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Resurrection of an East African house bat species *Scotophilus altilis* Allen, 1914 (Chiroptera: Vespertilionidae)

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Abstract

Several house bat specimens superficially resembling the white-bellied house bat *Scotophilus leucogaster* (Cretzschmar, 1830), were recently captured in southwestern Ethiopia and southern South Sudan. These *S.* cf. *leucogaster* differed from typical *S. leucogaster* by their slightly smaller size and ventral coloration, conforming instead with the original description of *S. altilis* Allen, 1914. *Scotophilus altilis* is an overlooked taxon known from the Blue Nile region in Sudan that is currently considered a junior synonym of *S. leucogaster*. Phylogenetic analysis of mitochondrial cytochrome *b* gene (*cytb*) sequences revealed *S.* cf. *leucogaster* as a sister clade to *S. leucogaster* with a genetic distance of ca. 10%. Comparative specimens of questionable *S. nigritellus* de Winton, 1899 from northwestern Ethiopia and a wing biopsy sample of another *S.* cf. *leucogaster* from western Kenya also fell within this clade. Sequence data from two nuclear markers (*zfy* and *fgb7*) corroborated the distinction of *S.* cf. *leucogaster* from *S. leucogaster*. Likewise, morphometric analysis of cranial data largely supported this distinction, as well as taxonomic affiliation with *S. altilis* based on comparison with the only available paratype specimen. The position of this paratype specimen within the new *Scotophilus* clade, inferred from analysis of a short fragment of *cytb*, confirmed its taxonomic identity. Based on the presented evidence, the overlooked East African taxon *S. altilis* should be resurrected as a full species within the genus *Scotophilus*.

Key words: yellow bat, white-bellied house bat, *Scotophilus leucogaster*, phylogeny, morphometrics

Introduction

Several house bats, genus *Scotophilus* Leach, of the family Vespertilionidae, were recently captured in southwestern Ethiopia and southern South Sudan and tentatively identified as the white-bellied house bat, *S. leucogaster* (Cretzschmar, 1830), a common species of the Sahelo-Sudanian zone of Africa. The specimens were slightly smaller than typical *S. leucogaster* and had aberrantly colored ventral pelage, light brown rather than white (Fig. 1). Due to sympatric occurrence with the unambiguously identified *S. leucogaster*, taxonomic affinity of these five *S.* cf. *leucogaster* specimens was challenged. The genus *Scotophilus* is known to be frequently misidentified and suffers from taxonomic uncertainties (Robbins *et al*. 1985; Goodman *et al*. 2005; Trujillo *et al*. 2009; Monadjem *et al*. 2010; Vallo *et al*. 2013; Vallo & Van Cakenberghe 2017; Demos *et al*. 2018). In 2013, the existence of a new species was reported from West Africa (Vallo *et al*. 2013). These taxa resembled in size the thus far smallest described *Scotophilus* species, *S. nigritellus* de Winton, 1899 although the ventral pelage coloration resembled *S. leucogaster*. Therefore, there may either be a relationship between the East African suspect *S.* cf. *leucogaster* and this West African form or two distinct taxa outside the content of the long acknowledged and familiar *S. leucogaster* may exist.

External morphology of the aberrant *S.* cf. *leucogaster* specimens matched the original description of *S. altilis* Allen, 1914, which was previously considered a candidate name for the West African *S.* aff. *nigritellus* (Vallo *et al*.

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2013). *Scotophilus altilis* is a neglected taxon currently considered a junior synonym of *S. leucogaster* (Aellen 1952; Koopman 1965, 1975, 1994; Kock 1969; Helgen & McFadden 2001; Simmons 2005; Van Cakenberghe & Happold 2013; Lanza *et al.* 2015). *Scotophilus altilis* was described as a new species from the Blue Nile region in Sudan as a comparably small bat with forearm length varying around 46 mm and grayish brown back, white chin and throat and pale drab chest and belly (Allen 1914; Fig. 1). Since its introduction, knowledge on this obscure, scarcely encountered form, has remained rather limited, both regarding actual distribution range and intrageneric taxonomic relationships. Only two bat specimens have ever been identified as *S. altilis* since its description, namely those from northeast of the nowadays Democratic Republic of the Congo (Allen *et al*. 1917). Thus, including the four specimens of the type series, the actual number of known specimens ever assigned to the name *S. altilis* is six.

Herein, taxonomic status of the suspect *S.* cf. *leucogaster* specimens from Ethiopia and South Sudan and its possible affiliation with *S. altilis* are assessed using phylogenetic analysis of partial sequences of one mitochondrial and two nuclear genes and morphometric analysis of cranial dimensions.

Material and methods

Sampling and DNA sequence analysis. Five specimens of *S.* cf. *leucogaster* originating from Mago National Park in southwestern Ethiopia (n=2) and Kajo Keji county in southern South Sudan (n=3) were included in this study (Fig. 2; Table 1). Additionally, two doubtful specimens of *S. nigritellus* from the Alatish NP, northwestern Ethiopia (cf. Kruskop *et al*. 2016), housed in the Zoological Museum of the Moscow State University, Russia (ZMMU), and a wing biopsy sample of *S.* cf. *leucogaster* captured at Lake Victoria in Kenya were included to confirm their taxonomic affinity (Fig. 2; Table 1). A paratype specimen of *S. altilis* from Bados in Sudan housed in the Field Museum of Natural History, Chicago, IL, USA, (FMNH) was also included in the analysis (Fig. 2; Table 1). The other three specimens from the type series were not readily available for comparison.

TABLE 1. Specimens of *S.* cf. *leucogaster* analyzed in this study. PT—paratype specimen of *Scotophilus altilis* Allen, 1914; *—originally identified as *S. nigritellus*; **—wing membrane biopsy only; †—partial 170-bp sequence; ††—amplified fragment identical to previously published sequences of *S. dinganii* morphospecies (Trujillo *et al*. 2009).

specimen	country	area	sex	coordinates	cytb	fgb7	zfy
NMP 95005	Ethiopia	Mago NP	m	05°40'N, 36°25'E	MK097177	MK097176	EU751004††
NMP 95006	Ethiopia	Mago NP	f	05°40'N, 36°25'E	MK097177	MK097176	-
ZMMU 189.608*	Ethiopia	Alatish NP	f	12°13'N, 35°53'E	MK097181	-	-
ZMMU 189.610*	Ethiopia	Alatish NP	m	12°23'N, 35°44'E	MK097182	-	-
USNM 590884	South Sudan	Kajo Keji	m	03°53'N, 31°39'E	MK097178	MK097176†	EU751004††
USNM 587015	South Sudan	Kajo Keji	f	03°57'N, 31°35'E	MK097179	MK097176†	-
USNM 587028	South Sudan	Kajo Keji	m	03°57'N, 31°35'E	MK097180	MK097176†	EU751004††
FMNH 34161 (PT)	Sudan	Bados	m	12°10'N, 34°19'E	MK097183	-	-
pww3006**	Kenya	Kisumu	f	00°07'S, 34°45'E	MH299586	-	-

