width (level of ethmoidal foramina), NCW—posterior nasal cavity ("choanae" in Meester, 1963) width (level of ethmoidal foramina), OL—orbital length (distance between postpalatine torus margin and foramen ovale), PGW—postglenoid width (measured between lateral parts of the entoglenoid processes), GW—greatest width (maximum transverse diameter of the braincase), LAL—lower antemolar row length, MRW—width of mandibular ramus (distance between M3 and base of condylar process), MBL—mandibular body length (distance between mandibular foramen and incisive notch), COR—height of mandibular coronoid process, APL—angular process length (distance between mandibular foramen and caudal end of pr.), LML—lower molar row length; MBH—mandibular body height (level of the m1 posterior margin). These 25 measurements are illustrated in figure 1. Some of these cranial variables (MBL) and their combinations (UAL + P4L + UML, LAL + LML, P4L + UML) are modifications of measurements (mandible length, upper tooth row, lower tooth row, P4-M3 length, respectively) usually used in previous studies on taxonomy and systematics of shrews.

Material of each species analysed includes voucher specimens identified using molecular or karyological methods and used in morphometric analyses (see Appendix 2). Holotypes of the 13 taxa mentioned below in the comparisons were examined by RH. Cranial and dental nomenclature follows that of Meester (1963) (general skull morphology), Repenning (1967) (general mandible morphology), and Wible (2008) (special terms, not used by earlier authors). Dental nomenclature follows that of Butler *et al.* (1989) (special terms for lower teeth morphology), Dannelid (1998) (general terms), and Ziegler (2009) (special terms for upper and lower teeth morphology). We use also some special features applied by Lopatin (2006), such as: postparacrista; premetacrista with different parts. The terminology of the three upper unicuspid teeth of *Crocidura* is still not settled; Hutterer (2005a) called them I2, I3, and C. For the purpose of this paper, we simply apply the term antemolar. In the use of the term "Lipotyphla" we follow Asher (2005).

Shapiro-Wilk test implemented in the PAST ver. 2.04 (Hammer *et al.*, 2002) program detected an absence of conclusive evidence for sexual dimorphism in cranial variables within studied species, and we therefore combined sexes in all subsequent analyses. Principal component analyses (PCA) were performed on 25 cranial and mandibular linear measurements using the program PAST ver. 2.04 (Hammer *et al.*, 2002). Principal components were extracted from the variance-covariance matrix because the variables were measured in the same unit (mm). Results of the PCA executed on both raw (untransformed) and log-transformed metrical data were very similar and only the former are presented in the paper. The "Broken-stick model" was used to find statistically significant principal components (PCs), because "this method provided a good combination of simplicity of calculation and accurate evaluation of dimensionality relative to the other statistical approaches" (Jackson, 1993: 2211–2212). The components located above the "broken-stick" were considered significant. We used this method for defining the number of PCs, which were examined further in the analysis.

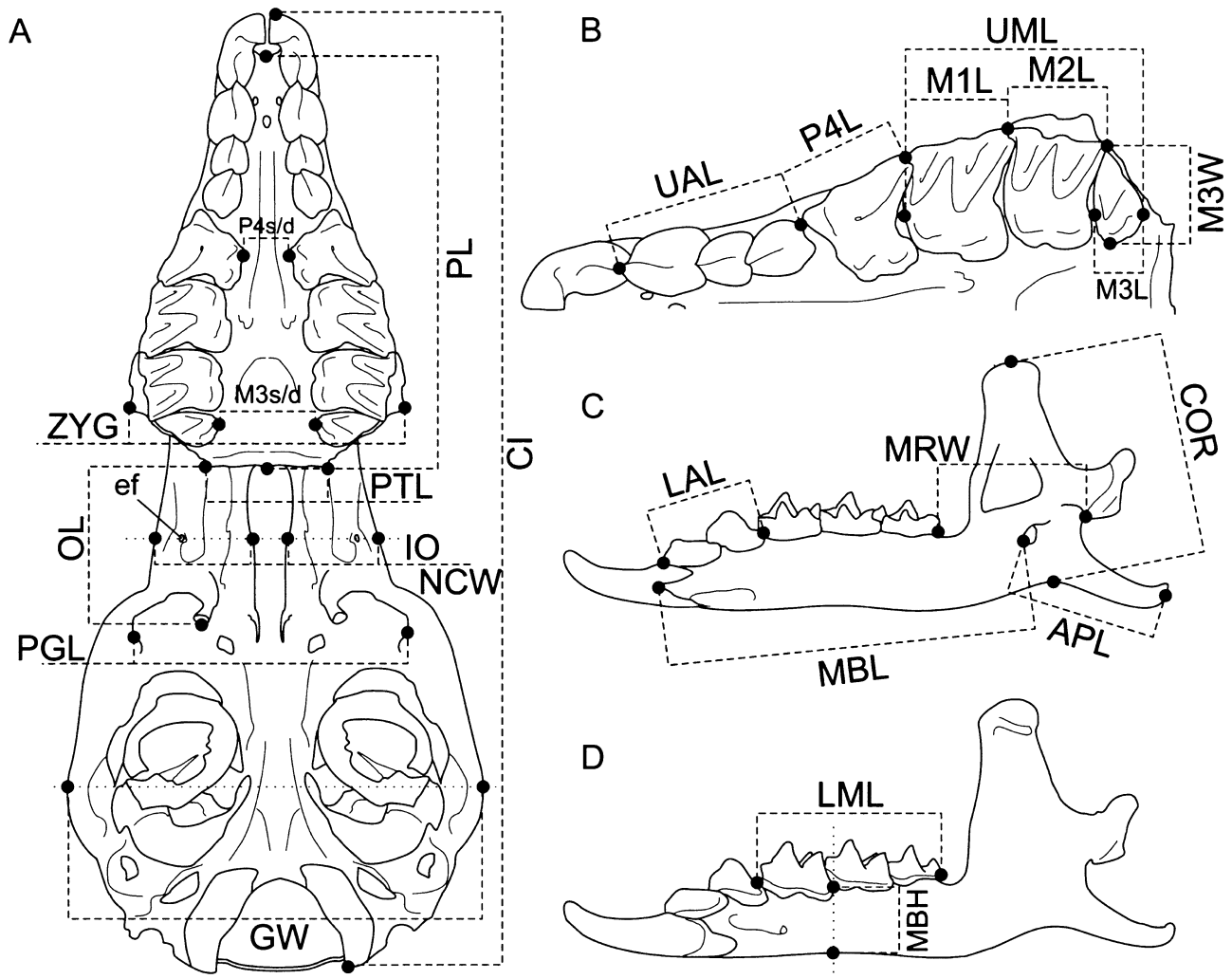


FIGURE 1. Diagrammatic images of the ventral view of the cranium of *Crocidura yaldeni* sp. nov. (A), occlusal view of the upper tooth row (B), medial (C) and lateral (D) views of the mandible, with landmark wireframe used for measuring. Measurement abbreviations see text; ef = ethmoidal foramen. Unscaled.

Results

Description of two new species of *Crocidura* from southern Ethiopia

Crocidura afeworkbekelei sp. nov.

Figs. 2A, 3A, 4A, 5A, 6A, 7; Table 1.

Crocidura lucina Dippenaar, 1980: Lavrenchenko *et al.*, 1997: 218 (partim)

Holotype. ZMMU S-162697; adult female, dry skin and skull; collector's number 189; collected by L.A. Lavrenchenko, 02 March 1995 (Figs 2, 3).

Type locality. Konteh Area of the Sanetti Plateau, Bale Mountains National Park, south-eastern Ethiopia, 06°51'N, 039°53'E, 4050 m a.s.l.

Paratypes. ZMMU S-162643 (adult female, body in ethanol, skull extracted, collector's number 187); ZMMU S-162644 (adult female, body in ethanol, skull extracted, collector's number 196); both specimens from the type locality, collected by L.A. Lavrenchenko, 01 March 1995.



FIGURE 2. Dorsal and ventral views of the cranium of *Crocidura afeworkbekelei* **sp. nov.** S-162697 (A), *C. glassi* S-164856 (B), *C. macmillani* S-166029 (C), *C. baileyi* S-172690 (D), *C. lucina* S-189286 (E). Scale 5 mm.

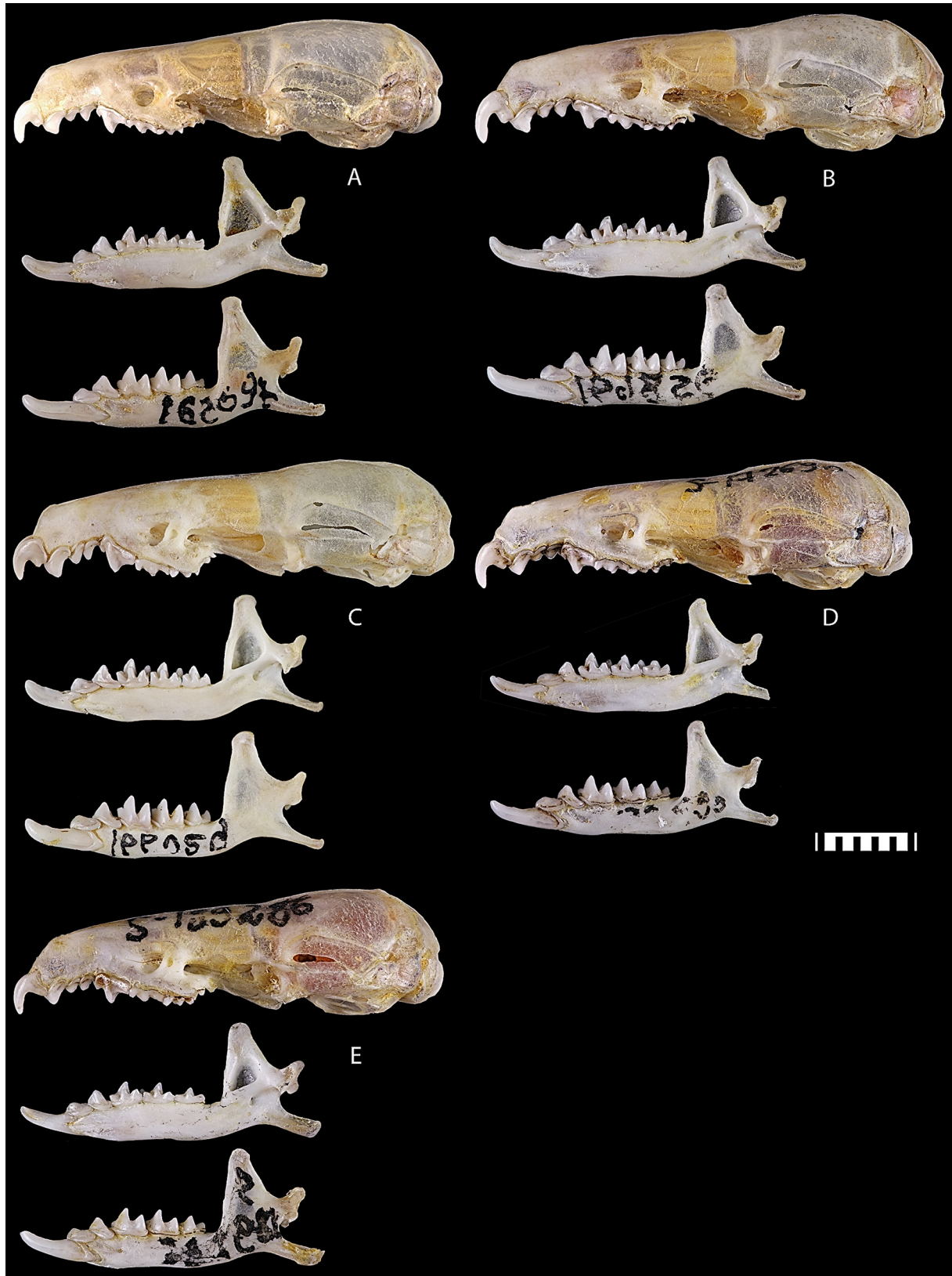


FIGURE 3. *Crocidura afeworkbekelei* sp. nov.; lateral views of the cranium, medial and lateral views of the mandible. Explanations as in figure 2.

