



Taxonomy/Taxonomie

Molecular taxonomy of *Crocidura* species (Eulipotyphla: Soricidae) in a key biogeographical region for African shrews, Nigeria

Joseph Igbokwe^{a,1}, Violaine Nicolas^{b,1}, Akinlabi Oyeyiola^c, Adeoba Obadare^c, Adetunji Samuel Adesina^d, Michael Olufemi Awodiran^a, Natalie Van Houtte^e, Elisabeth Fichet-Calvet^f, Erik Verheyen^{e,g}, Ayodeji Olayemi^{c,*}

^a Department of Zoology, Obafemi Awolowo University, HO 220005 Ile Ife, Nigeria

^b Institut de Systématique, Évolution, Biodiversité, ISYEB, UMR 7205 CNRS, MNHN, UPMC, EPHE, Muséum National d'Histoire Naturelle, Sorbonne Universités, 57 rue Cuvier, CP 51, Sorbonne, France

^c Natural History Museum, Obafemi Awolowo University, HO 220005 Ile Ife, Nigeria

^d Department of Biochemistry and Molecular Biology, Obafemi Awolowo University, HO 220005, Ile Ife, Nigeria

^e Biology Department, University of Antwerpen, Evolutionary Ecology Group, Universiteitsplein 1, B-2610 Wilrijk, Belgium

^f Bernhard-Nocht Institute of Tropical Medicine, Bernhard-Nocht-Straße 74, 20359 Hamburg, Germany

^g Royal Belgian Institute of Natural Sciences, Operational Direction Taxonomy and Phylogeny, Molecular Laboratory, Vautierstraat 29, 1000 Brussels, Belgium

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ABSTRACT

The taxonomy of African shrew species is still unresolved due to their conserved morphology. This also affects knowledge concerning their geographic distribution. In Nigeria, using mitochondrial Cytochrome *b* gene sequences, we carried out a survey for shrews from the genus *Crocidura* across various ecological zones to determine taxa that are present and also to assess their phylogeographic structure. Our analyses include 183 specimens collected with Sherman traps from 19 localities around the country. We detected six taxa: *Crocidura olivieri* lineages II, III and IV, *C. hildegardae*, *C. jouvenetae*, and *C. foxi*. Among these, *C. hildegardae* and *C. jouvenetae* are reported in Nigeria for the first time. Phylogenetic comparison of our genetic sequences to those generated from other parts of Africa demonstrate that all species in our study, as currently defined, are in need of taxonomic revision. Geographically, Nigeria seems to represent the easternmost boundary for *C. olivieri* lineage II and *C. jouvenetae*, and the western distribution limit of *C. olivieri* lineage IV and *C. hildegardae*. The Niger River appears to be the most significant topographical barrier restricting these taxa. This information is vital to preserving the diversity but also managing the epidemiological potential of these small mammals.

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* Corresponding author.

E-mail addresses: jospas2014@gmail.com (J. Igbokwe), violaine.colin@mnhn.fr (V. Nicolas), oyeyiola_akinlabi@yahoo.com (A. Oyeyiola), mekingarts@yahoo.com (A. Obadare), asadesina@yahoo.com (A.S. Adesina), michfemi@yahoo.com (M.O. Awodiran), natalie.vanhoutte@uantwerpen.be (N. Van Houtte), ecalvet@club-internet.fr (E. Fichet-Calvet), everheyen@naturalsciences.be (E. Verheyen), aolayemi@oauife.edu.ng, ayolayemi@yahoo.com (A. Olayemi).

¹ Joint first authors.

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1. Introduction

The shrew genus *Crocidura* (family Soricidae, order Eulipotyphla [1]) is the most speciose among African mammal genera [2]. These small mammals prey primarily on arthropods, earthworms, and molluscs [3], and are thus ecologically important as secondary consumers [4]. Shrews are relatively abundant, biologically and taxonomically diverse, have a restricted dispersal capacity, and are not subject to hunting pressure. Moreover, because of their short life span, they respond quickly to environmental changes. Thus they have been frequently used as model organisms for phylogeographic studies aimed at understanding factors driving faunal diversification in tropical Africa [5,6] and as bioindicators of habitat change [7–9].

African shrews also bear epidemiological significance because they are increasingly being discovered to be hosts of potentially zoonotic hantaviruses. In Guinea, *Crocidura theresae* and *Crocidura douceti* were detected as the reservoirs of Tanganya virus and Bowe virus, respectively [10,11]. In Ivory Coast, *Crocidura obscurior* was found to carry Azagny virus [12]. Within Tanzania, other shrews such as *Myosorex zinki* and *Myosorex geata* have been reported to host the Kilimanjaro virus and Uluguru virus respectively [13].

