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SPECIAL ISSUE: AFRICAN SMALL MAMMALS

Integrative taxonomy of Guinean *Lemniscomys* species (Rodentia, Mammalia)

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Abstract. In the Republic of Guinea (West Africa), the diversity and distribution of striped grass mice of the genus *Lemniscomys* is poorly known. In the course of long-term field surveys from 2003 to 2011, we collected 97 specimens from various regions of Guinea with the aim of characterizing the morphological and genetic diversity of the genus in the country. We performed an integrative study that allowed us to detect the existence of at least two species in the collected specimens. Two molecular clades, corresponding to different karyotypes, were recovered. By comparison with type specimens and using classical morphometric analyses, we are able to confirm the presence of *L. linulus* and *L. striatus* in Guinea. We redescribe the skull and dental characters of the poorly known *L. linulus* and report its standard karyotype formula (2N = 56, NFa = 66). We did not collect any *L. zebra* in Guinea despite its presence in South Mali. In conclusion, the distributions of *L. striatus* and *L. linulus* described for Guinea and, including the previously reported *L. bellieri*, three species are now known to occur in this country. We recognise these three species as valid pending further revision of the genus at a pan-African scale.

Key words: West Africa, Muridae, taxonomy, cytb, morphometrics, cytogenetics

Introduction

Grass mice of the genus *Lemniscomys* Trouessart, 1881 are semi-diurnal, medium-sized rodents displaying stripes on their pelage. They are found all over Africa except in dense forests and deserts. To date, 11 species are recognized within this genus according to Monadjem et al. (2015), of which four are found in West Africa: *L. bellieri* Van der Straeten, 1975 whose type comes from the Ivory

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Coast (Lamto); *L. linulus* Thomas, 1910 described from Senegal (Gamon); *L. striatus* Linnaeus, 1758 described from Sierra Leone (no precision) and *L. zebra* Heuglin, 1864 described from Sudan (Bahr el Ghazal) (Musser & Carleton 2005, Wilson et al. 2017). The taxonomy of the genus is still debated and many synonyms have been described (Monadjem et al. 2015).

Located in West Africa, Guinea harbours a high biodiversity and is situated at the western margin of the Guineo-Congolian forest block. This country is dominated by three main vegetation types: Sudanian savannah, Guinean savannah and forest (Denys et al. 2005, White 1986). The lowlands of the coastal region display remnants of Guineo-Congolian primary and secondary forests or deciduous forest and bush with edaphic grasslands, the highlands of the Fouta Djallon (from 500 to 1500 m) are covered by Guinean transition savannah zone and riverine forest along rivers and edaphic grassland savannahs (Guinean and Sudanian ones). In the South-east of the country some isolated mountain ranges (Mount Nimba, Mount Ziama, Simandou) harbour mountain forest mosaic and represent hotspots of biodiversity (Olson & Dinerstein 1998, Myers et al. 2000) (Fig. 1).

There have been few taxonomic investigations on the genus *Lemniscomys* in Guinea with only a few references available. Previous studies have shown that *L. striatus* is present in forest localities in Guinea (Mount Nimba, Macenta) (Heim de Balsac & Lamotte 1958, Roche 1971). In a general list of Guinean mammals, Barnett & Prangley (1997) highlighted four species of *Lemniscomys: L. barbatus* (incorrectly designated as "*L. barbarous* = *L. zebra*)") and *L. striatus* as confirmed, and *L. bellieri* and *L. linulus* as possible. However, no *L. zebra* were confirmed in Guinea in recent revisions by Monadjem et al. (2015) and Wilson et al. (2017) and it is not listed in the Global Biodiversity Information Facility database (htt://www.gbif.org). Later, Denys et al. (2005, 2009) reported *L. striatus* in central and coastal Guinea. In an ecological study in central Guinea, in the Faranah region, Fichet-Calvet et al. (2009) found two species, *L. striatus* and *L. linulus,* in two localities in upper Guinea. The species identification of several of these specimens was confirmed by molecular methods by Nicolas et al. (2008) in a large-scale phylogeographic study of *L. striatus*. Ziegler et al. (2002) reported the presence of *L. bellieri* and *L. striatus* in woodlands of central Guinea in the Upper Niger National Park (Faranah NP). This is the single locality were *L. bellieri* has been reported in Guinea.

In the surrounding countries, Granjon & Duplantier (2009, 2011) confirmed *L. linulus* in South Mali (Mandingues Mountains, Bafing) and suggested its probable presence in Guinea in the same Sudanian savannah environment. Bellier & Gautun (1967) and Van der Straeten (1980) recorded *L. linulus* in the north of Ivory Coast (RCI). Thomas (1911) and Rosevear (1969) reported the species in Gemenjulla (West Senegal) (locality of the paratype of *L. linulus*), with the presence of a second species attributed to *L. barbarus oweni* = *L. zebra* according to Carleton & Van der Straeten (1997). Granjon & Duplantier (2009) indicated its sympatry with *L. linulus* in Sudanian savannah in Mali. Konečný et al. (2010) and Bâ et al. (2013) identified only *L. zebra* in the Niokolo Koba National Park on the Senegal side of the park, which borders Guinea, so it is highly possible that this species is present in the north of the country. *Lemniscomys striatus* was shown to be widely distributed in RCI and Sierra Leone (Nicolas et al. 2008, Decher et al. 2010).