Diagnosis. A small greyish-brown *Crocidura* similar in external measurements (HB) to *C. glassi* Heim de Balsac, and slightly larger than *C. lucina* Dippenaar, *C. baileyi* Osgood, and *C. macmillani* Dollman. Cranial size (CI) comparable on average to *C. lucina*, *C. baileyi* and *C. macmillani*, but smaller than *C. glassi* (Figs 2, 3).

Distinguished from these species by the following combination of characters: moderately short and uniformly colored tail, relatively long hindfoot, tapering outline of nasal aperture, first upper incisor with a simple talon, relatively small upper anteromolars (Fig. 4, A), convex posterior edge of the upper third anteromolar (Fig. 4, A-c), relatively short upper fourth premolar, gentle occlusal outline of the upper third molar (Fig. 6, A-a).

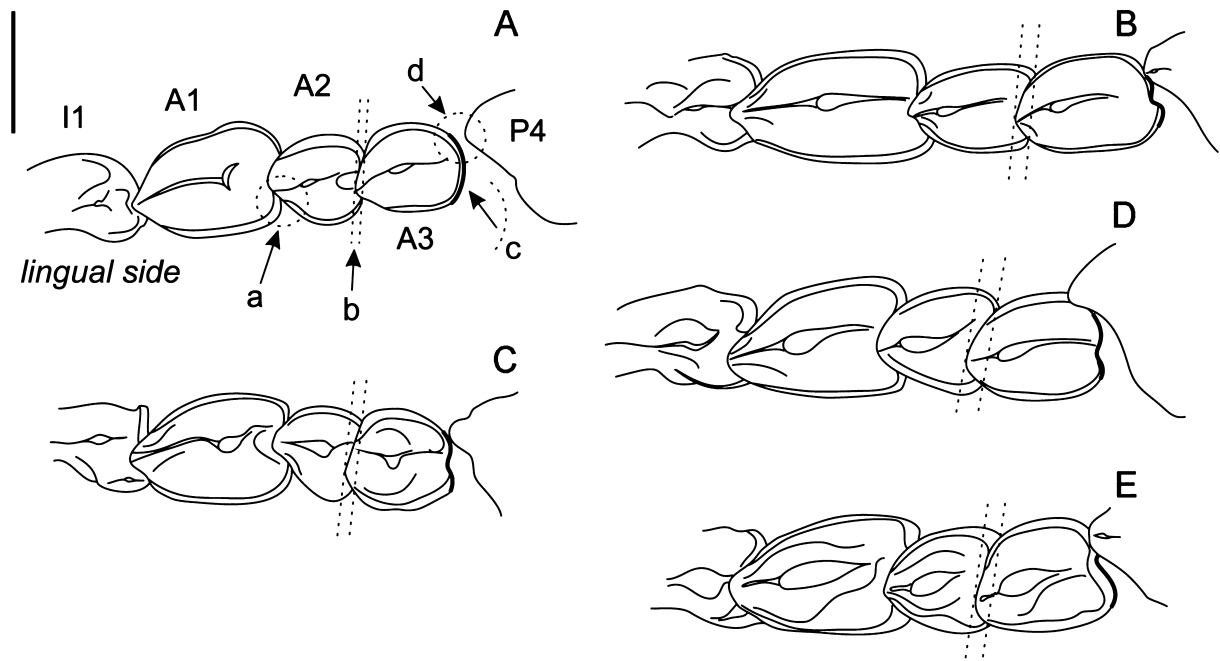


FIGURE 4. Upper anteromolar rows (occlusal view) of five Ethiopian *Crocidura*. A–E see figure 2. Specific characters of *C. afeworkbekelei* sp. nov.: a—the position of the anterior ridge of A2 relative to the postero-lingual cingulum of A1; b—A3 slightly overlapping A2; c—convex posterior edge of A3; d—A3 not in contact with the parastyle of P4. Scale 1 mm.

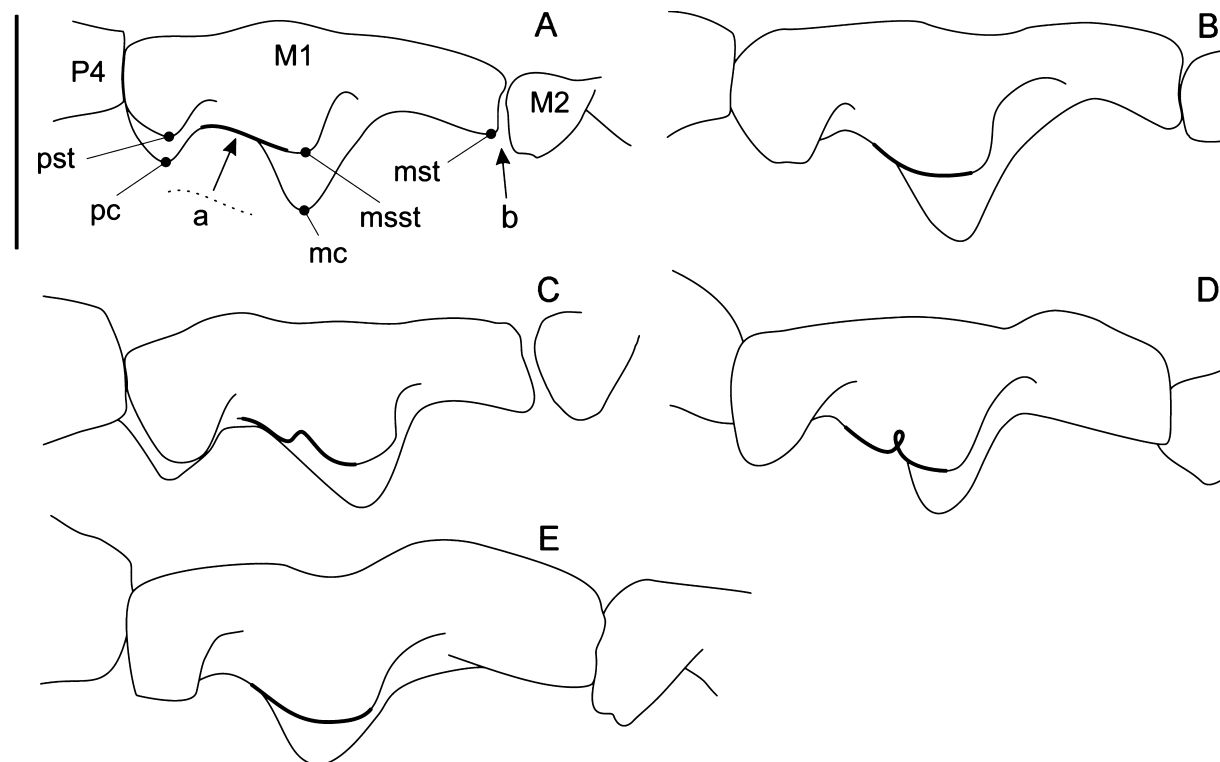


FIGURE 5. Upper M1 in lateral view of five Ethiopian *Crocidura*. A–E see figure 2; Abbreviations: pst = parastyle, pc = paracone, msst = mesostyle, mc = metacone, mst = metastyle. Specific characters of *C. afeworkbekelei* sp. nov.: a—postparacrista straight without incision; b—metastyle of M1 not connected to parastyle of M2. Scale 1 mm.

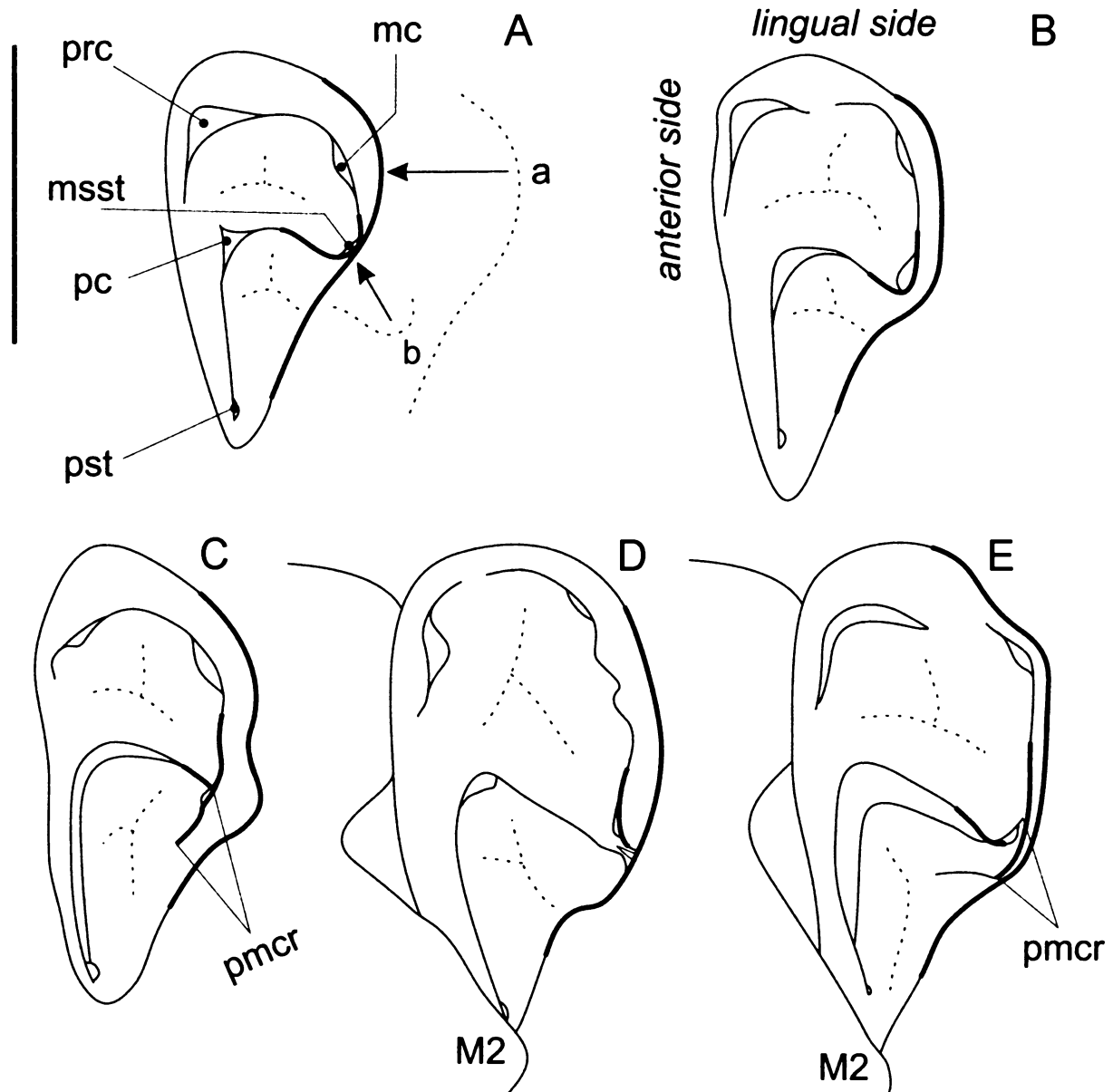


FIGURE 6. Upper M3 (in occlusal view) of five Ethiopian *Crocidura*. A–E see figure 2; Abbreviations: pmcr = developed mesostylar part of the premetacrista; prc = protocone; also see figure 5. Specific characters of *C. afeworkbekelei* sp. nov.: a—shape of the outline of the posterior edge; b—mesostylar part of premetacrista (pmcr) not developed.