Identifying *Crocidura* specimens is notoriously difficult because of the high morphological similarity between species. The ensuing taxonomic uncertainties have resulted in the frequent grouping of taxa in so-called “species complexes” within which the number of species and their geographical distributions are highly debated. This lack of knowledge is a major problem for attempts to delineate appropriate units for biodiversity conservation and for investigations into the distribution ranges of species that may be carriers of zoonotic diseases. Nonetheless, contemporary studies using genetic sequences are beginning to contribute new insight [5,6,14–16].

Very little is known about the taxonomic diversity of shrews and their distribution ranges in Nigeria. In 1983, Hutterer and Happold [17] reviewed the bibliographical data and museum specimens available for this country. Since then, almost no work has been carried out on Nigerian shrews, and specimens from this country are only exceptionally included in recent regional phylogeographic or phylogenetic studies. Up to now, the few published shrew genetic sequences from Nigeria have been generated from a single locality in the southwestern part of the country, Ile Ife [6,18]. In a recent small mammal survey across vast portions of Nigeria, Olayemi *et al.* [19] listed all their shrew specimens as *Crocidura* spp. in order to avoid taxonomic misinterpretation.

Nigeria possesses topographical features such as major rivers already shown to be involved in the speciation of other small mammals [20,21]. Therefore, this geographic region not only represents a significant knowledge gap, it also offers a distinct opportunity to contribute to earlier studies on the molecular biogeography of Afrotropical shrews. For instance, the distribution ranges of certain *Crocidura* clades described in Jacquet *et al.* [6] that extend only up to the west or only to the east of Nigeria appear to

have their boundaries within the country. Furthermore, high altitude could also potentially affect species distribution. That the Jos plateau is home to endemics as the Nigerian Gerbil *Taterillus nigeriae*, the Ochre Mole-rat *Cryptomys ochraceocinereus* and the Klipspringer *Oreotragus* [22] illustrates this point. Another example is the unique montane forest ecosystem on the Mambilla plateau, where a new shrew species *Sylvisorex corbeti* was described [23] and collection records were made for the first time in Nigeria of other shrews *S. camerunensis*, *S. ollula*, and *Crocidura attila* [24]. Therefore, geographical distribution records, including those for *Crocidura* shrews, need to be adequately described.

Our objectives in the present investigation are, using mitochondrial gene sequences, to survey the *Crocidura* taxa present within Nigeria and to describe their distribution according to main rivers and ecological zonation.

2. Materials and methods

2.1. Specimen collection and sequencing

Using Sherman live-traps, the 183 shrew specimens included in this study were collected during 2011–2017 in 19 localities around Nigeria. These localities are distributed across key ecological zones such as the western and eastern flanks of both the Niger and Benue Rivers and along the Guinea savanna and rainforest vegetative belts (Fig. 1). Jos (Jos Plateau, 1280 m above sea level; locality 19) and Ngel Nyaki (Mambilla Plateau, 1650 m above sea level; locality 15) are situated on highlands where several endemic and rare small mammal species have been recorded [22,24]. During the period of the study, each locality was visited at least once in a session of three trap-nights, but certain localities were visited multiply. Traps were set in diverse habitats: inside houses (in kitchens, bedrooms and food storage areas), outdoors in domestic surroundings (including gardens and other sites close to the houses) and outdoors in wild vegetation (e.g., forest, savanna or river bank, depending on the locality). A broad designation of the habitat in which each specimen was captured appears in Appendix A. Our capture methods are described in detail in Olayemi *et al.* [19], with all voucher specimens preserved in ethanol at the Natural History Museum, Obafemi Awolowo University, Nigeria.

No experiments were carried out on living animals. Kidneys were dissected from euthanized specimens and preserved in ethanol. Total DNA was extracted from the kidneys using the Nucleospin Tissue kit (Machery Nagel, Düren, Germany) and the DNeasy blood and tissue kit (QIAGEN, Valencia CA, USA). The cytochrome *b* gene (*Cyt b*) was amplified using the following primers: L7 (ACC AAT GAC ATG AAA AAT CAT CGT T) and H15915 (TCT CCA TTT CTG GTT TAC AAG AC) [26]. Initial denaturation was carried out at 95 °C for 3 min, followed by 35 cycles of 94 °C for 30 s, 52 °C for 40 s, and 72 °C for 90 s. Amplicons were Sanger-sequenced and submitted to GenBank with accession numbers from MH996698 to MH996882 (Appendix A).