Partial sequences of the mitochondrial cytochrome *b* gene (*cytb*) and introns of nuclear genes for beta fibrinogene (*fgb7*) and male-only zinc finger protein (*zfy*), respectively, were obtained from the ethanol-preserved tissue samples and analyzed as previously published by Vallo *et al*. (2013, 2015) using phylogenetic tree (for *cytb*) and network (for *fgb7*, *zfy*) approaches in programs MrBayes (Ronquist & Huelsenbeck 2003) and PAUP (Sinauer Associates, Sunderland, MA, USA), and Network (Fluxus Technology, Clare, Suffolk, UK; Bandelt *et al*. 1999), respectively. The respective sequence alignments included comparative sequences of African congeneric species from Vallo *et al*. (2013, 2015) and Trujillo *et al*. (2009). Due to the nature and age of the paratype specimen, a modified protocol was used for processing of DNA. In order to minimize contamination, the workplace and tools were sterilized using UV light and kit chemicals were used from yet unopened original containers. Remnants of dry tissue were scraped from inside of the skull with a dissecting needle. Prior to DNA extraction, the tissue was soaked overnight in sterile de-ionized water to soften. Tissue DNA Microprep Kit (Zymo Research, USA) was

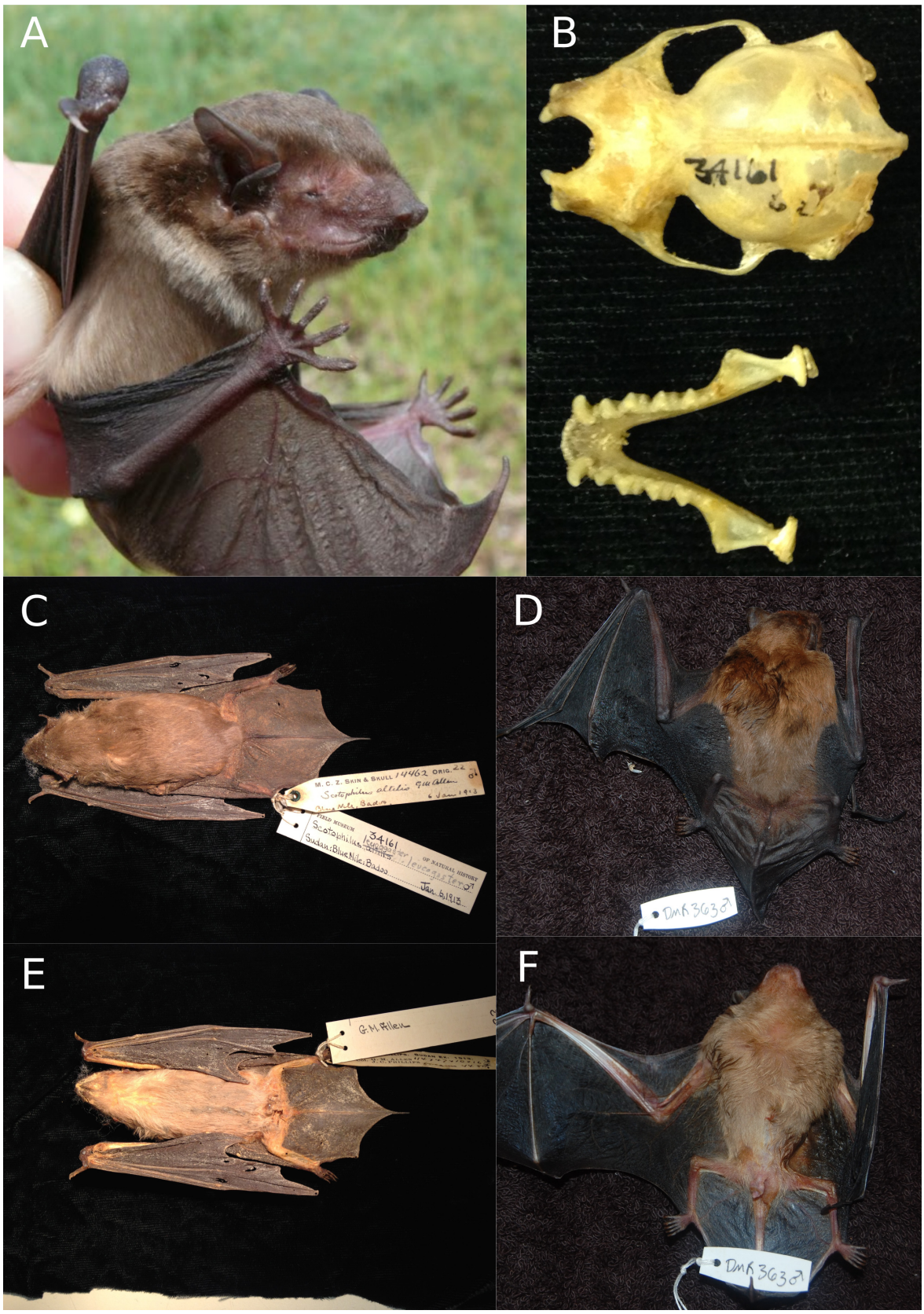

FIGURE 1. (A) External appearance of *Scotophilus* cf. *leucogaster* from SW Ethiopia; (B) dorsal view of skull and jaw, and (C) dorsal and (D) ventral view of the skin of the paratype specimen of *S. altilis* (FMNH 34161) from Bados, Kordofan, Sudan; (E) dorsal and (F) ventral view of *Scotophilus* cf. *leucogaster* (USNM 587028) from Kajo Keji, South Sudan. Photograph by A: P. Kaňuch, B–F: D.A.Reeder.

used for the DNA extraction following the manufacturer's protocol, with the elution step carried out twice using 10 µl of of elution buffer preheated to 60 ºC. A 181-bp fragment from 5'-end and a 110-bp fragment from the mid-section of *cytb* was amplified using the primer F1 (cf. Vallo *et al*. 2011, 2013, 2015) and the newly designed *Scotophilus*-specific primer scot_iR182 (5'-GYGACGGAGYTGAATGCTG-3'), and the *Scotophilus*-specific primer pair scot_iF518 (5'-GYGACGGAGYTGAATGCTG-3') and scot_iR629 (5'-GYGACGGAGYTGAATGCTG-3'). The PCR cocktail further contained TP 2x Master Mix (Top-Bio, Czech Republic), a hot-start PCR chemical mix containing trehalose and 1,2-propandiol for amplification of hard-to-amplify samples containing inhibitors of PCR. PCR products were purified using Small Fragments Purification Kit (Geneaid, Taiwan), and sequenced and analyzed in the same way as in the previous samples.