Description. Relatively small-sized, head and body length 78–85 mm with a moderately short tail, ranging between 50.6–61.5% of head and body length (Table 1). Dorsal pelage greyish-brown; hairs grey at base, brown at tip. Ventral pelage grey; hairs grey at the base, pale-yellowish at tip. Dorsal surface of forefoot pale grey, hindfoot (19–21.7% of HB) yellowish-grey. Tail brown above and brownish-grey below (similar to *C. macmillani* and *C. baileyi*), not appearing as bicolored (as in *C. glassi* and *C. lucina*). Long bristle hairs are present throughout the tail. Skull (see Figs. 2, 3) with a moderately short and broad rostrum (similar to *C. macmillani*), and relatively broad maxillary and interorbital regions. The medial tip of the posterior margin of the nasal aperture is absent. Lacrimal foramen is at height of the M1–M2 joint. Mandible with a moderately broad body and a high and massive ramus. The oblong pterygoid spicule is moderately developed and lies below the margin of the upper sigmoid notch; the coronoid spicule is well-developed and inclined. Mandibular condyle articular surface is sub-triangular. Angular process with hooked tip.

First upper incisor (I1) relatively small in size (similar or slightly more than in *C. macmillani*), talon reduced. Its lateral cingulum is weak and extends dorsally no further than 2/3 of the I1 base height. The occlusal part of the

talon not well developed. First upper antemolar (A1) bigger than the following antemolars; the buccal face of the crown is undulated; the main cusp is slightly crested with indistinct basal prominence of the anterior ridge. The second upper antemolar (A2) is approximately 1/3 the height of A1 and half the height of the A3; the buccal cingulum is very broad; the antero-posterior axis in occlusal view is shifted lingually; the anterior ridge is in close contact with the postero-lingual cingulum of A1 (Fig. 4, A-a); A3 slightly overlapping A2 (Fig. 4, A-b). The posterior margin of the third upper antemolar (A3) is not in contact with the parastyle of P4 (Fig. 4, A-d); its posterior edge is convex (Fig. 4, A-c). The parastyle of the fourth upper premolar (P4) is well defined but falls short of A3; the upper outline in lateral view undulates with a visible mesial inflection; the tooth is sealed against the root by a cingulum that extends to the posterior edge of P4; the paracone possesses a hook-like shape. The first upper molar (M1) has a straight postparacrista (Fig. 5, A-a), its metastyle not connected to parastyle of M2 (Fig. 5, A-b). The third upper molar (M3) is relatively short and narrow; the posterior edge is not undulated (Fig. 6, A-a); in contrast to *C. macmillani* the mesostylar part of the premetacrista is not developed (see Fig. 6, A-b vs. C-pmcr). The first lower incisor (i1) has one faint denticulation on the cutting ridge and a well-marked postero-buccal cingulum, which extends into the upper half of the basis of this tooth. The second incisor (a1) is elongated; approximately half of the lower border of the tooth is in contact with i1; its posterior border is considerably (about 1/3) overlapped by the fourth lower premolar (p4). The basal prominence on the anterior ridge of p4 is present, but indistinct. The hypoconulids of the first (m1) and second (m2) lower molars are developed, but not visible from the medial side of the teeth (see Fig. 9 for description of *Crociodura yaldeni* **sp. nov.**). The crown base of the third lower molar (m3) is surrounded by a cingulum, which is interrupted below the hypoconid and not visible from the medial side of the tooth.

The chromosomal set of *C. afeworkbekelei* **sp. nov.** ($2n = 36$, $NFa = 50$) comprises 4 pairs of metacentric, 4 pairs of submetacentric and 9 pairs of acrocentric autosomes. The X-chromosome is large metacentric, the Y-chromosome is small submetacentric (Lavrenchenko *et al.*, 1997).

TABLE 1. Comparison of the external and cranial measurements of *C. afeworkbekelei* **sp. nov.**, *C. glassi*, *C. macmillani*, *C. baileyi* and *C. lucina*. Measurements in millimeters are presented as the mean, standard error of mean, standard deviation, range and number of specimens in parentheses.

	<i>C. afeworkbekelei</i> sp. nov.	<i>C. glassi</i>	<i>C. macmillani</i>	<i>C. baileyi</i>	<i>C. lucina</i>
HB	80.66/78.0–85.0 (3)	78.0±1.34/4.03/ 70.0–82.0 (9)	72.50 (2)	76.0 (1)	73.0 (1)
TL	45.66/43.0–48.0 (3)	55.41±1.68/5.06/ 46.0–64.0 (9)	56.0/55.0–57.0 (2)	44.0 (1)	49.0 (1)
HL _(-n)	15.66/15.0–15.50 (3)	16.18±0.30/0.91/ 15.0–18.0 (9)	14.12/13.75–14.50 (2)	13.0 (1)	15.0 (1)
HL _(+n)	16.76/16.30–17.0 (3)	17.7±0.34/1.04/ 16.50–20.0 (9)	14.75/14.30–15.20 (2)	—	—
EL	9.16/8.50–10.0 (3)	10.22±0.24/0.73/ 8.90–11.0 (9)	7.25/5.50–9.0 (2)	8.0 (1)	9.0 (1)
CI	22.10/21.82–22.37 (3)	23.70±0.16/0.49/ 22.76–24.51 (9)	22.42/22.30–22.53 (2)	22.32 (1)	22.67 (1)
PL	9.24/8.85–9.48 (3)	9.92±0.09/0.28/ 9.48–10.33(9)	9.07/9.02–9.13 (2)	9.16 (1)	9.59 (1)
UAL	2.82/2.70–2.93 (3)	3.12±0.02/0.08/ 2.95–3.21 (9)	2.79/2.75–2.83 (2)	2.82 (1)	2.65 (1)
P4L	2.01/2.01–2.02 (3)	2.18±0.03/0.09/ 2.08–2.36 (9)	2.18/2.14–2.22 (2)	2.12 (1)	2.35 (1)
M1L	1.7/1.65–1.74 (3)	1.84±0.02/0.06/ 1.74–1.94 (9)	1.83/1.76–1.90 (2)	1.76 (1)	1.87 (1)
M2L	1.39/1.34–1.42 (3)	1.54±0.02/0.08/ 1.40–1.66 (9)	1.59/1.57–1.61 (2)	1.66 (1)	1.66 (1)

.....continued on the next page

TABLE 1. (continued)

	<i>C. afeworkbekelei</i> sp. nov.	<i>C. glassi</i>	<i>C. macmillani</i>	<i>C. baileyi</i>	<i>C. lucina</i>
M3W	1.49/1.48–1.49 (3)	1.60±0.03/0.09/ 1.44–1.73 (9)	1.68/1.64–1.71 (2)	1.60 (1)	1.59 (1)
M3L	0.78/0.77–0.79 (3)	0.77±0.01/0.04/ 0.70–0.84 (9)	0.80/0.76–0.84 (2)	0.87 (1)	0.78 (1)
UML	3.65/3.55–3.74 (3)	3.95±0.03/0.11/ 3.72–4.09 (9)	4.0/3.90–4.10 (2)	4.13 (1)	4.10 (1)
P4s/d	1.36/1.28–1.44 (3)	1.27±0.02/0.08/ 1.10–1.40 (9)	1.29/1.16–1.42 (2)	1.06 (1)	1.08 (1)
ZYG	6.57/6.41–6.66 (3)	6.80±0.07/0.23/ 6.47–7.09 (9)	6.85/6.83–6.88 (2)	6.47 (1)	6.58 (1)
M3s/d	2.67/2.58–2.76 (3)	2.67±0.04/0.13/ 2.40–2.84 (9)	2.71/2.63–2.78 (2)	2.43 (1)	2.69 (1)
PTL	3.13/3.02–3.21 (3)	3.22±0.04/0.13/ 3.0–3.38 (9)	3.15/3.14–3.16 (2)	2.82 (1)	3.24 (1)
IO	5.64/5.61–5.66 (3)	5.80±0.05/0.17/ 5.45–6.0 (9)	5.56/5.40–5.71 (2)	5.42 (1)	5.38 (1)
NCW	0.92/0.88–0.96 (3)	0.94±0.04/0.12/ 0.80–1.15 (9)	0.90/0.83–0.98 (2)	0.86 (1)	1.10 (1)
OL	3.90/3.87–3.94 (3)	4.06±0.06/0.19/ 3.74–4.33 (9)	4.03/3.94–4.12 (2)	3.97 (1)	3.86 (1)
PGW	6.79/6.67–6.92 (3)	6.80±0.07/0.23/ 6.35–7.11 (9)	6.86/6.76–6.96 (2)	6.52 (1)	6.88 (1)
GW	10.03/9.74–10.23 (3)	10.40±0.08/0.26/ 9.90–10.76 (9)	9.89/9.78–9.99 (2)	9.72 (1)	9.76 (1)
LAL	2.29/2.21–2.37 (3)	2.56±0.01/0.05/ 2.46–2.63 (9)	2.57/2.57–2.58 (2)	2.47 (1)	2.44 (1)
MRW	3.63/3.58–3.67 (3)	3.91±0.04/0.12/ 3.75–4.09 (9)	3.59/3.55–3.62 (2)	3.58 (1)	3.76 (1)
MBL	8.82/8.61–8.94 (3)	9.66±0.08/0.25/ 9.23–10.05 (9)	9.10/9.04–9.16 (2)	9.05 (1)	9.31 (1)
COR	5.48/5.45–5.54 (3)	5.53±0.05/0.17/ 5.27–5.75 (9)	5.35/5.23–5.47 (2)	5.15 (1)	5.29 (1)
APL	3.51/3.36–3.61 (3)	3.71±0.03/0.11/ 3.59–3.95 (9)	3.66/3.63–3.68 (2)	3.42 (1)	3.58 (1)
LML	4.25/4.18–4.34 (3)	4.59±0.05/0.16/ 4.41–4.92 (9)	4.73/4.65–4.81 (2)	4.71 (1)	4.78 (1)
MBH	1.48/1.46–1.51 (3)	1.57±0.03/0.10/ 1.42–1.72 (9)	1.44/1.42–1.46 (2)	1.63 (1)	1.57 (1)

Variation. In external measurements the holotype and both paratypes show a comparable hindfoot size (15.0–15.5 mm); paratype S-162644 is larger in head and body length (85 mm, vs. 78–79 mm) and has a slightly shorter tail (50.6% of head and body length) than the other type specimens (58.2–61.5%). In cranial size the holotype is smaller in the following parameters: CI, PI, NCW, MBL. The qualitative characters are relatively homogeneous except for the ethmoidal foramina of paratype S-162643 which extend postero-dorsally from the sphenorbital fissure depression; mandibular angular process showed high intraspecific variability of relative position of the pterygoid muscle facets.