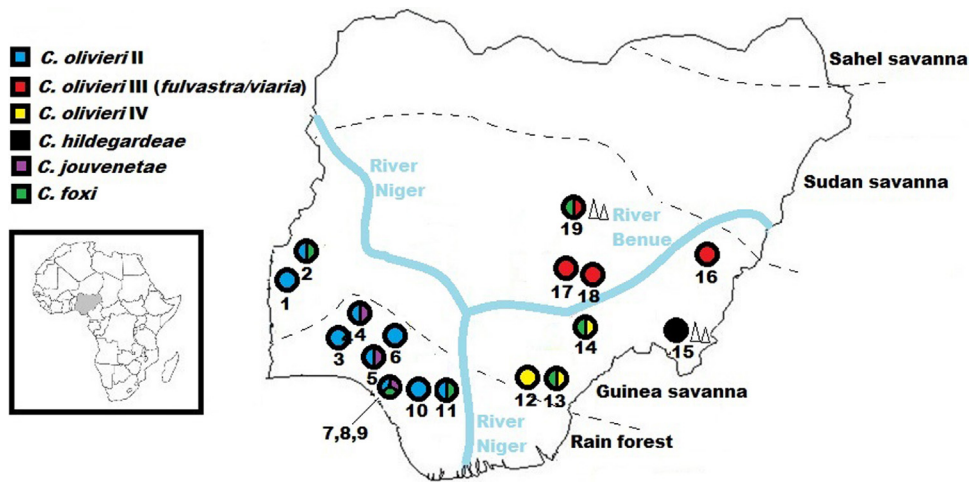


Fig. 1. Geographic distribution of *Crocidura* species and lineages resolved in this study. To the left is a map of Africa, with Nigeria in inset. Colours within the circles indicate the presence of each taxon (but not its relative abundance). Numbers below the circles represent localities as listed: 1) Bwen, 2) Gwanara, 3) Abagboro, 4) Kako, 5) Okeluse, 6) Ifon, 7) Eguare Egoro, 8) Ekpoma, 9) Ebudin, 10) Opoji, 11) Okhuesan, 12) Ndubia, 13) Abakaliki, 14) Onmba Abena, 15) Ngel Nyaki, 16) Mayo Ranewo, 17) Lafia, 18) Obi, 19) Jos. Localities in close proximity (7,8,9) are grouped under the same circle. Geographical coordinates are listed in the [Appendix](#). Triangles designate localities (15 & 19) within highland. Broken lines separate vegetative zones (adapted from Federal Ministry of Environment, Nigeria [25]). It must be noted that patches of derived savanna are scattered over the area classed under rain forest.

2.2. Phylogenetic analyses

The obtained sequences were compared to reference sequences in GenBank through a standard Nucleotide BLAST analysis (https://blast.ncbi.nlm.nih.gov/Blast.cgi?PAGE_TYPE=BlastSearch). As explained in the introductory section, the taxonomy of many *Crocidura* species is poorly known. Thus, the aim of our BLAST analysis was simply to be able to attribute each sequence to a given species complex. For each species complex, we then compared our sequences to all relevant published data and/or to unpublished sequences obtained by our team in recent years (details in [Appendices B–E](#)). Relationships among sequences were estimated by constructing phylogenetic trees using Neighbour Joining (NJ) phylogenetic analyses. NJ analyses were performed with PAUP 4b10 [27] using the K2P genetic distance. Bootstrap analysis (100 replicates) was used to estimate the robustness of the internal nodes. Note that the aim of this study was not to resolve the phylogeny or taxonomy of the analysed groups, but to provide new information about the distribution ranges of well-differentiated evolutionary lineages using the classical barcoding approach based on mitochondrial sequences in combination with available integrative taxonomy data in the selected groups.

3. Results and discussion

3.1. Notes on individual taxa

3.1.1. *C. olivieri* species complex Lesson, 1827

The 149 sequences attributed to the *C. olivieri* species complex based on the BLAST analysis were compared to those published by Jacquet *et al.* [6]. These authors highlighted the need for taxonomic revision of this complex: the species *C. olivieri* is polyphyletic and divided

into five geographical clades showing allopatric or parapatric distributions, while specimens of *C. viaria* and *C. fulvastra* form a single genetic clade. Our Nigerian specimens appear in three different clades: *C. olivieri* clade II, *C. olivieri* clade IV and the *C. viaria-fulvastra* clade III ([Figs. 1 and 2](#)). In Nigeria specimens of clade II were only captured west of the Niger River, which seems to represent the easternmost limit of its distribution range. Specimens of this clade were captured both in the Guinea savanna and rainforest zones. We record for the first time the presence of clade IV in Nigeria. This clade was only captured in the Guinea savanna east of the Niger River, which seems to represent the westernmost limits of its geographical distribution. According to Jacquet *et al.* [6], clade III is widely distributed from Senegal to Cameroon and Chad, but no specimen from Nigeria was previously sequenced. Our specimens fall within the genetic variability already recorded for that species. Clade III specimens were only captured in the Guinea savanna zone. According to Hutterer and Happold [17] *C. viaria* and *C. fulvastra* can be differentiated by ventral pelage and tail coloration. Based on these external characters, all our specimens from Nigeria fit more closely with *C. fulvastra*.