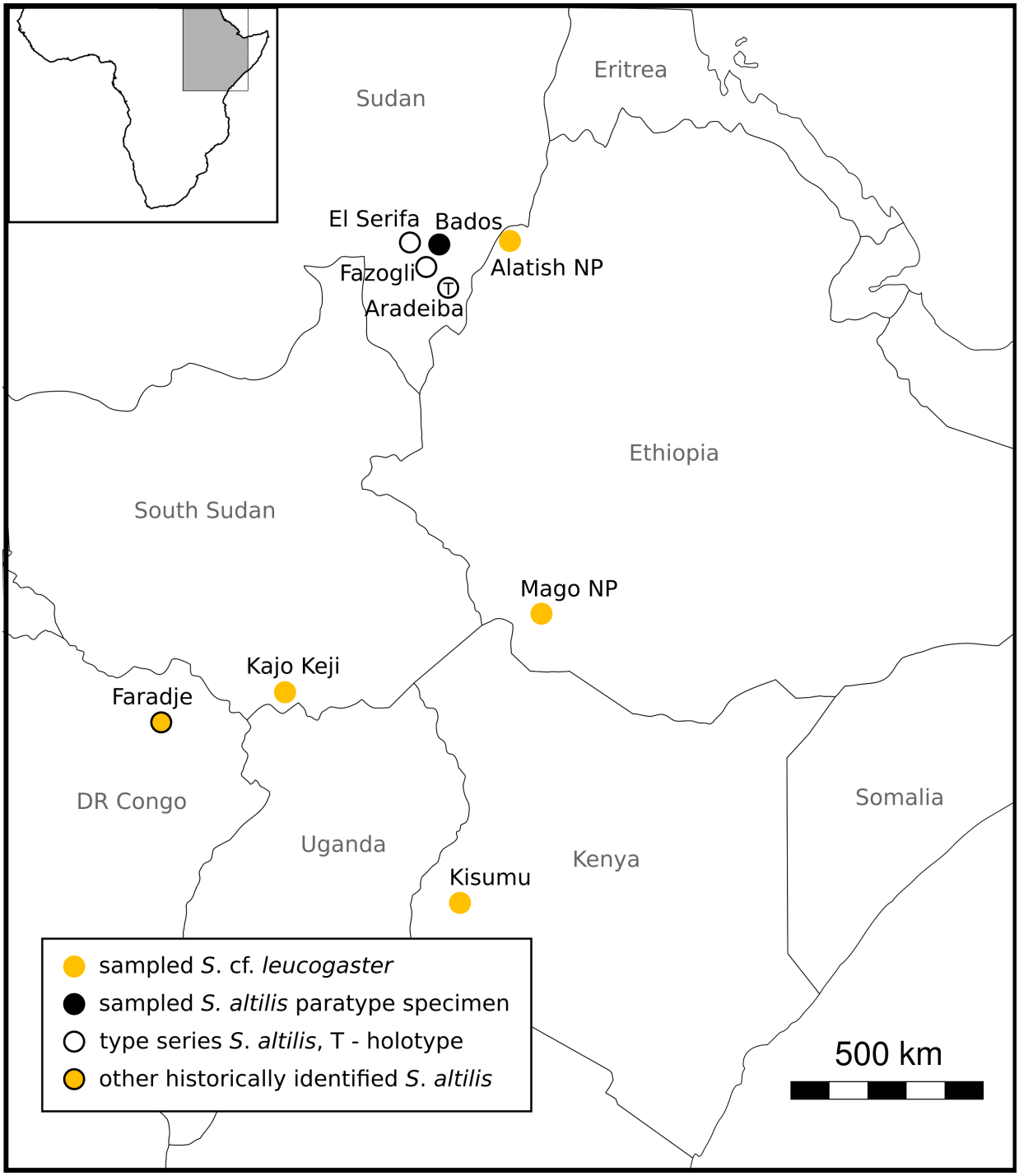

FIGURE 2. Distribution of localities of origin of the newly sampled and/or analyzed *Scotophilus* cf. *leucogaster* and known specimens of *S. altilis* based on Allen (1914) and Allen *et al*. (1917). The paratype specimen of *S. altilis* from Bados was included in the molecular and morphometric comparisons.

Morphological analysis. All specimens in the morphometric comparison were adult, as assumed from ossification status of large bone epiphyses. The analysis was carried out using comparative datasets from previously published study by Vallo *et al*. (2013) under univariate and multivariate approaches in program Statistica v.6 (StatSoft Inc., Tulsa, Ok, USA). The datasets included measurements of selected specimens of *S. leucogaster*, *S. nigritellus*, and *S.* aff. *nigritellus* (sensu Vallo *et al*. 2013). All comparative individuals were previously genetically identified. *S. nigritellus* and *S.* aff. *nigritellus* were chosen as size-relevant taxa of the category of small-sized *Scotophilus*, laying close to the size range of *S.* cf. *leucogaster*. Of the rather larger species *S. leucogaster*, the smallest individuals were chosen, to enable comparison within a reasonable size scale.

The specimens were measured at following dimensions: LAt—forearm length (incl. wrist); LCr—greatest length of skull; LCb—condylobasal length; LaZ—zygomatic width; LaI—width of interorbital constriction; LaInf—rostral width between foramina infraorbitalia; LaN—neurocranium width; LaM—mastoidal width; ANc—neurocranium height; LBT—largest horizontal length of tympanic bulla; CC—rostral width across upper canines; M^3M^3—rostral width across upper third molars; CM^3—length of upper tooth-row across canine and third molar; LMd—condylar length of mandible; ACo—height of coronoid process; CM^3—length of lower tooth-row across canine and third molar.

Results

***Mitochondrial* cytb.** A 920-bp fragment of *cytb* was obtained from the five new *S.* cf. *leucogaster* specimens from southwestern Ethiopia and southern South Sudan, and the two presumed *S. nigritellus* from northwestern Ethiopia and *S.* cf. *leucogaster* from Kenya. The specimens from southwestern Ethiopia and the specimens from northwestern Ethiopia were respectively represented by an identical haplotype. All these haplotypes clustered in a clade, which was in sister relationship to *S. leucogaster,* including the closely related mtDNA haplotype of *S.* aff. *nigritellus* (Fig. 3). Genetic divergence between haplotypes within the *S.* cf. *leucogaster* clade reached up to 2%. Genetic divergence of the *S.* cf. *leucogaster* clade from congeneric species varied between a minimum of 11.5–12.2% from *S. leucogaster* (including the *S.* aff. *nigritellus* haplotype) to a maximum of 18.8–19.4% from *S. kuhlii*.