Comparisons. This is a small to medium shrew, comparable in general size to the Ethiopian endemics of the "*C. glassi* complex" (*sensu* Dippenaar & Meester, 1989): *C. glassi*, *C. lucina*, *C. macmillani*, and *C. baileyi* (Table 1). It is much larger than the following Ethiopian Afromontane–Afroalpine species: *C. bottegoides* Hutterer et

Yalden, 1990 (CI = 14.3–15.1 mm; Hutterer, 2013a), *C. bottegi* Thomas (CI = 14.9 mm, 15.2 mm; Hutterer, 2013b), *C. cf. hildegardae* Thomas (CI = 18.9 mm; S-165167 from Bale Mountains National Park), *C. haremma* Hutterer & Yalden, 1990 (CI = 18.7–19.2 mm; Hutterer & Yalden, 2013), *C. phaeura* Osgood (CI = 18.9–20.6 mm; Happold & Yalden, 2013), and *C. parvipes* Osgood (CI = 19.3–20.7 mm; Hutterer, 2013c). It is considerably smaller than the other Ethiopian species of *Crociodura* that are found in the Afromontane–Afroalpine biotic zone: *C. thalia* Dippenaar (CI = 25.5–25.9 mm; see Table 2), *C. zaphiri* Dollman (CI = 26.5 mm; Hutterer, 1980), and *C. olivieri* (Lesson) (CI = 32.0–34.3 mm; Churchfield & Hutterer, 2013).

The principal component analysis of 25 cranial and mandibular measurements reveals a clear separation between the small-sized (*C. haremma*, *C. parvipes*), the medium-sized (*C. glassi*, *C. lucina*, *C. macmillani*, *C. baileyi*, *C. afeworkbekelei* **sp. nov.**) and the large-sized (*C. thalia*, *C. yaldeni* **sp. nov.**) shrews (see Fig. 7A). The highly significant first component (according to the "Broken-stick model") accounted for 95.35% of the total variance. This axis is most correlated with measures of the general size of the skull and mandible, such as CI ($r = 0.708$), PL ($r = 0.334$), MBL ($r = 0.306$) and GW ($r = 0.240$), indicating that the first component can be interpreted as a variant of size dimension. Because the second and following components were not significant, the further (second) principal component analysis of all 25 measurements was performed separately for the medium-sized group.

The second PCA (see Fig. 7B) reveals that *C. afeworkbekelei* **sp. nov.** is clearly separated from *C. glassi* along the first component, and from *C. macmillani*, *C. baileyi* and *C. lucina* along the second and third component. The PC 1 is positive correlated with skull, mandible and rostral length (CI, $r = 0.740$; MBL, $r = 0.357$; PL, $r = 0.375$); the PC 2 is positive correlated with maximum transverse diameter of the braincase (GW, $r = 0.510$), basicranial (PGL, $r = 0.342$) and orbital width (IO, $r = 0.290$); the PC 3 is positive correlated with rostral width (ZYG, $r = 0.501$) and lower molar row length (LML, $r = 0.409$). The first three components were statistically significant, and accounted for 73.69%, 10.06% and 5.40% of the total variance, respectively.

Detailed comparisons with other middle-sized species: *C. afeworkbekelei* **sp. nov.** differs from *C. glassi* in its smaller PL, UAL, UML, M1L, MBL, LAL; larger on average for P4s/d; more rounded edge of the anterior opening of the infraorbital canal; smaller and faintly developed I1 talon; the shape of the angular process facets.

Crociodura afeworkbekelei **sp. nov.** differs from *C. macmillani* in the occlusal outlines of the antemolars (A1–A3); curved outline of the A3 posterior edge; faintly developed I1 talon; straight postparacrista of the M1 (Fig. 5, A-a); gentle outline of the M3 posterior edge (Fig. 6, A-a); absent mesostylar part of premetacrista of the M3 (Fig. 6, A-b).

Crociodura afeworkbekelei **sp. nov.** differs from *C. baileyi* in straight postparacrista of the M1; occlusal outline of the M3; distinctly smaller M3 (M3W); relatively position of hypoconulids of the m1–m2 (hypoconulids are not visible from medial side of teeth); cingulum of the m3 not visible from medial side of tooth.

Crociodura afeworkbekelei **sp. nov.** differs from *C. lucina* in slightly overlapped anterior margin of A3 by the adjoining posterior margin of A2; smaller size of the A2 relative to A3; gentle outline of the M3 posterior edge; shape of the angular process facets.

In general, *C. afeworkbekelei* **sp. nov.** can be distinguished from other medium-sized species of Ethiopian *Crociodura* by the following features: shortest P4; largest transverse distance between left/right P4; the largest height of the mandibular ramus relative to the length of the mandibular body (62.1% vs. 56.8–58.8% in comparable species).

The standard karyotype is fully identical (at least at the level of the routine staining) to that of another Ethiopian endemic, *C. haremma*, but differs significantly from the chromosomal sets of syntopic *C. glassi* and *C. lucina* ($2n = 36$, NFA = 52) (Lavrenchenko *et al.*, 1997—in this paper the data on *C. lucina* refer in fact to *C. afeworkbekelei* **sp. nov.**, and the data on *Crociodura* sp. A to *C. lucina*). According to our allozyme data, *C. afeworkbekelei* **sp. nov.** differs from syntopic *C. glassi* and *C. lucina* by alternative alleles fixed for five (Hbb-1, Hbb-2, Me-1, Got-1, Lap-1) and two (Lap-2 and Es-4) loci, respectively (Lavrenchenko *et al.*, 1997).

Distribution. Only known from the Konteh Area of the Sanetti Plateau (06°51'N, 039°53'E, 4050 m a.s.l.). It remains possible that the new species inhabits other parts of the Plateau. It is likely that *C. afeworkbekelei* **sp. nov.** is endemic to the Bale Mountains.

Habitat. The specimens were captured in Sherman live traps in the Afroalpine belt with sparse and short vegetation. Three other small mammal species, *C. glassi*, *C. lucina*, and *Stenocephalemys albocaudata* Frick were also caught at the same site. The females showed no reproductive activity when examined.

TABLE 2. Comparison of the external and cranial measurements of *C. yaldeni* sp. nov. and *C. thalia*. Measurements in millimeters are presented as the mean, standard error of mean, standard deviation, range and number of specimens in parentheses.

	<i>C. yaldeni</i> sp. nov.	<i>C. thalia</i>
HB	93.87±3.49/6.98/84.0–99.50 (4)	90.50±2.3/5.75/ 85.0–100.0 (6)
TL	65.62±3.10/6.20/60.0–73.0 (4)	63.25±1.57/3.86/ 57.50–69.0 (6)
HL _(-n)	18.20±0.42/0.85/17.0–19.0 (4)	17.33±0.24/0.60 /17.0–18.50 (6)
HL _(+n)	20.20±0.76/1.53/18.50–22.20 (4)	18.81±0.09/0.20/ 18.50–19.0 (5)
EL	10.50±0.28/0.57/10.0–11.0 (4)	11.16±0.38/0.93/ 10.0–12.50 (6)
CI	26.52±0.49/0.98/25.07–27.24 (4)	25.76±0.06/0.15/ 25.53–25.98 (6)
PL	11.36±0.24/0.48/10.65–11.69 (4)	10.67±0.06/0.15/ 10.51–10.97 (6)
UAL	3.49±0.09/0.18/3.23–3.61 (4)	3.47±0.04/0.10/ 3.3–3.60 (6)
P4L	2.43±0.05/0.11/2.29–2.57 (4)	2.39±0.01/0.04/ 2.35–2.45 (6)
M1L	2.05±0.05/0.10/1.91–2.18 (4)	1.97±0.02/0.06/ 1.87–2.03 (6)
M2L	1.92±0.01/0.03/1.88–1.95 (4)	1.62±0.02/0.05/ 1.53–1.67 (6)
M3W	2.02±0.04/0.09/1.93–2.10 (4)	1.71±0.01/0.04/ 1.66–1.77 (6)
M3L	1.0±0.03/0.06/0.95–1.10 (4)	0.85±0.01/0.04/ 0.78–0.90 (6)
UML	4.65±0.08/0.16/4.41–4.8 (4)	4.25±0.03/0.09/ 4.11–4.35 (6)
P4s/d	1.30±0.03/0.06/1.24–1.39 (4)	1.43±0.03/0.07/ 1.31–1.54 (6)
ZYG	7.88±0.06/0.13/7.74–8.07 (4)	7.37±0.06/0.15/ 7.12–7.54 (6)
M3s/d	2.62±0.02/0.05/2.56–2.67(4)	2.82±0.06/0.15/ 2.61–3.02 (6)
PTL	3.54±0.02/0.05/3.48–3.62 (4)	3.45±0.05/0.12/ 3.29–3.59 (6)
IO	6.26±0.07/0.14/6.08–6.39 (4)	6.22±0.05/0.14/ 6.06–6.41 (6)
NCW	1.04±0.05/0.10/0.95–1.20 (4)	0.88±0.05/0.12/ 0.67–1.03 (6)
OL	4.47±0.04/0.09/4.34–4.57 (4)	4.56±0.09/0.24/ 4.11–4.82 (6)
PGW	7.86±0.09/0.18/7.64–8.08 (4)	7.38±0.09/0.23/ 6.99–7.58 (6)
GW	11.64±0.15/0.31/11.19–11.90 (4)	11.19±0.05/0.12/ 11.03–11.36 (6)
LAL	3.03±0.09/0.18/2.77–3.18(4)	2.92±0.03/0.08/ 2.83–3.09 (6)
MRW	4.32±0.10/0.21/4.01–4.49 (4)	4.24±0.06/0.15/ 4.03–4.43 (6)
MBL	10.83±0.23/0.46/10.17–11.24 (4)	10.66±0.08/0.21/ 10.39–10.94 (6)
COR	6.82±0.18/0.36/6.29–7.10 (4)	6.12±0.03/0.07/ 6.01–6.23 (6)
APL	4.26±0.19/0.38/3.76–4.66 (4)	3.89±0.05/0.12/ 3.73–4.09 (6)
LML	5.41±0.04/0.09/5.28–5.50 (4)	5.03±0.03/0.07/ 4.95–5.13 (6)
MBH	1.88±0.09/0.18/1.61–2.02 (4)	1.87±0.04/0.10/ 1.72–1.98 (6)

Etymology. We dedicate this new species to our colleague and friend Prof. Dr. Afework Bekele in appreciation of his promotion of research on Ethiopian mammals (Fig. 11). As the vernacular name for the new species we propose Sanetti Shrew.

***Crocidura yaldeni* sp. nov.**

Figs. 7A, 8A, 9A, 10; Table 2.

Crocidura sp. B: Bannikova *et al.*, 2001: 56.

Crocidura sp. B: Bannikova *et al.*, 2005: 47.

Crocidura sp. B: Lavrenchenko *et al.*, 2009: 57.

Holotype. ZMMU S-165342; adult male, dry skin and skull; collector's number 30; collected by L.A. Lavrenchenko on 16 April 1997.

Type locality. Beletta Forest, south-western Ethiopia, 07°34'N, 036°31'E, 1900 m a.s.l.

Paratypes. ZMMU S-165340 (adult female, dry skin and skull, collector's number 20); ZMMU S-165341 (adult male, dry skin and skull, collector's number 28); ZMMU S-165343 (adult male, dry skin and skull, collector's number 35; Fig. 8A); all three specimens from the type locality collected by L.A. Lavrenchenko between 13 and 19 April 1997.