3.1.2. *C. hildegardae* species complex Thomas, 1904

One specimen (NGE777) was attributed to the *C. hildegardae* complex based on our BLAST analysis (88–89% identity with *C. hildegardae* from Tanzania and Kenya recently published by Stanley *et al.* [16]). This species complex is in need for revision. Based on 16S mitochondrial sequences, Quérouil *et al.* [28] and Dubey *et al.* [29] showed that *C. hildegardae* from Burundi, Gabon and Republic of Congo and *C. denti* from Central African Republic, Cameroun, and Democratic Republic of Congo cluster together and do not form separate genetic clades. In our NJ tree, we included all *C. hildegardae* sequences

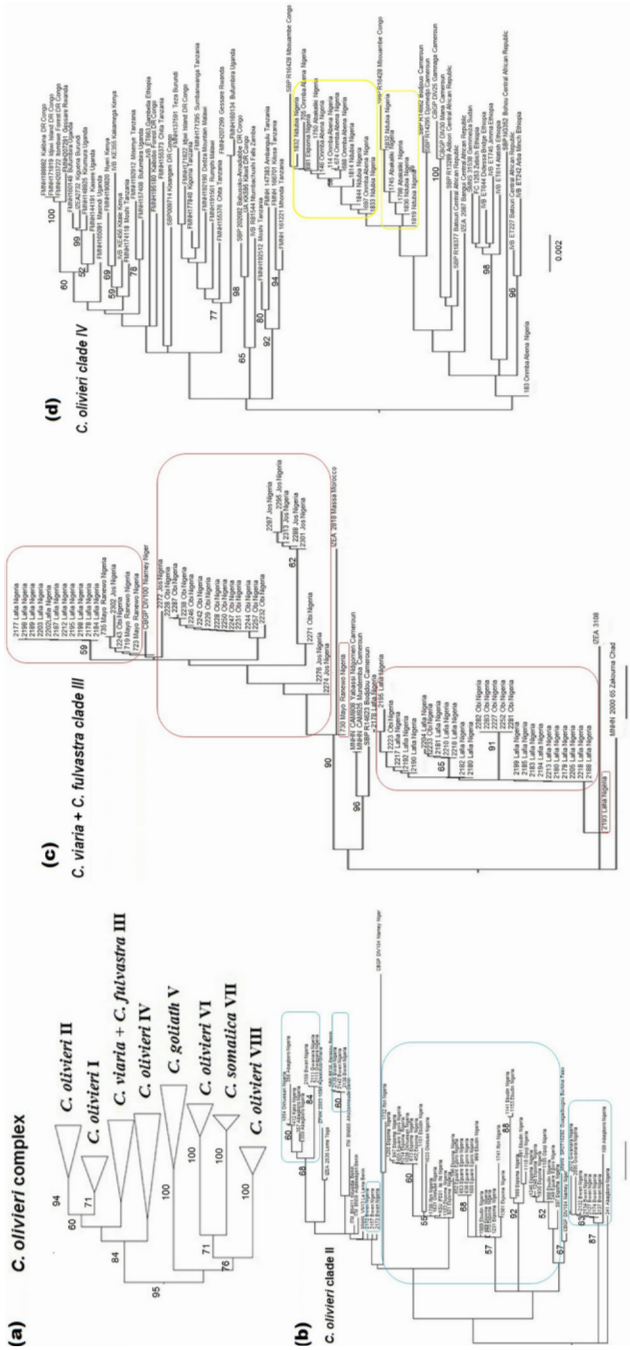


Fig. 2. Neighbour joining tree of the *Cyt b* gene including the sequences used by Jacquet et al. [6] in their Fig. 2. a: Condensed tree displaying various taxa within the species complex; b: *C. olivieri* clade II, with Nigerian sequences enclosed in blue; c: *C. varia* + *C. fulvastra* clade III, with Nigerian sequences enclosed in red; d: *C. olivieri* clade IV, with Nigerian sequences enclosed in yellow.

available in GenBank [30] as well as unpublished *C. hildegardae* and *C. denti* from Central Africa, and several representatives of the *C. poensis* species complex, which is known as the sister clade of the complex *C. hildegardae* – *C. denti* [29]. Our analyses confirm that *C. hildegardae* and *C. denti* are closely related and do not form two distinct monophyletic groups (Fig. 3). Moreover, within *C. hildegardae* – *C. denti*, two main clades can be identified: one grouping specimens from Central Africa (Nigeria, Gabon, Congo Republic and Central African Republic) and one grouping specimens from East Africa (Tanzania, Burundi, Kenya). This analysis confirms the urgent need for an integrative taxonomic revision of *C. hildegardae* and