The paratype of *S. altilis* from Bados yielded a 291-bp compound *cytb* fragment covering nucleotide positions 1–181 and 519–628. It was almost identical with the respective portions of the haplotypes of *S.* cf. *leucogaster*, differing from all of them by one unique T/C synonymous transition on position 174. The paratype specimen further shared two synonymous transitions with the haplotype of presumed *S. nigritellus* from northwestern Ethiopia, T/C and G/A on positions 588 and 612, respectively, which equaled a genetic distance of 0.3%. In the rather poorly resolved MP maximum parsimony tree, the 291-bp haplotypes of *S. altilis* and *S.* cf. *leucogaster* created a compact clade with internal genetic distance reaching up to 1.4% and differing by at least 9.3% from other *Scotophilus* species (Fig. 3).

Nuclear introns. *Fgb7* sequences 390 bp long were obtained from all five *Scotophilus* cf. *leucogaster* specimens (Table 1). The two specimens from southwestern Ethiopia were homozygous and their sequences identical (GenBank accession number MK097176). The South Sudanese specimens yielded an identical sequence to the Ethiopian specimens at the first 170 bp of the amplified fragment and showed length polymorphism of alleles beyond this position. The *fgb7* haplotype of *S.* cf. *leucogaster* differed from *S. leucogaster* by a 21-bp indel starting at position 153 of the alignment, which was 411 bp long after introduction of gaps, and two unique substitutions at positions 324 and 403. Additional six substitutions to those formerly mentioned and an indel 1-bp shorter than that in *S. leucogaster* were the differences to *S.* aff. *nigritellus*. The reconstructed network showed *S.* cf. *leucogaster* in a close relationship to *S. nigritellus*, from which it differed by only one substitution at position 324 and with which it shared the substitution at position 403, separating them from *S. leucogaster* (Fig. 4A).

Zfy sequences obtained from three males of *S.* cf. *leucogaster* in the length of 314 bp were identical and corresponded to partial haplotype of the *S. dinganii* morphospecies (EU751004–EU751010). It further differed by a 4-bp indel from *S. nigritellus*, by two substitutions and a 3-bp indel from *S.* aff. *nigritellus*, and by a 152-bp indel and five substitutions from *S. leucogaster* (Fig. 4B). Similarly as in the *fgb7* network, the sister relationship between *S.* cf. *leucogaster* and *S. leucogaster* inferred from mtDNA was not corroborated.

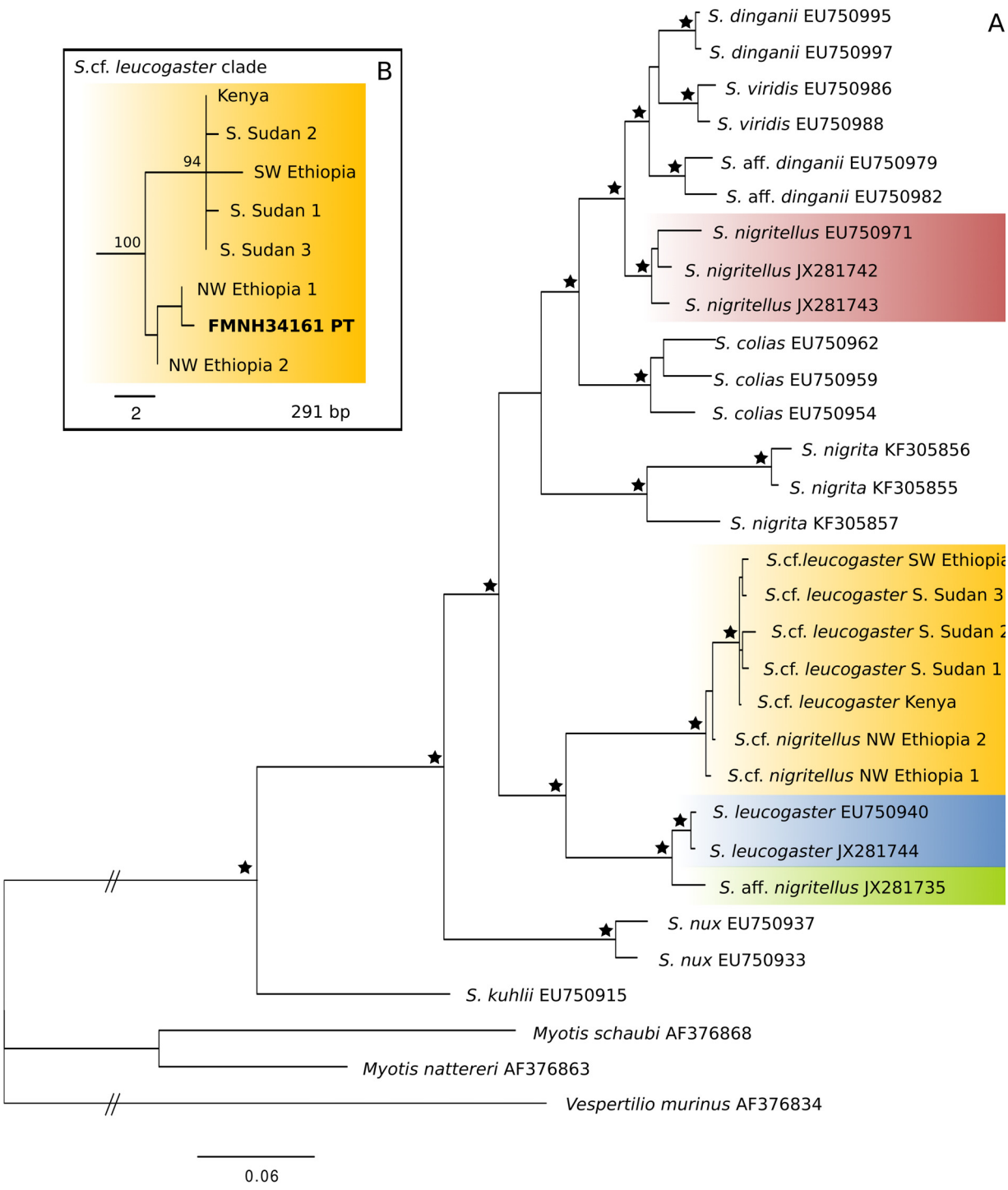

FIGURE 3. (A) Bayesian *cytb* tree based on 920-bp alignment showing phylogenetic position of *Scotophilus* cf. *leucogaster* within the genus *Scotophilus*. Posterior probability ≥ 0.95 is indicated with a star at the respective nodes. Branches of outgroup taxa are shortened for representational purpose. (B) MP *cytb* tree section based on 291-bp alignment showing relationship of *S.* cf. *leucogaster* and the paratype specimen of *S. altilis*. MP bootstrap support is indicated for the target clade. Color scheme introduced for easier visual identification of relevant species in this and all subsequent figures.