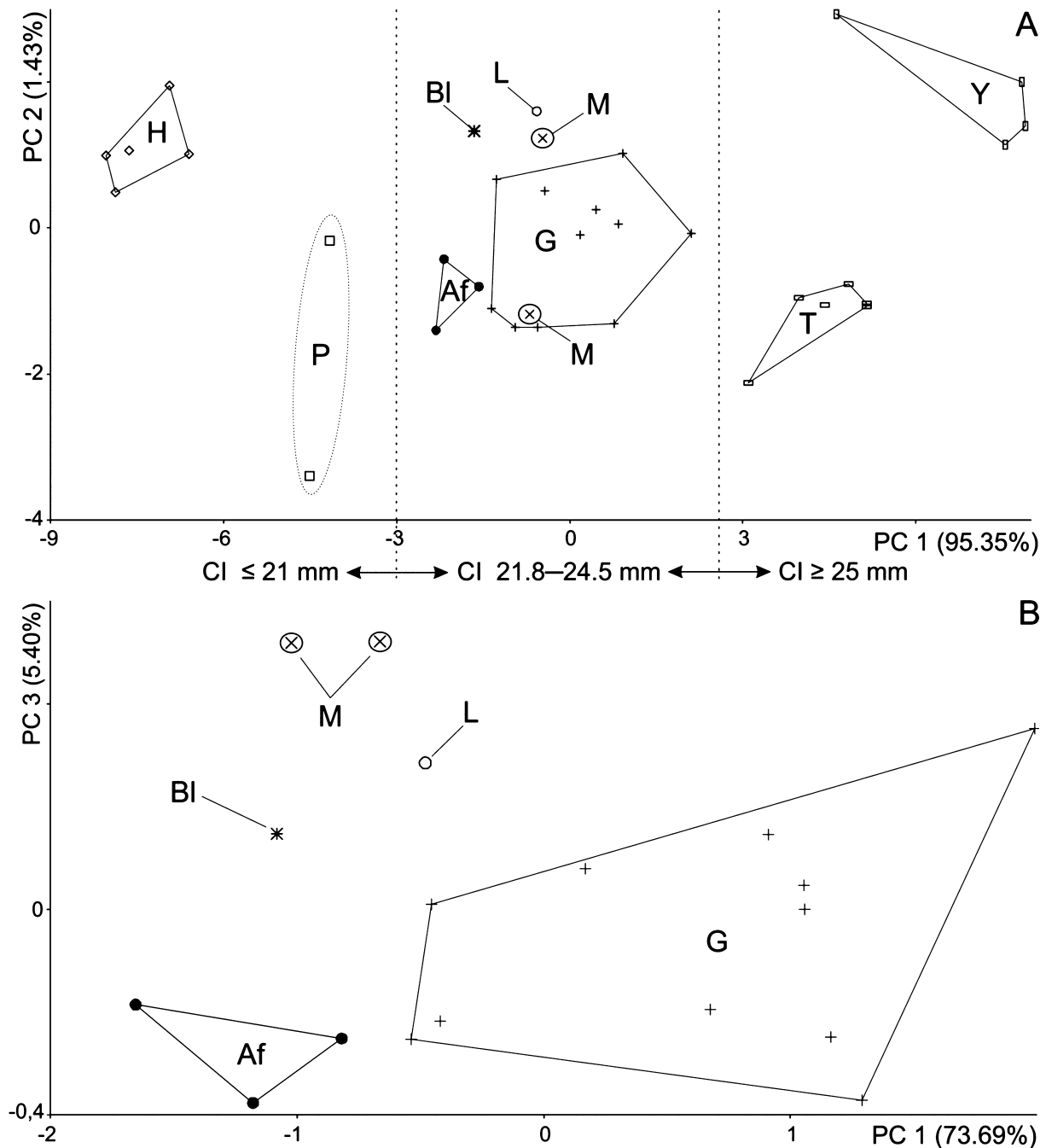


FIGURE 7. Principal components plots: A—for all specimens of *Crocidura* (1st versus 2nd axis); B—for five middle-sized species (1st versus 3rd axis). Abbreviations: Af = *C. afeworkbekelei* sp. nov.; BI = *C. baileyi*; G = *C. glassi*; H = *C. haremma*; L = *C. lucina*; M = *C. macmillani*; P = *C. parvipes*; T = *C. thalia*; Y = *Crocidura yaldeni* sp. nov. Below upper plot size ranges for small-, middle-, and large-sized groups shown by condylo-incisive length (CI) along PC 1.

Diagnosis. A large-sized, greyish-brown *Crocidura* similar in external measurements (HB, TL) to *C. thalia* but slightly larger, on average, in cranial size (Table 2). Distinguished from the latter species by the following features: moderately longer hindfoot and claws; relatively uniformly colored tail; bristle hairs of tail bicolored and longer; skull large; nasal aperture wide; dorsal profile of skull looks concave at the midpoint and, slightly convex above the

upper tooth row (Fig. 8, A); upper first incisor with a hook-like apex; lingual outline of the second upper molar with a distinct symmetric incision (Fig. 9, A1-a); second and third upper molar in firmly contact (Fig. 9, A1-b); occlusal outline of the third upper molar more undulated (Fig. 9, A1-c); hypoconulids of the lower molars visible in medial view (Fig. 9, A2-d); postcingulid of m3 forming a notch (Fig. 9, A3-e).

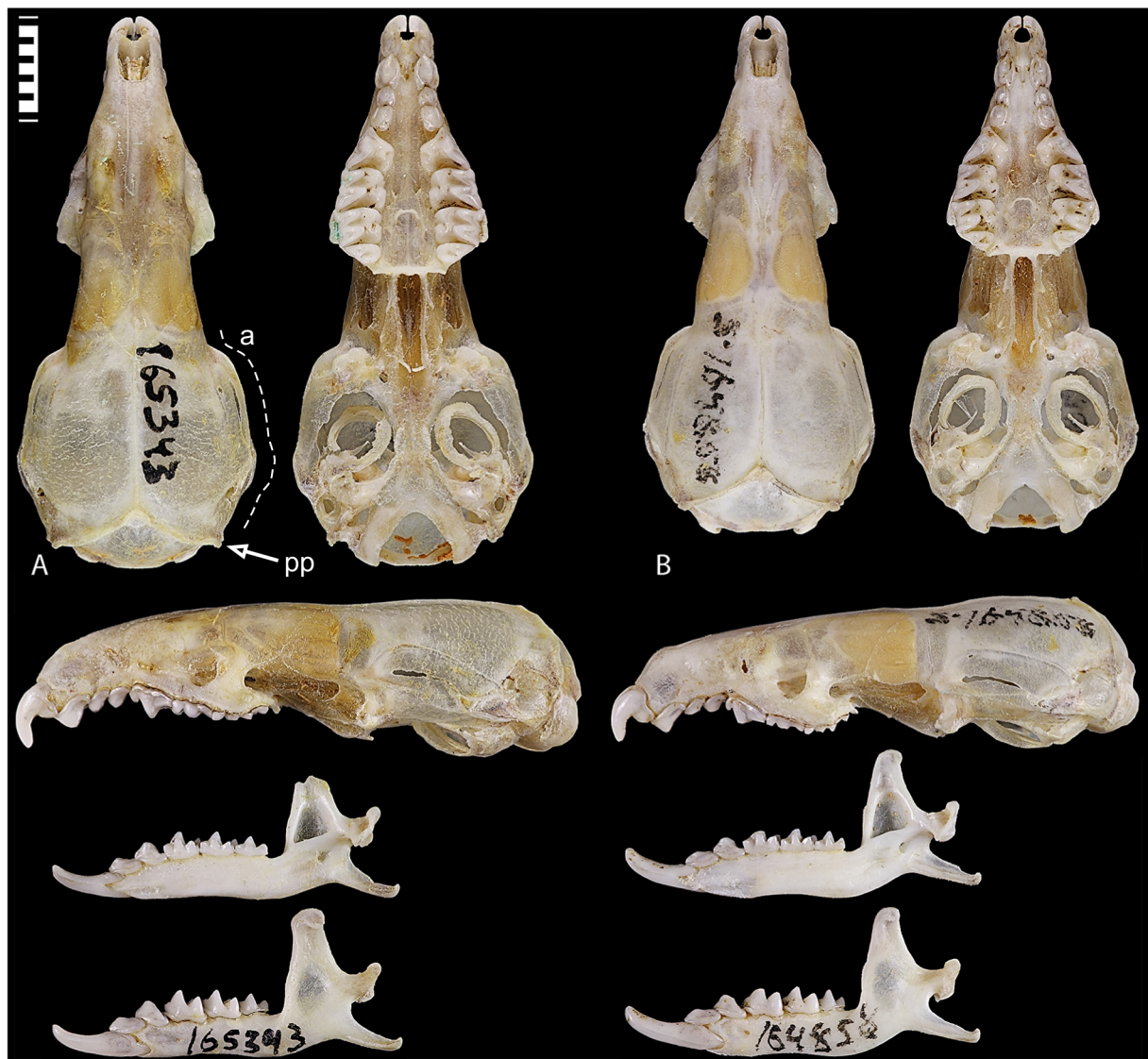


FIGURE 8. Dorsal, ventral, and lateral views of the cranium, and medial and lateral views of the mandible of *Crocidura yaldeni* sp. nov. S-165343 (A) and *C. thalia* S-164858 (B). Abbreviations: a = outline of lateral profile of the braincase; pp = paraoccipital process. Scale 5 mm.

Description. Large-sized *Crocidura* (head and body length 84.0–99.5 mm; here regarded as large-sized shrew in comparison to examined species) with a moderately long tail, ranging between 62.2–77.6% of head and body length. Dorsal pelage grey-brown with pale ochre shades (differs from *C. thalia* in slightly less intensive shades); dorsal hairs grey at base, brown at tip. Ventral pelage blackish-grey with pale ochre wash; ventral hairs dark grey at base, pale-yellowish at tip. Dorsal surface of fore- and hindfoot brownish. Tail uniformly colored, dark grey-brown above and brown below. Bristle hairs are long, dark-grey at base, pale-grey at tip, and present along the full length of the tail.

Skull (Fig. 8, A) with a long rostrum and wide braincase. The rostral part is distinctly inflated (similar to *C. thalia* and differs from others Ethiopian endemic and Afroalpine species). The nasal aperture is wide; the posterior margin of the aperture has no medial tip. The dorsal outline of the orbital parts is slightly flexed. The lateral profile of the braincase is slightly angulated (Fig. 8, A-a). The nuchal crests are well-developed; their postero-lateral ends are prolonged and joint with noticeable paraoccipital processes (Fig. 8, A-pp). The sagittal

crest is faint (in adult specimens); the temporal line is clearly recognizable. Mandible with broad body; its lower margin running in a shallow convex inward curve; body achieving its maximum depth below p4–m3. Coronoid spicule massive. External temporal fossa well-developed and wide. Angular process with hooked tip (Fig. 8, A).