C. denti. Neither *C. hildegardae* nor *C. denti* were previously known to occur in Nigeria.

3.1.3. *C. cf. juvenetae* Heim de Balsac, 1958

Nine specimens were identified as *C. cf. juvenetae* (93% identity with *C. cf. juvenetae* published by Vogel et al. [15] based on the BLAST analysis). *Crocidura juvenetae* was referred to as a subspecies of *C. crossei* [31–33]. However, Hutterer [34] considers the larger-sized *juvenetae* to represent a separate species. According to Happold [2] *C. juvenetae* is found in the rainforest biotic zone of West Africa, in southern Guinea, Liberia, and southern Ivory Coast, and it may also occur in Sierra Leone. *Crocidura*

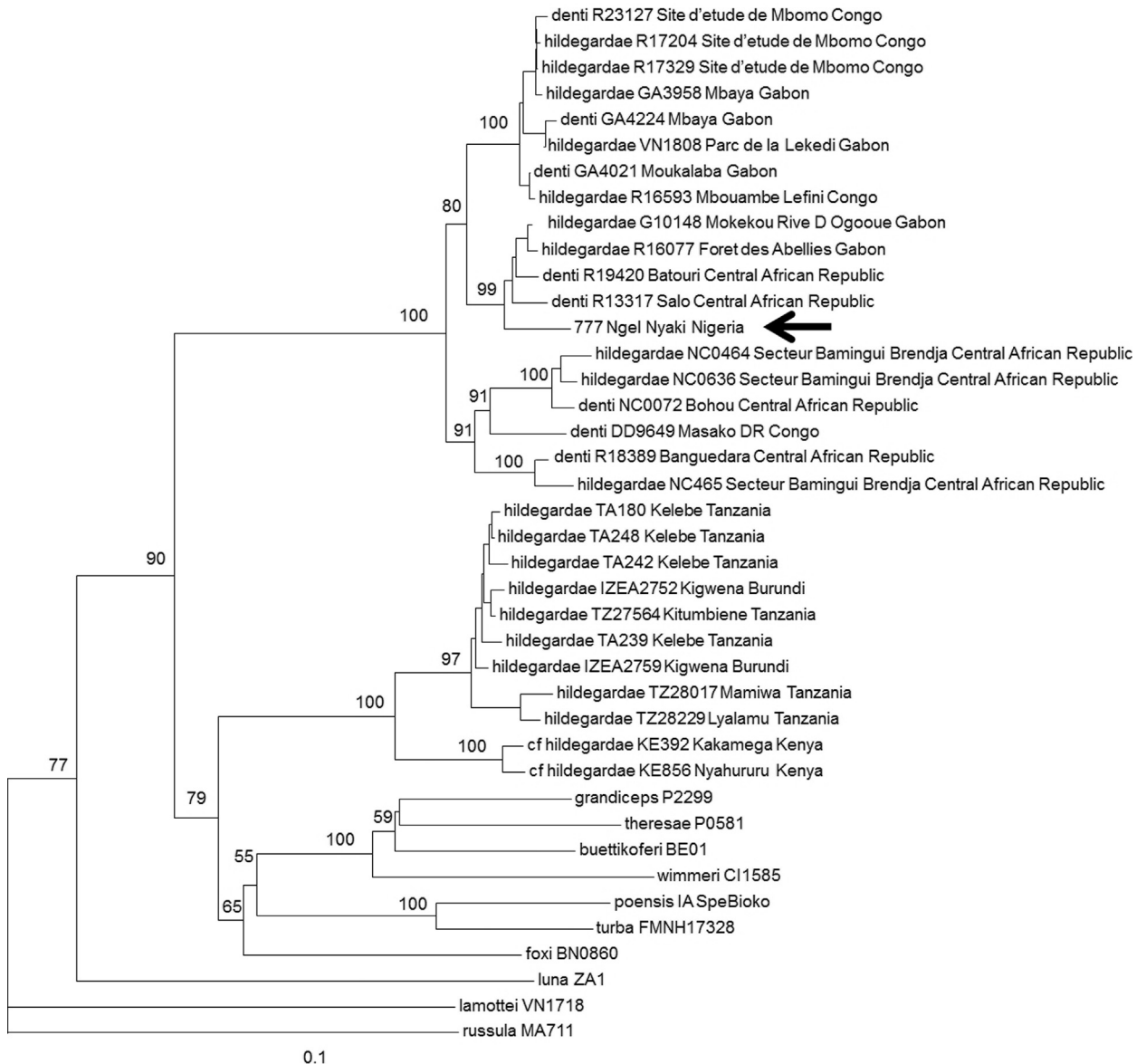


Fig. 3. Neighbour joining tree based on Cyt b sequences (1069 bp) of *C. denti* and *C. hildegardae* specimens. Representatives of the *C. poensis* species complex (*C. theresae*, *C. grandiceps*, *C. buettikoferi*, *C. wimmeri*, *C. turba*, *C. poensis*, *C. foxi*) were also included in this analysis, and *C. luna*, *C. lamottei* and *C. russula* were used as outgroups. The specimen from Nigeria (NGE777) is indicated by an arrow.