Cranial morphometrics. Comparison of cranial dimensions revealed the specimens of *S.* cf. *leucogaster* from southwestern Ethiopia and southern South Sudan and two presumed *S. nigritellus* from northwestern Ethiopia, to represent a morphotype of its own, differing in a series of characters from compared small-sized congeneric

species. In general skull size (LCb 15.28–16.67 mm; mean 16.11 mm), these bats roughly correspond to the larger specimens of *S. nigritellus*, being on average slightly larger. They are also larger than the samples of *S.* aff. *nigritellus* (Table 3). The largest individuals of *S.* cf. *leucogaster* overlap with the smaller specimens of *S. leucogaster*; the paratype specimen of *S. altilis* also falls within this overlap zone (Fig. 5; Table 2). However, *S.* cf. *leucogaster* skulls differ from the comparative specimens through their relative width (LaZ/LCb 0.75–0.71; mean 0.777; LaN/LCb 0.52–0.56; mean 0.546; LaM/LCb 0.67–0.70; mean 0.683). Moreover, their rostra are relatively the widest and shortest in the compared set (CM^3/LCb 0.35–0.38; mean 0.369 mm; LaInf/LCb 0.39–0.32; mean 0.404; CC/CM^3 0.97–1.05; mean 1.008). The examined paratype specimen of *S. altilis* falls within the variation range of *S.* cf. *leucogaster* at all skull dimensions (Table 3).

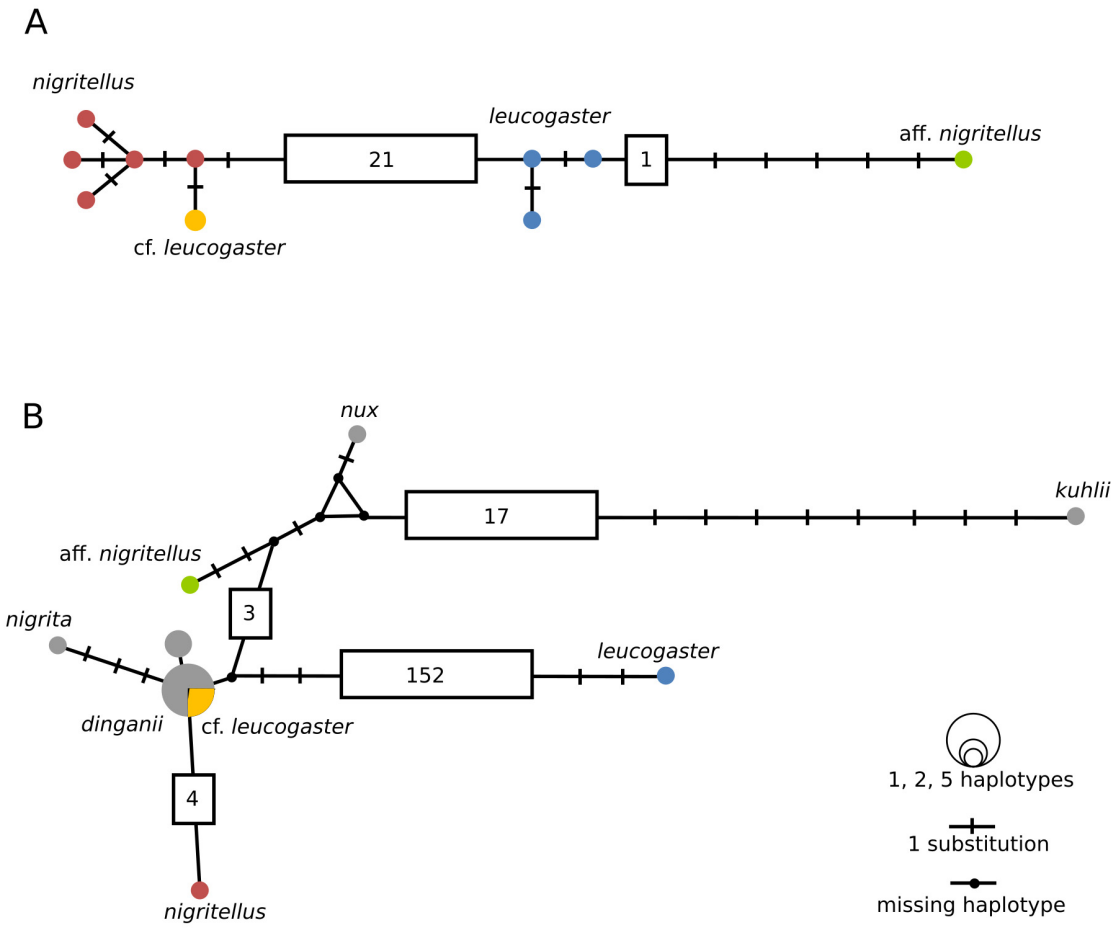

FIGURE 4. (A) *Fgb7* and (B) *zfy* median-joining networks showing alternative relationships of *Scotophilus* cf. *leucogaster* to other species of the genus *Scotophilus*. Haplotype frequencies are considered only in B, where identity of several sequences of *S. dinganii* morphospecies and *S.* cf *leucogaster* (section not proportional) was thus indicated. Color scheme as in previous figures.

The results of the principal component analysis (PCA) confirmed the mutual separation of all examined morphotypes of the small-sized *Scotophilus* bats (Fig. 6). For the PCA calculation, all 15 skull dimensions (see Table 3) and the above-mentioned relative dimensions were used. Eleven variables (LCr, LCb, LaZ, LaM, ANc, CC, M^3M^3, CM^3, LMd, ACo, CM_3) showed the highest loadings with absolute value exceeding 0.9 on the first principal component (PC1, 65.2% of variance explained), while the second principal component (PC2) was notably smaller (12.0% of variance explained) and influenced mostly by five variables describing the shape of rostrum and skull width (LaI, LaN, CM^3/LCb, CC/CM^3, LaN/LCb) with absolute value of loadings above 0.5. Each comparative set of specimens was constituted by a separate cluster; the cluster representing *S.* cf. *leucogaster*, best characterized by PC2 > 0.3, comprised also the paratype specimen of *S. altilis* (Fig. 6). On the other hand, the

holotype specimen of *S. nigritellus* clustered with other samples assigned to this species and was positioned neither close to the cluster of *S.* cf. *leucogaster* nor that of *S.* aff. *nigritellus*.