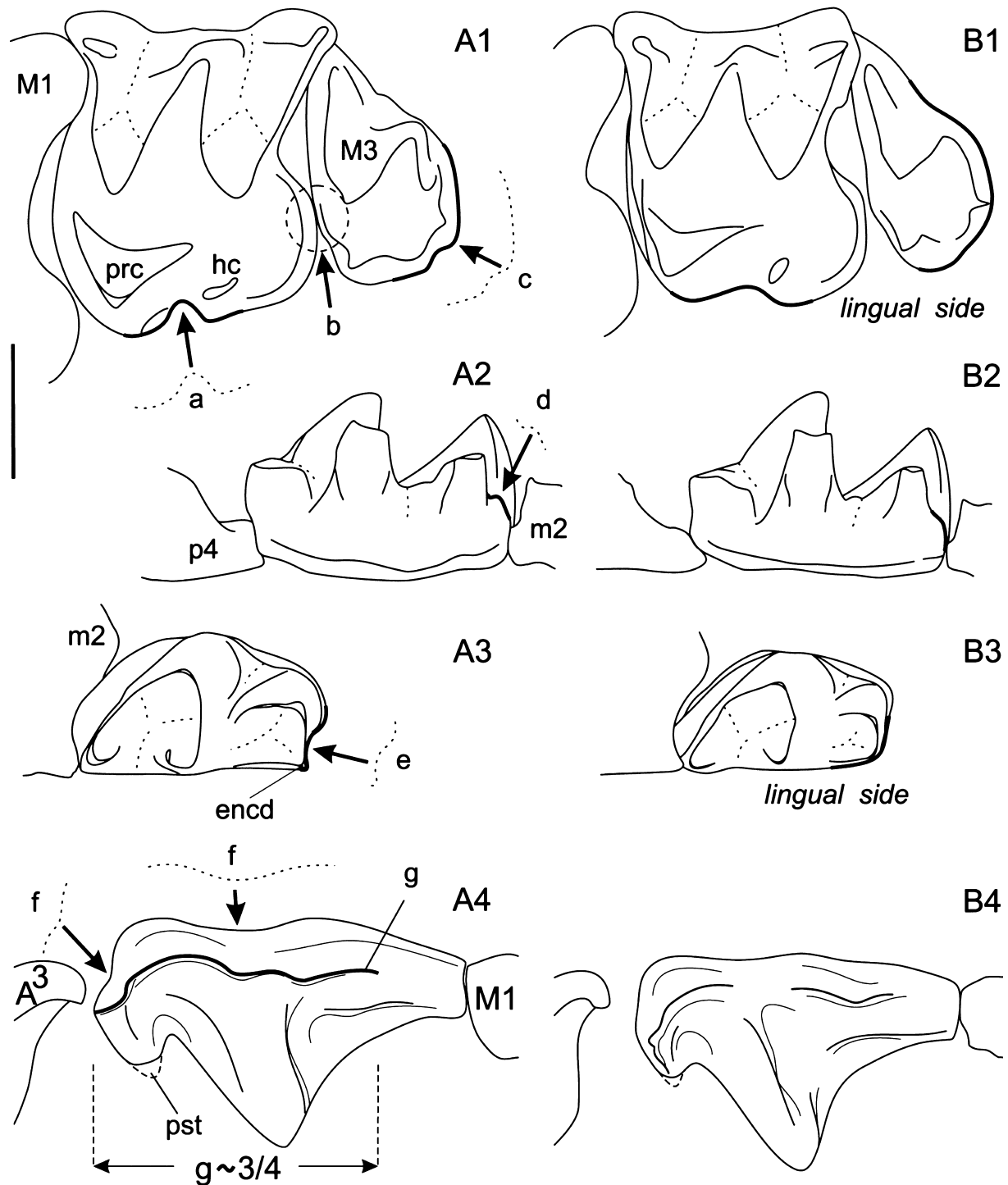


FIGURE 9. Specific features of *Crocidura yaldeni* sp. nov. S-165343 (A1–A4) and *C. thalia* S-164858 (B1–B4). A1, B1—occlusal view of the M2 and M3; A2, B2—lingual side of the m1; A3, B3—occlusal view of the m3; A4, B4—lateral view of the P4. Abbreviations: encd = entoconid; hc = hypocone; also see figure 5. Specific characters of *C. yaldeni*: a—the symmetric and distinctly curved incision of the M2; b—postero-lingual part of the M2 in contact with M3; c—the shape of the outline of the posterior edge of M3; d—the hypoconulid shoulder of the m1 in medial view; e—postcingulid of m3 forming a notch; f—the undulated upper margin of P4 in lateral view; g—three-quarters of the crown base of P4 surrounded by a cingulum. Scale 1 mm.

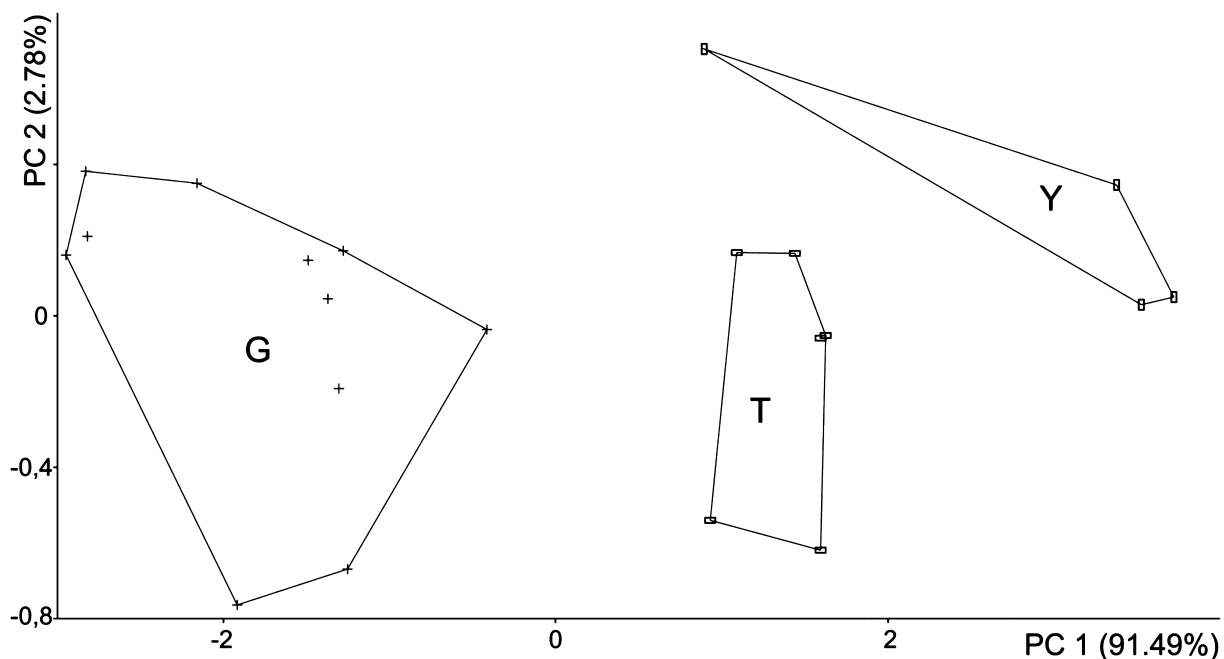


FIGURE 10. Principal components plot for two large-sized species and *C. glassi* (1st versus 2nd axis). Abbreviations: G = *C. glassi*; T = *C. thalia*; Y = *Crocidura yaldeni* sp. nov.

First upper incisor (I1) is robust; the apex (partly worn) is comparably long and hooked. The talon is well-developed, with distinct lingual ridge (lingual cingulum). The posterior ridge of the talon apex is strongly-developed. Lateral cingulum is weak and extending dorsally about 3/4 of I1 base height, with a faint bulge on the inferior part. Upper antemolars (A1–A3) are well-spaced, with a weak buccal cingulum and postero-buccal small cuspules. The upper first antemolar (A1) is very large; basal prominence of the anterior ridge is absent. The upper second antemolar (A2) is smallest, approximately 1/3 the height of A1, and 3/4 the height of A3. The upper third antemolar (A3) with straight buccal outline; the posterior edge is not strongly curved and connected with P4. The parastyle of the fourth upper premolar (P4) is well defined (tip partly worn); the upper margin (lateral view) is undulated and distinctly concave above parastyle and main cusp (Fig. 9, A4-f); three-quarters of the crown base is surrounded by a cingulum (Fig. 9, A4-g). The upper molars (M1–M2) are comparably wide. The lingual edge of the upper second molar (M2) has a well-developed and symmetrically curved incision (Fig. 9, A1-a). The upper third molar (M3) is relatively long and wide, in close contact with M2 (Fig. 9, A1-b), posterior edge is undulated (Fig. 9, A1-c).

The first lower incisor (i1) is wide at base, with a blunt tip; the tooth is partly worn in all specimens, and therefore the denticulation of the cutting ridge is unknown. The second incisor (a1) is elongated, approximately 1/3 of the lower border of the tooth is in contact with i1; its posterior border is considerably (about 1/4) overlapped by the fourth lower premolar (p4); the postero-lateral ridge has a bulge. The basal prominence on the anterior ridge of p4 is present but indistinct, the lingual cusp (metaconid) is small. The hypoconulids of the lower molars (m1-m3) are well-developed and visible from the medial side of the teeth (Fig. 9, A2-d). The postcingulid of the lower third molar (m3) forms a visible notch buccal to the entoconid (Fig. 9, A3-e).

The chromosomal set of *C. yaldeni* sp. nov. ($2n = 36$, $NFa = 52$) comprises 4 pairs of metacentric, 5 pairs of subtelocentric and 8 pairs of acrocentric autosomes. The X-chromosome is large metacentric; the Y-chromosome is small subtelocentric.

Variation. Specimens of the type series are uniformly colored. In external and skull measurements S-165340 (female) is slightly smaller (HB = 84.0 mm, vs. 94.0–99.5 mm in males). The qualitative characters are relatively homogeneous.

Comparisons. This is a large-sized shrew, comparable in external size (HB, TL) to *C. thalia*, but slightly larger in cranial size (Table 2). It is substantially larger than the following Ethiopian Afroalpine species: *C. bottegoides*, *C. cf. bottegi*, *C. cf. hildegardeae*, *C. haremma*, *C. phaeura*, *C. parvipes*, *C. afeworkbekelei* sp. nov., *C. lucina*, *C. macmillani*, *C. baileyi*, and *C. glassi*. The values of CI for all mentioned species range

between 14.3–24.51 mm. The new species is considerably smaller than the other Ethiopian *Crocidura* species found in the Afromontane–Afroalpine biozones: *C. zaphiri* (HB = 105 mm, CI unknown; Churchfield & Jenkins, 2013a), and *C. olivieri* (CI = 32.0–34.3 mm; Churchfield & Hutterer, 2013).

The first PCA (see above, and Fig. 7A) revealed significant differences between the groups of smaller, medium-sized and larger shrews along significant PC 1. Therefore, a further PCA was performed on two larger species and *C. glassi*.

The third PCA (Fig. 10) of all 25 cranial and mandibular linear measurements reveals that the smaller *C. glassi* is clearly separated from the larger *C. thalia* and *C. yaldeni* **sp. nov.** along PC 1. This statistically significant axis accounted for 91.49% of the total variance and is most correlated with measures of the general size of the skull and mandible, such as CI ($r = 0.674$), PL ($r = 0.316$), MBL ($r = 0.297$) and COR ($r = 2.788$). The second component accounted only for a small percentage of the total variance (2.78%), and therefore was not significant. The PC 2 is most positively correlated with cranial width (PGW, $r = 0.576$; ZYG, $r = 0.349$; GW, $r = 0.261$). As can be seen from Fig. 10, *C. thalia* and *C. yaldeni* **sp. nov.** are clearly distinguished along the first two principal components. The difference between the two species along the first axis reflects the larger average size of *C. yaldeni* **sp. nov.**, while the second component is associated with changes in skull shape.