crossei has a larger distribution: it is known from the rainforest biotic zone, northern rainforest – savanna mosaic and Guinea savanna biotic zone from Guinea and Sierra Leone to western Cameroon. We compared our

sequences to all previously published *C. crossei* and *C. juvenetae* sequences [15,29,35] and Kang et al. (unpublished sequences available in Genbank) (Fig. 4). Our results confirm that the complex *C. juvenetae-crossei* is in urgent

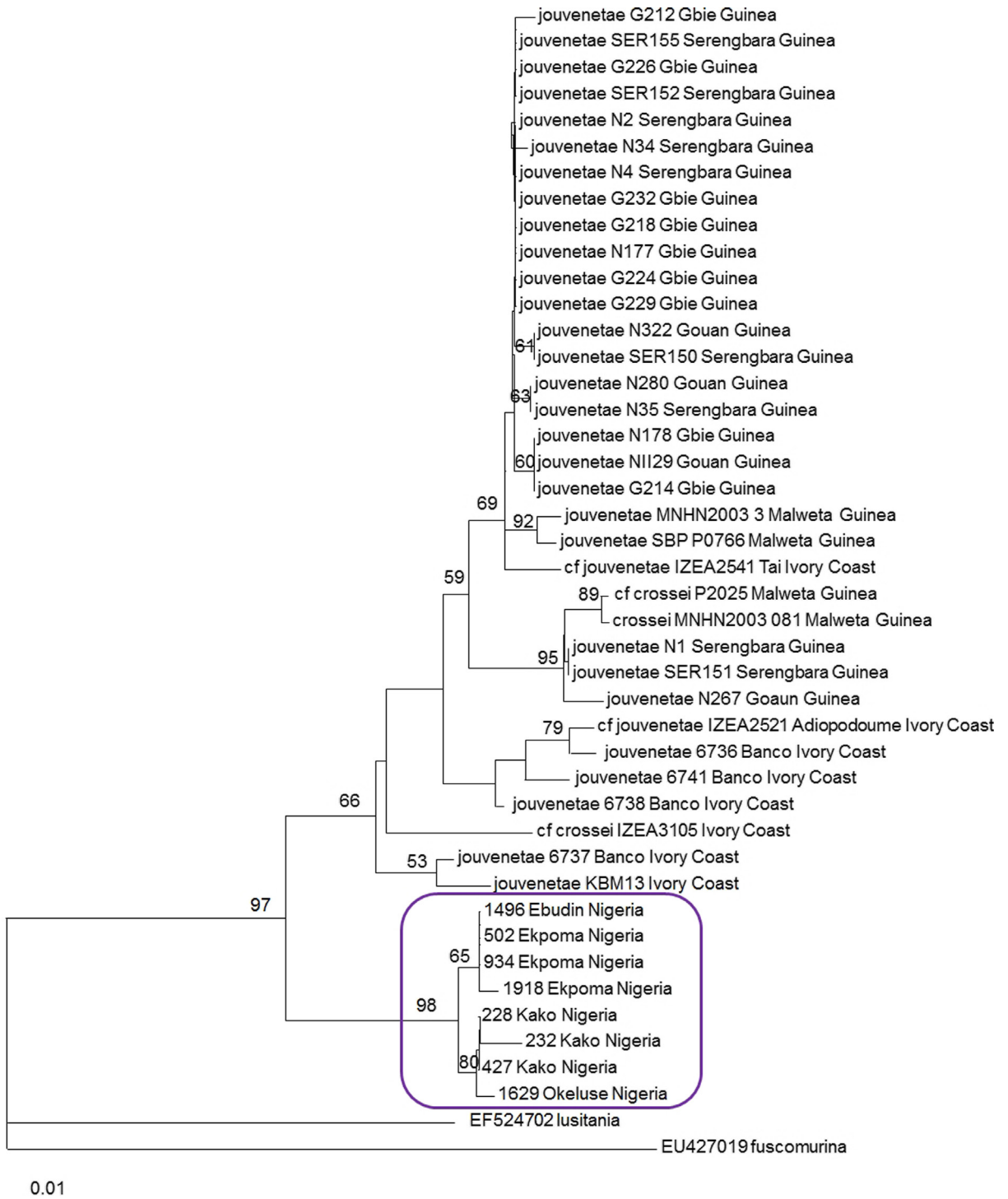


Fig. 4. Neighbour joining tree based on all available Cyt b sequences (402 bp) of *C. juvenetae* and *C. crossei*. The species *C. lusitania* and *C. fuscomurina* were used as outgroups. Specimens from Nigeria are encased in purple.