TABLE 2. Measurements of specimens of *S.* cf. *leucogaster* analyzed in this study. PT—paratype specimen of *Scotophilus altilis* Allen, 1914

dimension	NMP 95005	NMP 95006	USNM 590884	USNM 587015	USNM 587028	FMNH 34161 (PT)	ZMMU 189.608	ZMMU 189.610
LAt	43.7	45.3	49	48.1	46.4	44.5	47.1	46.9
LCr	16.53	17.21	17.02	17.79	17.46	17.31	16.62	16.93
LCb	15.28	16.18	16.45	16.67	16.39	16.23	15.92	15.88
LaZ	11.93	12.51	12.78	12.77	13.22	12.62	11.98	12.44
LaI	4.57	4.83	5.05	5.19	4.8	4.94	4.43	4.61
LaInf	6.02	6.37	6.9	6.93	6.72	6.83	6.36	6.24
LaN	8.38	8.91	9.05	9.25	8.98	9.35	8.34	8.63
LaM	10.68	11.02	11.24	11.17	11.19	11.16	10.68	10.98
ANc	7.01	6.81	6.94	7.12	6.9	6.88	6.94	6.86
LBT	3.58	3.54	3.11	3.13	2.91	3.19	3.68	3.75
CC	5.76	6.11	6.3	6.26	6	6.25	5.68	5.82
M^3M^3	7.63	8.05	8.27	8.05	8.09	8.05	7.64	7.46
CM^3	5.78	6.17	5.99	6.21	6.10	6.10	5.84	5.52
LMd	12.14	12.41	13.07	13.32	12.45	12.49	12.48	12.23
ACo	4.79	5.18	5.21	5.54	5.14	5.18	5.02	4.98
CM_3	6.51	6.94	7.00	7.24	6.75	6.83	6.67	6.43

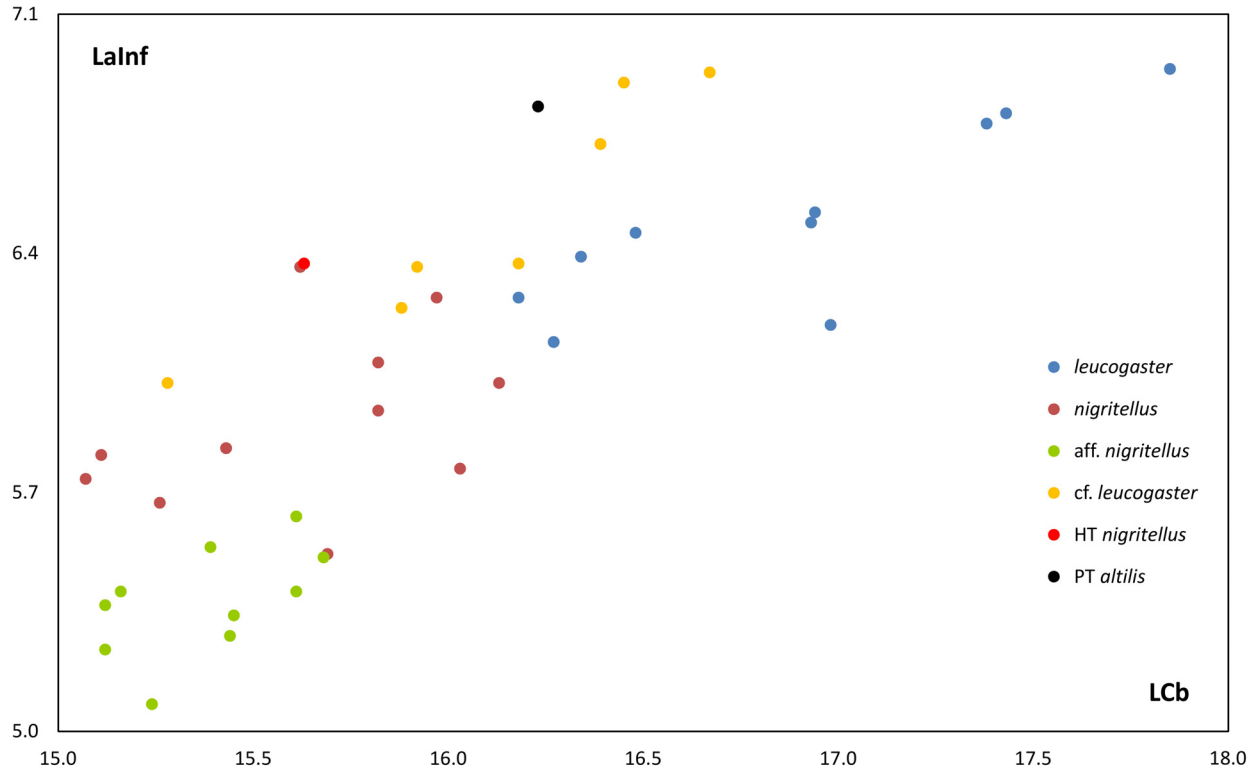

FIGURE 5. Bivariate plot of skull dimensions of examined *Scotophilus* specimens, using two specific measures: condylo-basal length of skull (LCb) and rostral width between foramina infraorbitalia (LaInf). PT—paratype specimen of *Scotophilus altilis*, HT—holotype specimen of *Scotophilus nigritellus*. Color scheme as in previous figures.

TABLE 3. Summary statistics of measurements of *Scotophilus* specimens analyzed in this study.