FIGURE 11. Afework Bekele (left, photograph taken by Viola Clausnitzer in March 2000) and the late Derek Yalden (right, photograph taken by Pat Morris), two biologists who greatly contributed to the knowledge of the mammal fauna of Ethiopia.

Detailed comparison between similar in size species: *C. yaldeni* **sp. nov.** differs from *C. thalia* in: smaller P4s/d, M3s/d; bigger M2L, M3W, M3L, UML, ZYG, PGW, LML; longer hindfoot and claws (Table 2); the uniformly colored tail (tail of *C. thalia* is mottled with brown and pale ochre); the bicolored and longer bristle hairs of tail; more massive I1; more compact upper antemolars row; stronger developed incision on lingual edge of the M2 (Fig. 9, A1-a vs. B1); the expression of hypoconulids on the lower molars (Fig. 9, A2-d).

The standard karyotype is identical to that of two related species, *C. thalia* and *C. glassi* (Lavrenchenko *et al.*, 1997). Phylogenetic analyses based upon repetitive DNA elements (taxonomic DNA fingerprint) and inter-SINE-PCR (IS-PCR) revealed that genetic distances between *C. yaldeni* **sp. nov.** and its two closest relatives, *C. thalia* and *C. glassi*, fell within the range usually recorded for interspecific genetic differentiation within *Crocidura* (Bannikova *et al.*, 2001; Bannikova *et al.*, 2005). The former analysis strongly supported that *C. yaldeni* **sp. nov.** is a sister species to *C. thalia*; in the latter analysis *C. thalia* and *C. glassi* had a tendency to form a clade against *C.*

yaldeni **sp. nov.** The phylogenetic analysis of an extended set of *Crocidura* species using mitochondrial cytochrome b gene sequences (Lavrenchenko et al., 2009) revealed that *C. yaldeni* **sp. nov.** and *C. macmillani* form the most basal branch of the group of Ethiopian endemics (including *C. glassi*, *C. thalia*, *C. lucina* and *C. baileyi*), whereas *C. thalia* appears as sister to *C. glassi*.

Distribution. The new species has been found only in the Beletta Forest (07°34'N, 36°31'E, 1900 m a.s.l.). We failed to trap *C. yaldeni* **sp. nov.** in any other site of this forest and other humid Afromontane forest blocks of SW Ethiopia: the Sheko Forest (07°04'N, 35°30'E, 1930 m a.s.l.), the Dushi Area of the Godare Forest (07°21'N, 35°13'E, 1200 m a.s.l.), the Meti Area of the Godare Forest (07°17'N, 35°16'E, 1370 m a.s.l.) and the Inegawa Forest (07°25'N, 35°24'E, 2340 m a.s.l.). Therefore, the currently known distribution range of this new species is extremely small.

Habitat. All four specimens of *C. yaldeni* **sp. nov.** were captured in the riverine variant of humid Afromontane forest on the bank of the small river (trees: *Schefflera abyssinica*, *Croton macrostacis*, *Allophylus abyssinicus*, *Aningeria altissima*, *Malacanta alnifolia*, *Phoenix reclinata*, *Brucea antiderinterica*, *Polyscias fulva*; small trees: *Vepris dainelii*, *Teclea nobilis*, *Dracaena afromontana*, *D. fragrans*; shrubs: *Coffea arabica*, *Canthium oligocarpum*, *Galimiera coffeoides*; climbers: *Embelia schimperi*, *Phychotria neglecta*; ferns: *Pteris dentatum*, *Asplenium sandersoni*, *Pleopeltis* sp.; herbs: *Afromomum* sp.). Three rodent species, *Lophuromys chrysopus* Osgood, *Mus mahomet* Rhoads, and *Stenocephalemys albipes* (Rueppell) were also collected at the same trapping site. All individuals of the new shrew were caught in Sherman live traps placed on the ground no more than 1 m from the river bank. Probably the very restricted range of *C. yaldeni* **sp. nov.** is associated with yet unknown habitat requirements, presumably more specific than 'river edge'. However, no morphological adaptations to some specific life style (including semi-aquatic adaptations) were observed.

Etymology. The new species is named in honor of the late Dr. Derek W. Yalden (1940-2013), who has contributed greatly to our knowledge on Ethiopian small mammals (Fig. 11). As the vernacular name for the new species we propose Beletta Shrew.

A review of the diversity of Ethiopian shrews

Currently, we recognize two species of *Suncus* and 26 named species of *Crocidura* in Ethiopia, with two of the latter being described in the present paper (Table 3). This checklist is provisional. The sole specimen of *C. cf. hildegardae* (ZMMU S-165167, collected 31 December 1995 by Leonid Lavrenchenko in *Schefflera-Hagenia* belt of the Harena Forest, 06°45'N, 039°44'E, 2760 m a.s.l.) may indicate the presence of a further new species endemic to Ethiopia. Both newly described shrews, *C. afeworkbekelei* and *C. yaldeni*, possess extremely small distributional ranges (single Afroalpine plateau or forest, respectively). We predict that further discoveries will be most probably confined to the still poorly-explored forested and high-altitude areas: lowland/montane forests in the southwestern sector of the country and high plateaus around Mt Guna, Abune Yosef, Amba Ferit and Abbiye Meda. Moreover, distribution ranges of poorly known species can be enlarged as a result of field surveys. For example, two endemic shrews, *C. macmillani* and *C. phaeura*, were known only from their type localities. The former species was collected in the Middle Godjeb Valley and the Sheko Forest (Lavrenchenko, 2008), and the latter in the Nachisar National Park (Duckworth *et al.*, 1993). Furthermore, *C. parvipes* reported for the first time from Ethiopia by Hutterer & Yalden (1990) on the evidence of a single specimen from Bulcha Forest, was currently found to be rather numerous in the Middle Godjeb Valley and near the Koi River (37 km SW of the Bebeke Coffee Farm) (our unpublished data).

An eco-geographic analysis of Ethiopian *Crocidura* indicates that 38% of the shrew fauna is primarily associated with savanna of different types, 46% with forest habitats, and 16% with Afroalpine moorlands. 10 shrew species (38% of the total) are currently considered to be endemic; all of them are forest (6 species) or Afroalpine (4 species) forms (Table 3). Two endemic species, *C. thalia* and *C. bottegoides*, known as associated with "forest/grassland" are predominantly forest species inhabiting riverine habitats inside forests. Thus, the Ethiopian endemic shrew fauna consists of forest and montane species known to occur only within the altitudinal range of 1200–4050 m a.s.l. The remarkable number of endemic *Crocidura* species clearly shows that the Ethiopian Plateau is an important centre of high diversity and adaptive radiation for the genus.

TABLE 3. A list of shrews recorded from the territory of Ethiopia with information about endemism, habitats and distribution; C = *Crocidura*, S = *Suncus*.

nn	Species	Ethiopian endemic	Habitat	Distribution
1	<i>C. afeworkbekelei</i> sp. nov.	Yes	Afroalpine belt with sparse and short vegetation	East of the Ethiopian Rift Valley (Bale Mts)
2	<i>C. baileyi</i>	Yes	Humid localities with tall grasses in afroalpine moorland and humid heather forest [1]	West of the Ethiopian Rift Valley (Simien Mts, Amedamit Mts, Enjiabara, Debre Sina and Ankober) [1]
3	<i>C. glassi</i>	Yes	Upland grasslands, ericaceous scrub and afroalpine moorland, over a range of altitudes [2]	East of the Ethiopian Rift Valley (Bale Mts, Mt Badda and Chercher Highlands) [2]
4	<i>C. lucina</i>	Yes	Afroalpine moorland, and grasslands at lower altitudes [3]	East of the Ethiopian Rift Valley (Bale Mts and Mt Badda) [3]
5	<i>C. bottegoides</i>	Yes	Relict forest [4]	Two regions in Ethiopia: Harenna Forest in the Bale Mts, and Mt Albasso, Arussi [4]
6	<i>C. harenna</i>	Yes	Schefflera-Hagenia montane forest [5]	Ethiopia (Harenna forest, Bale Mts) [5]
7	<i>C. macmillani</i>	Yes	Ethiopian montane tropical forest and humid woodland Terminalia-Combretum savanna with high grasses [6]	Western Plateau of Ethiopia (Middle Godjeb Valley and Sheko Forest) [6]
8	<i>C. phaeura</i>	Yes	Forest localities, including riverine forest at Nachisar and Guramba Mt [7]	SW Ethiopia (Guramba Mt and Nechisar Nat. Park) [7]
9	<i>C. thalia</i>	Yes	Open habitats from humid woodland savanna to highland grasslands and scrub [8]	East and west Ethiopian Rift Valley [8]
10	<i>C. yaldeni</i> sp. nov.	Yes	Humid afroalpine forest	SW Ethiopia (Beletta Forest)
11	<i>C. fulvastra</i> (Sundevall)	No	Drier savanna; also in mesic habitats [9]	Mali, N Nigeria, S and C Sudan, Ethiopia (Rift Valley), N Kenya [9]
12	<i>C. fuscumurina</i> (Heuglin)	No	Woodland savannas and semi-arid regions [10]	Many countries in W, E, EC and S Africa [10]
13	<i>C. lusitania</i> Dollman	No	Savanna and semi-desert	S Morocco to Senegal, Mauritania, Mali, Nigeria, Sudan and Ethiopia [11]
14	<i>C. nana</i> Dobson	No	Dry grassland and scrub [12]	Somalia and Ethiopia [12]
15	<i>C. pasha</i> Dollman	No	Semi-arid savannas [13]	Sahel Savanna and Sudan Savanna; Known in Sudan, Ethiopia (Awash Nat. Park), N Mali [13]
16	<i>C. somalica</i> Thomas	No	Dry savanna, semi-desert, granite rocks and sandy valleys [14]	Sudan Savanna, Somalia-Masai Bushland, three localities in Ethiopia, Sudan (Kordofan Prov.), Mali [14]
17	<i>C. viaria</i> (I. Geoffroy)	No	Savanna	S Morocco to Senegal and east to Sudan, Ethiopia and Kenya [11]
18	<i>C. voi</i> Osgood	No	Savanna	Kenya and Somalia to Ethiopia and Sudan [11]
19	<i>C. yankariensis</i> Hutterer & Jenkins	No	Primarily dry savanna. In Ethiopia species was found amongst shrubs and boulders in wet grasslands [15]	Sudan Savanna, and parts of Somalia-Masai Bushland; also recorded from Nigeria, Cameroon, Sudan, Ethiopia, NW Kenya and Somalia [15]
20	<i>C. bottegi</i>	No	Grassy clearings within the forest [16]	Three localities in the Ethiopia and Marsabit, N. Kenya [17]

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TABLE 3. (Continued)

nn	Species	Ethiopian endemic	Habitat	Distribution
21	<i>C. hildegardeae</i>	No	Dry forest and wetter forests of montane and highland areas in eastern Africa [18]	SE Cameroon and Congo to Kenya and Tanzania, S Ethiopia [18]
22	<i>C. nigrofusca</i> Matschie	No	Damp habitats near water-courses, secondary forest, forest patches, swampy areas in forest-savanna mosaic [19]	S Ethiopia, S Sudan, most of E Africa, Zambia, Angola and C and S DR Congo [19]
23	<i>C. olivieri</i>	No	Mostly in well-vegetated moist habitats including lowland and montane evergreen forest, riverine and flood plain grassland and swamp [20]	From Senegal eastwards to Sudan and Ethiopia, and southwards towards southern Africa [20]
24	<i>C. parvipes</i>	No	Dry savanna habitats and occasionally in gallery forest [21]	Cameroon, Central African Republic, S Sudan, Uganda, Ethiopia, Kenya, Tanzania, DR Congo, Zambia and Angola [21]
25	<i>C. smithii</i> Thomas	No	Dry Sahelian savanna [22]	The lowland Ethiopia and Senegal [23]
26	<i>C. zaphiri</i>	No	Forest [24]	SW Ethiopia and SW Kenya [25]
27	<i>S. cf. etruscus</i> Savi	No	Mediterranean-type habitats [26]	Mediterranean; one isolated record from Ethiopia [27]
28	<i>S. megalura</i> (Jentink)	No	Moist savanna, swamps and forest edges [28]	Highlands of SW Ethiopia, and Guinea to Mozambique [28]