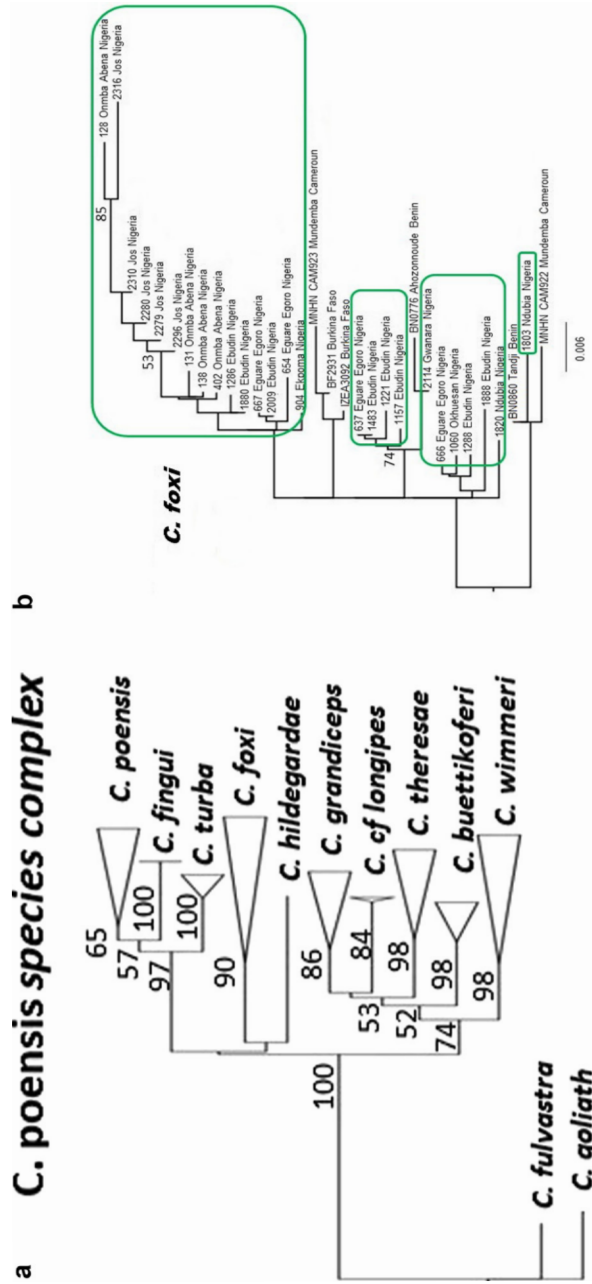


Fig. 5. Neighbour joining tree of the *C. poensis* species complex (1063 bp of the Cyt *b* gene), with a special emphasis on the species *C. foxi*. a: Condensed tree displaying various taxa within the species complex; b: *C. foxi*, with sequences from Nigeria enclosed in green.

need for integrative taxonomic revision, none of these species being monophyletic. All specimens from Nigeria cluster together with a strong bootstrap support, and they form the sister clade composed of all specimens from Guinea and Ivory Coast. All Nigerian specimens occur in the rainforest zone (Fig. 1).

3.1.4. *C. foxi* Dollman, 1915

Twenty-six specimens were identified as closely related (99% identity) to two specimens from Burkina Faso available in Genbank (DQ305278 and DQ521043) (Fig. 5). These two specimens are identified as “*Crocridura Crocidura theresae*” in GenBank and original publications [36,37], but they were later called *Crocridura cf. foxi* in subsequent studies [15,28]. *Crocridura foxi* and *C. theresae* both belong to the *C. poensis* complex, which was recently reviewed by Nicolas et al. [38]. The comparison of our sequences with those from Nicolas et al. allowed us to unambiguously identify the Nigerian specimens as *C. foxi*. This species is widespread in Nigeria: we caught it to the west and east of both the Niger and Benue Rivers, and both within the Guinea savanna and the rainforest (Fig. 1).

3.2. Biogeographical summary

The number of shrew taxa recorded in this study is small (6) compared to what has been described for Nigeria in the past (24 species in Hutterer and Happold [17], for instance). A reason for our low diversity could be the fact that we used only Sherman traps, which possibly attracts only certain taxa. Surveys in Gabon [39] and in the Congo Democratic Republic [40] demonstrated that pitfall traps are more efficient than Sherman traps for capturing shrews. Also, increasing our effort beyond the three trap-nights we spent in some localities might have yielded more variety. Nevertheless, our survey reports the

presence of two taxa detected within Nigeria for the first time: *C. juvenetae* and *C. hildegardeae*.