	S. cf. *leucogaster*					*S. leucogaster*				
	n	M	min	max	SD	n	M	min	max	SD
LAt	7	46.64	43.7	49.0	1.755	10	48.53	44.0	51.1	2.160
LCr	7	17.080	16.53	17.79	0.448	10	18.071	17.03	19.17	0.845
LCb	7	16.110	15.28	16.67	0.464	10	16.878	16.18	17.85	0.560
LaZ	7	12.519	11.93	13.22	0.459	10	13.025	12.44	13.94	0.501
LaI	7	4.783	4.43	5.19	0.271	10	4.744	4.54	4.87	0.121
LaInf	7	6.506	6.02	6.93	0.348	10	6.499	6.14	6.94	0.271
LaN	7	8.791	8.34	9.25	0.348	10	9.021	8.61	9.47	0.309
LaM	7	10.994	10.68	11.24	0.234	9	11.526	10.48	12.34	0.633
ANc	7	6.940	6.81	7.12	0.102	10	7.835	7.04	8.66	0.532
LBT	7	3.386	2.91	3.75	0.329	10	3.817	3.69	4.04	0.112
CC	7	5.990	5.68	6.30	0.245	10	6.344	5.94	6.91	0.290
M^3M^3	7	7.884	7.46	8.27	0.303	10	8.260	7.81	8.74	0.264
CM^3	7	5.944	5.52	6.21	0.247	10	6.443	6.13	6.71	0.206
LMd	7	12.586	12.14	13.32	0.440	10	13.302	12.92	14.18	0.386
ACo	7	5.123	4.79	5.54	0.233	10	5.283	4.91	5.98	0.315
CM_3	7	6.791	6.43	7.24	0.287	10	7.442	7.13	7.79	0.213
CM^3/LCb	7	0.369	0.348	0.381	0.011	10	0.382	0.375	0.396	0.006
LaZ/LCb	7	0.777	0.753	0.807	0.017	10	0.772	0.758	0.784	0.009
CC/CM^3	7	1.008	0.973	1.054	0.033	10	0.985	0.951	1.030	0.028
LaInf/LCb	7	0.404	0.393	0.419	0.011	10	0.385	0.365	0.392	0.008
LaM/LCb	7	0.683	0.670	0.699	0.010	9	0.680	0.648	0.710	0.023
LaN/LCb	7	0.546	0.524	0.555	0.010	10	0.535	0.510	0.567	0.015
	S. nigritellus					*S.* aff. *nigritellus*				
LAt	10	44.43	42.6	46.6	1.520	10	42.07	40.6	43.2	0.817
LCr	10	16.603	15.86	17.03	0.322	10	16.210	15.92	16.54	0.234
LCb	11	15.632	15.07	16.13	0.369	10	15.382	15.12	15.68	0.213
LaZ	9	12.009	11.53	12.49	0.296	8	11.305	10.98	11.44	0.151
LaI	11	4.183	3.98	4.43	0.139	10	4.457	4.36	4.55	0.062
LaInf	11	5.910	5.52	6.36	0.255	10	5.381	5.08	5.63	0.159
LaN	11	8.175	7.68	8.44	0.248	10	8.567	8.27	8.85	0.167
LaM	10	10.147	9.38	10.62	0.389	8	9.889	9.58	10.02	0.139
ANc	10	6.831	6.31	7.14	0.299	10	6.249	5.94	6.48	0.167
LBT	11	3.495	3.29	3.76	0.154	10	3.498	3.27	3.74	0.151
CC	11	5.735	5.49	5.92	0.157	10	5.481	5.31	5.58	0.085
M^3M^3	11	7.621	7.44	7.88	0.149	10	7.234	7.02	7.41	0.125
CM^3	11	5.857	5.76	6.09	0.108	10	5.628	5.48	5.84	0.110
LMd	11	12.095	11.78	12.61	0.253	10	11.666	11.32	11.93	0.189
ACo	11	4.768	4.47	5.09	0.167	10	4.367	4.17	4.47	0.090
CM_3	11	6.552	6.33	6.82	0.139	10	6.380	6.21	6.56	0.128
CM^3/LCb	11	0.375	0.364	0.386	0.008	10	0.366	0.355	0.372	0.005
LaZ/LCb	9	0.767	0.747	0.782	0.012	8	0.735	0.724	0.755	0.010

.....continued on the next page

TABLE 3. (Continued)

	S. cf. *leucogaster*					*S. leucogaster*				
	n	M	min	max	SD	n	M	min	max	SD
CC/CM[3]	11	0.980	0.901	1.021	0.037	10	0.974	0.950	1.005	0.017
LaInf/LCb	11	0.378	0.352	0.407	0.015	10	0.350	0.333	0.361	0.009
LaM/LCb	10	0.647	0.604	0.679	0.025	8	0.643	0.633	0.656	0.008
LaN/LCb	11	0.523	0.479	0.553	0.022	10	0.557	0.546	0.573	0.010

Discussion

Cytb sequence data from the suspicious *S.* cf. *leucogaster* specimens provide interesting evidence of the presence of yet another new evolutionary lineage within African *Scotophilus*. Its sister relationship with the sympatric *S. leucogaster* and pairwise genetic divergence over 10% to any congeneric taxon would support status of *S.* cf. *leucogaster* as a separate species (Baker & Bradley 2006; for *Scotophilus* cf. Jacobs *et al*. 2006; Trujillo *et al*. 2009; Vallo *et al*. 2011, 2013; Demos *et al*. 2018). Analysis of nucDNA also supports distinction of *S.* cf. *leucogaster* from *S. leucogaster*, although their sister relationship was not corroborated. The revealed nucDNA structure in both markers rather suggests incomplete lineage sorting, with the partial *zfy* haplotype corresponding with *S. dinganii* morphospecies and *fbg7* showing close relationship to *S. nigritellus.*

This newly identified *S.* cf. *leucogaster* clade, however, has a strong connection with a clade identified in a recent study by Demos *et al*. (2018; labeled as clade 7), which contains three specimens from Kisumu, Kenya. These taxonomically unidentified specimens likely originate from the same population as our sample and all four sequences are basically identical. This confirms that the herein presented *S.* cf. *leucogaster* and the *Scotophilus* sp. clade 7 by Demos *et al*. (2018) represent one and the same taxon.

Morphological separation of *S.* cf. *leucogaster* from compared *Scotophilus* species mirrors the separation revealed by DNA sequence data and supports its status as a distinct species. As the paratype specimen of *S. altilis* falls within the variation range of *S.* cf. *leucogaster* in molecular and morphological comparisons, the taxonomic identity of this species appears straightforward. It is interesting that this species with a rather broad latitudinal distribution has remained unnoticed for almost a hundred years. Obviously, this species has been present in museum collections or captured in recent bat surveys, like the specimens from the Alatish NP in northwestern Ethiopia identified as *S. nigritellus* (Kruskop *et al*. 2016) or the specimen sampled at Kisumu in Kenya. Earlier, Robbins *et al*. (1985) mentioned two small-sized *Scotophilus* from Ethiopia under the likely incorrect name *S. viridis* (Peters) that may also belong here, one from Mabil, 240 km south-east, the other one from Gambela, ca. 480 km south of the Alatish NP. Additionally an earlier report on bats of Sudan by Wettstein (1918) also mentions several small-sized and aberrantly colored *S. leucogaster* from nowadays northeastern South Sudan, ca. 400 km south-west from the type locality. Taxonomic identity of these specimens, however, is yet to be confirmed.