Notes. [1]—Lavrenchenko (2013a: 59); [2]—Lavrenchenko (2013b: 82); [3]—Lavrenchenko (2013c: 98); [4]—Hutterer (2013a: 62); [5]—Hutterer & Yalden (2013: 87); [6]—Lavrenchenko (2008); [7]—Happold & Yalden (2013: 122); [8]—Lavrenchenko (2013d: 138); [9]—Churchfield & Jenkins (2013b: 79); [10]—Dippenaar & Baxter (2013: 81); [11]—Hutterer (2005b); [12]—Churchfield & Jenkins (2013c: 111); [13]—Churchfield & Jenkins (2013d: 121); [14]—Hutterer (2013d: 133), Jacquet *et al.* (2015); [15]—Hutterer (2013e: 147); [16]—Hutterer & Yalden (1990); [17]—Hutterer (2013b: 61); [18]—Stanley (2013: 88); [19]—Hutterer (2013f: 114); [20]—Churchfield & Hutterer (2013: 118); [21]—Hutterer (2013c: 120); [22]—Hutterer *et al.* (2008); [23]—Happold (2013: 132); [24]—Hutterer & Oguge (2008); [25]—Churchfield & Jenkins (2013a: 148); [26]—Aulagnier & Fons (2013: 174); [27]—Corbet & Yalden (1972); [28]—Baxter & Dippenaar (2013: 179).

Chromosomal analyses (Lavrenchenko *et al.*, 1997; Bannikova *et al.*, 2001) demonstrated that all cytogenetically studied endemic Ethiopian *Crocidura* species except for *C. macmillani* (2n = 28) (including *C. bottegoides*, *C. glassi*, *C. thalia*, *C. harensa*, *C. lucina*, *C. yaldeni* **sp. nov.**, and *C. afeworkbekelei* **sp. nov.**) have similar karyotypes (2n = 36, NF = 52–56). The karyotype of *C. macmillani* (2n = 28, NF = 56), composed entirely of biarmed chromosomes, apparently originated from the 36-chromosomal set of the remaining Ethiopian endemics by Robertsonian translocations. It is a rather unexpected result because most African species of *Crocidura* have a high diploid number, generally with around 50 chromosomes and over 60 chromosomal arms. By contrast, all Palearctic and Oriental species have about 40 chromosomes or fewer and a relatively low fundamental number (Maddalena & Ruedi, 1994). Although African species of *Crocidura* are extremely numerous and cytogenetically diverse, only two species with diploid numbers of 36 were found in the rest of Sub Saharan Africa (*C. obscurior* from Ivory Coast and *C. luna* from Burundi) (Maddalena & Ruedi, 1994; Schlitter *et al.*, 1999). The only other 28-chromosomal karyotype (NF = 56) was found in *C. luna* from Zambia (Castiglia *et al.*, 2009). The karyotypes of *C. canariensis* Hutterer, López-Jurado & Vogel, 1987 (endemic to the Canary Islands), *C. sicula* Miller (endemic to Sicily and Malta), and *C. tarfayaensis* Vesmanis & Vesmanis (SW Morocco) are almost identical to those of the 36-chromosome Ethiopian endemics (Hutterer *et al.*, 1987; Vogel, 1988; Vogel *et al.*, 1990, 2006). The karyotypes of these species are strikingly similar to the presumed ancestral chromosome set of the genus *Crocidura* (2n = 38, NF = 54–58, Xm, Yst) reconstructed on the basis of chromosome banding homology (Maddalena & Ruedi, 1994). Therefore, we can suspect that a set of African species, including Ethiopian endemics, derived from an ancestral Palearctic branch of the genus.

Phylogenetic relationships within a restricted set of Ethiopian *Crocidura* were examined on the basis of repetitive DNA elements (taxonomic DNA fingerprint) and inter-SINE-PCR (IS-PCR) (Bannikova *et al.*, 2001; Bannikova *et al.*, 2005). In both cases it was concluded that all 36 chromosomal species endemic to Ethiopia that have been studied, form a monophyletic group of relatively recent origin. The latter analysis suggests that two other endemic species, *C. macmillani* (2n = 28) and *C. baileyi* (karyotype unknown), form a cluster, sister to the group comprising the 36 chromosomal endemics. The phylogenetic analysis of cytochrome b gene sequences (Lavrenchenko *et al.*, 2009) confirmed the monophyly of the group of Ethiopian endemics (*C. glassi*, *C. thalia*, *C. macmillani*, *C. baileyi*, *C. lucina*, and *C. yaldeni* **sp. nov.**) which was phylogenetically remote from the Afrotropical clade. Moreover, the analysis revealed sister relationships, although not confirmed statistically, between this group and the clade comprising species cytogenetically close to it (*C. canariensis*, *C. sicula*, *C. cf. bottegi*) and the Cretan endemic *C. zimmermanni* Wettstein characterized by a similar karyotype (2n = 34, NF = 44, Vogel *et al.*, 1990). Based on the results of the study, it was suggested that, in spite of their morphological diversity, all *Crocidura* species endemic to Ethiopia have resulted from a relatively recent adaptive radiation of an ancient lineage of *Crocidura* (Lavrenchenko *et al.*, 2009). Further detailed analysis of extended data sets (including *C. afeworkbekelei* **sp. nov.**) is needed to test this hypothesis.

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APPENDIX 1. List of specimens housed in the Zoological Museum of Moscow State University (ZMMU; Russia) used in the morphometrical analyses. Information given in the following order: specific name, abbreviation for figs 7 and 10 in parentheses, geographical locality, geographical coordinates in parentheses, year of capture, specimen ID, field IDs in parentheses, sample sizes in parentheses.

- Crocidura afeworkbekelei* sp. nov. (Af): Konteh Area of the Sanetti Plateau, Bale Mountains National Park, SE Ethiopia (06°51'N, 039°53'E), 1995—S-162643–644 (187, 196), S-162697 (189), (n = 3).
- Crocidura yaldeni* sp. nov. (Y): Western Plateau, Beletta Forest, SW Ethiopia (07°34'N, 036°31'E), 1995—S-165340–343 (20, 28, 30, 35), (n = 4).
- Crocidura* cf. *bottegi*: Central Ethiopia, Debre-Sina (09°50'N, 039°44'E), 2011—S-189291 (1924), (n = 1).
- Crocidura bottegoides*: Harena forest, Kacha, Bale Mountains National Park, SE Ethiopia (06°43'N, 039°44'E), 1995—S-162635 (73), (n = 1).
- Crocidura* cf. *hildegardeae*: Upper belt of the Harena Forest, Bale Mountains National Park, SE Ethiopia (06°45'N, 039°44'E), 1995—S-165167 (419), (n = 1).
- Crocidura harena* (H): Eastern Plateau, Bale Mountains, Shawe River, Harena Forest, SE Ethiopia (06°38'N, 039°44'E), 1995—S-162618 (61), S-162620–622 (63, 66, 67), S-162625 (74), (n = 5).
- Crocidura parvipes* (P): Western Plateau, Middle Godjeb Valley, SW Ethiopia (07°15'N, 036°47'E), 1998—S-166033–034 (757, 758), (n = 2).
- Crocidura glassi* (G): Eastern Plateau, Bale Mountains, Dinsho area, SE Ethiopia (07°06'N, 039°47'E), 1995—S-162638–640 (168–170), S-162698 (247), S-164853 (373), S-164855–856 (380, 378), S-164860–861 (505, 522), S-165161–162 (409, 417), (n=11).
- Crocidura lucina* (L): Central Ethiopia, Debre-Sina (09°50'N, 039°44'E) 2011—S-189286 (1905), (n = 1).
- Crocidura baileyi* (Bl): Northern Amhara region, Mount Guna near Yitba, NW Ethiopia (11°43'N, 038°15'E), 2001—S-172690 (1089), (n = 1).
- Crocidura macmillani* (M): Western Plateau, Middle Godjeb Valley, SW Ethiopia (07°15'N, 036°47'E), 1998—S-166029 (734), S-166031 (741), (n = 2).
- Crocidura thalia* (T): Eastern Plateau, Bale Mountains, Shawe River, Harena Forest, SE Ethiopia (06°38'N, 039°44'E), 1995—S-162627 (40); 1996—S-164858–859 (460, 465), S-165164–166 (466, 468, 473), (n = 6).
- Crocidura olivieri*: Western Plateau, Middle Godjeb Valley, SW Ethiopia (07°15'N, 036°47'E), 1998—S-166027 (733), (n = 1).

APPENDIX 2. List of voucher specimens housed in ZMMU analyzed with molecular or cytogenetic methods and used for qualitative morphological comparisons. Information is in the following order: specific name, specimen ID (followed by field ID in parenthesis), references, method of analysis, GenBank number in parenthesis.

- Crocidura afeworkbekelei* sp. nov.: S-162697 (189)—Lavrenchenko *et al.* (1997), cytogenetic analysis.
- Crocidura yaldeni* sp. nov.: S-165342 (30)—Bannikova *et al.* (2001, 2005), Lavrenchenko *et al.* (2009), molecular analysis (GenBank: EU742595.1); S-165343 (35)—Bannikova *et al.* (2001), molecular analysis.
- Crocidura glassi*: S-164853 (373)—Bannikova *et al.* (2001, 2005), molecular analysis; S-164856 (378)—Bannikova *et al.* (2001, 2005), Lavrenchenko *et al.* (2009), molecular analysis (GenBank: EU742598.1); S-164860 (505)—Bannikova *et al.* (2001), molecular analysis.
- Crocidura lucina*: S-189286 (1905)—unpublished data (corresponding to voucher specimen from GenBank: EU742603.1), molecular analysis.
- Crocidura baileyi*: S-172690 (1089)—Bannikova *et al.* (2005), Lavrenchenko *et al.* (2009), molecular analysis (GenBank: EU742596.1).
- Crocidura macmillani*: S-166029 (734)—Bannikova *et al.* (2001, 2005), Lavrenchenko *et al.* (2009), chromosomal and molecular analysis (GenBank: EU742601.1); S-166031 (741)—Bannikova *et al.* (2001), chromosomal and molecular analysis.
- Crocidura parvipes*: S-166033–034 (757, 758)—Bannikova *et al.* (2001, 2005), chromosomal and molecular analysis.
- Crocidura harena*: S-162620 (63)—Lavrenchenko *et al.* (1997), cytogenetic analysis; S-162621 (66), S-162625 (74)—unpublished data, cytogenetic analysis.
- Crocidura thalia*: S-165165 (468)—Bannikova *et al.* (2001, 2005), molecular analysis; S-165166 (473)—Bannikova *et al.* (2001, 2005), Lavrenchenko *et al.* (2009), molecular analysis (GenBank: EU742599.1); S-164858 (460)—Bannikova *et al.* (2001), molecular analysis.