As could be expected, the Niger River appears to represent a significant physical barrier for several taxa, limiting *C. olivieri* lineage II and *C. juvenetae* on its right bank to western Nigeria (and by extension, West Africa) and *C. olivieri* lineages III, IV, and *C. hildegardeae* on its left bank to central and eastern Nigeria (expanding into northern, central and eastern Africa) (Fig. 6). Happold [22] reported 13 mammal species within Nigeria that occurred only on one side of the Niger River, but not on the other. The results of this study also show that the Benue River and/or the drier conditions towards the Sudan savanna in the North might play a combined role with the Niger River in limiting *C. olivieri* lineage IV and *C. hildegardeae* to eastern Nigeria.

Elevated topography (represented by the Jos and Mambilla plateaus) apparently does not influence the distribution ranges of the taxa encountered in this study. None of the species was endemic to the Jos plateau. The only *C. hildegardeae* specimen from Nigeria was found in montane forest within the Mambilla plateau, but specimens from Gabon, Republic of Congo, and Central African Republic were recorded in the lowlands [38].

With regard to habitat, specimens from this study belonging to the *C. olivieri* lineages and *C. foxi* were captured indoors, but also outdoors, in a wide range of domestic and wild vegetations (including lowland forest, savanna grassland, banana plants and fallow farmland; see Appendix). *Crocridura juvenetae*, on the other hand, was collected outdoors in domestic and wild vegetation (including lowland forest and grassland in forest clearings), while *C. hildegardeae* was captured only in wild vegetation (montane forest). Many *Crocridura* taxa have been described as commensal [2]. In Ekpoma, one of the localities sampled in this study, Olayemi et al. [41] detected two *Crocridura* specimens (later identified by Cyt b

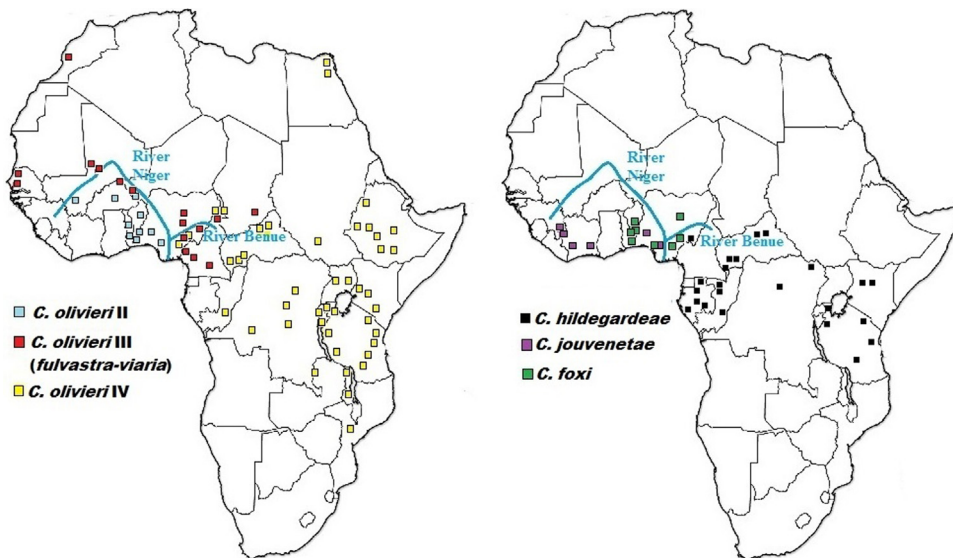


Fig. 6. Updated geographical distribution for *Crocridura* species detected in this study from Nigeria relative to molecular data compiled across Africa by Jacquet et al. [6] (to the left) and Nicolas et al. [38] (to the right).

sequencing as *C. olivieri* and *C. juvenetae*) with antibodies to the Lassa virus, which causes a deadly viral haemorrhagic fever in humans. They concluded that this was probably the result of a spill-over infection from proximity to the rodent *Mastomys natalensis*, which is known as the natural reservoir of this virus. These animals are usually found in the same peridomestic habitat. Again, this commensality along with the recent detection of hantaviruses [10–13] and bacteria [42] in *Crociodura* shrews highlights their zoonotic potential.

Overall our findings, like other recent studies employing molecular data, support the need for taxonomic revision of several taxa within the genus *Crociodura*. In addition, our survey demonstrates that Nigeria represents the geographical boundary of many *Crociodura* shrews, and is a region that must not be overlooked in the conservation and management of these animals.

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Disclosure of interest

The authors declare that they have no competing interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version at: <https://doi.org/10.1016/j.crv.2019.03.004>.

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