Taxonomic implications

Scotophilus altilis has likely been neglected over time due to its vague taxonomic delimitation and repeated synonymizations with other, largely acknowledged species, with only two specimens identified as *S. altilis* except the type series (Allen *et al*. 1917). A quarter of a century after the description of *S. altilis*, Allen (1939) himself synonymized this name with *murinoflavus* von Heuglin, 1861, another rather obscure taxon described from what is today Eritrea. Since this synonymization, the name *S. altilis* virtually disappeared from contemporary bat science. Several decades later Kock (1969) extracted *S. altilis* from *S. murinoflavus*, and placed it within the content of the currently acknowledged species *S. leucogaster*, as earlier suggested by Aellen (1952). This taxonomic opinion was later shared also by Koopman (1965, 1975, 1994). An alternative synonymization was suggested by Robbins *et al*. (1985), who tentatively included *S. altilis* into *S. viridis*, whose northern populations are currently recognized as *S. nigritellus* (Trujillo *et al*. 2009). Most recently, Helgen & McFadden (2001), Simmons (2005) and Van Cakenberghe & Happold (2013) returned to the opinion of Aellen (1952), Kock (1969) and Koopman (1965, 1975, 1994) and listed *S. altilis* again under the synonymy of the name *S. leucogaster*.

The herein presented molecular and morphological evidence clearly confirms the separate position of the newly captured specimens from Ethiopia, South Sudan and Kenya to other contemporary acknowledged *Scotophilus* species. Additional studies are required regarding another possible names for this distinct species, given the earlier synonymization with *S. murinoflavus*. This later taxon was recently mentioned as one of possible names existing for the yellow-bellied forms pertaining to the morphospecies *S. dinganii* in Ethiopia and Kenya by Vallo *et al*. (2011), for which *S. colias* Thomas, 1904, or later *S. andrewreborii* Brooks and Bickham, 2014, and *S. ejetai* Brooks and Bickham, 2014, were proposed. Based on its size and external appearance it seems that the earlier synonymization of *S. altilis* with *S. murinoflavus* by Allen (1939) was not justified. Later, Vallo *et al*. (2013) discussed the possible link of *S. altilis* to a newly discovered and yet undescribed small-sized *Scotophilus* species from West Africa (*S.* aff. *nigritellus*). However, these two morphologically delimited allopatric forms clearly represent independent evolutionary units as shown in the molecular genetic analysis. For the above mentioned reasons, we suggest the resurrection of the long neglected taxon name *S. altilis* for the respective populations of East African *Scotophilus* cf. *leucogaster*.

According to the available evidence, the newly resurrected *S. altilis* represents a small-sized representative of the genus, occurring in ca. 1400 km long belt of rather low elevation areas of the Nile basin (Fig. 2). This belt could be demarcated by the Blue Nile regions in southeastern Sudan and northwestern Ethiopia in the north, the area of most abundant records from five localities in an area of ca. 150×100 km, and the eastern banks of Lake Victoria in southwestern Kenya. Its southern distribution may extend westwards to northeastern DR Congo, as assumed from earlier comparison of the Faradje specimens to the paratype specimen from Bados by Allen *et al*. (1917). In this range, *S. altilis* occurs in broad sympatry with *S. leucogaster* (e.g. Kruskop *et al*. 2016), from which the former could be distinguished by slightly smaller size, but mainly by the conspicuous greyish-brown coloration of the belly (Fig. 1). It also occurs in sympatry or close parapatry with *S. colias* (sensu Vallo *et al.* 2011; unpubl. records), which, however, markedly differs by its bright pelage coloration, the yellow belly and reddish-brown back.

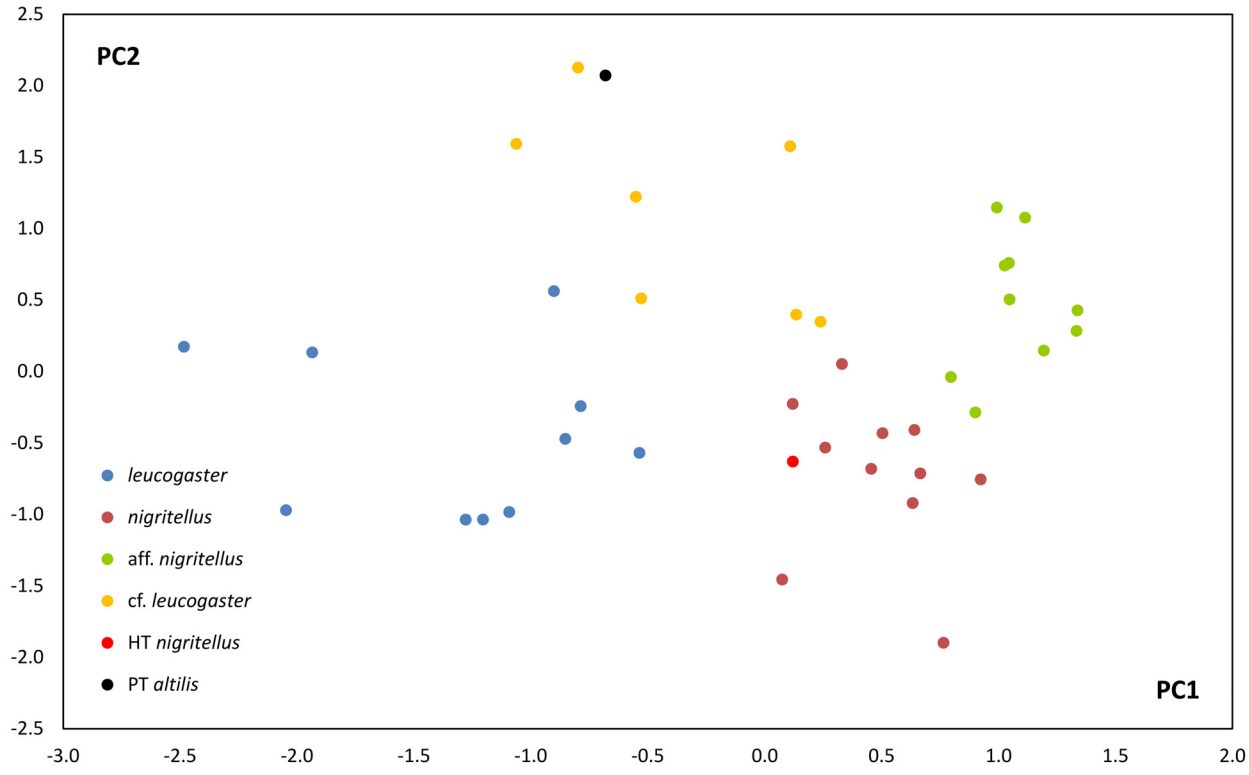

FIGURE 6. Plot of the first and the second principal component of the principal component analysis based on 15 skull dimensions of the examined *Scotophilus* specimens. PT—paratype specimen of *Scotophilus altilis*, HT—holotype specimen of *Scotophilus nigritellus*. Color scheme as in previous figures.

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