Several cytogenetic works have been conducted on West African *Lemniscomys* (Table 1) and data are currently available for *L. bellieri*, *L. striatus*, *L. macculus* and *L. zebra*. Regarding Guinean specimens, a single published karyotype is available for *L. striatus* from coastal Guinea (Denys et al. 2009). No image of the karyotype of *L. linulus* is available for the region and only the standard formula was provided by Granjon & Duplantier (2009). *L. linulus* is known only from 11 specimens (three from east Senegal and eight from RCI). This species has never been genotyped and its morphological features have not been adequately illustrated. There is a similar paucity of information for *L. bellieri* for which species diagnosis is based only upon relative craniometrical characters (Van der Straeten 1975, 1980). No specimens of these two species have been examined using an integrative taxonomic analysis and by reference to type specimens.

Recent fieldwork (2003-2011) in Guinea enabled us to collect new specimens that can serve to fill the knowledge gap on the taxonomic diversity and geographical distribution of *Lemniscomys* species in Guinea. The aims of this paper are: 1) to redescribe *L. linulus* and *L. bellieri* using an integrative

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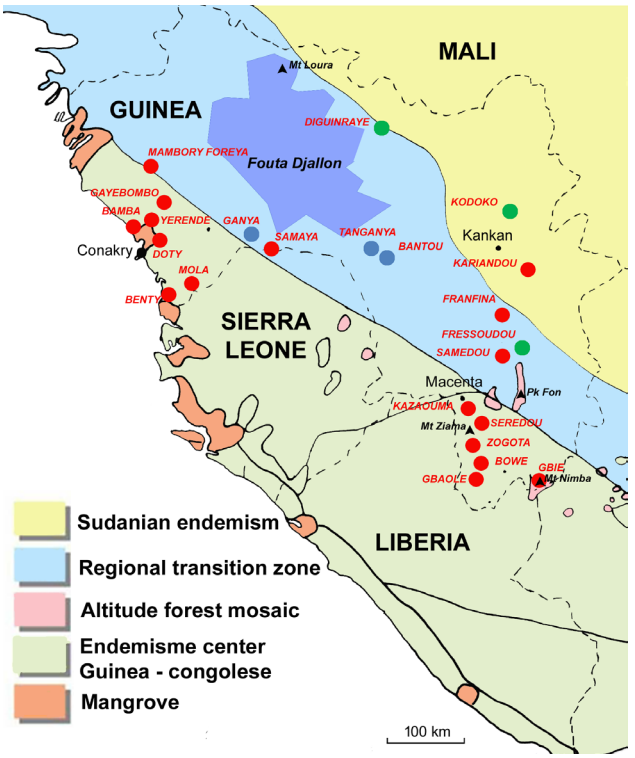


Fig. 1. Vegetation map of Guinea (after White 1986) with the distribution of sample sites and associated taxa. Blue dots: localities where *L. linulus* and *L. striatus* are found together, green dots: *L. linulus* only, red dots: *L. striatus* only. In purple the Fouta Djallon Plateau. Mt = Mount, Pk = Peak.

approach, 2) to propose a new identification key for the four species of *Lemniscomys* in West Africa, based upon genetically typed specimens and on examination of type specimens; and 3) to provide a basis for understanding the distribution and the number of *Lemniscomys* species in Guinea.

Material and Methods

Sampling

Between 2003 and 2011 we collected 97 *Lemniscomys* specimens in Guinea from 25 localities (Fig. 1). Superficially at least, these specimens divided into two morphological groups: 19 specimens bearing a single dorsal black stripe and 78 specimens with multiple dorsal stripes. Rodents were sacrificed following the recommendation of Sikes et al. (2016) and standard measurements were taken (weight, body length, tail length, hind foot length, ear length), as well as notes on their reproductive state. Liver and spleen samples were fixed in ethanol for molecular analyses. Bone marrow was extracted from femurs for preparation of standard karyotypes. Carcasses of whole animals were preserved in 5% formalin and skulls were cleaned and prepared for measurement.

Table 1. Standard karyotypes of West African *Lemniscomys* species from the literature and this study.

Species	Karyotype	Country	Reference
L. bellieri	2N = 56, NF = 78	Lamto, RCI	Van der Straeten & Verheyen 1978
L. bellieri	2N = 56	Lamto, Foro RCI	Tranier & Gautun 1979
L. bellieri	2N = 56, NFa = 60	Lamto, RCI	Volobouev, unpublished
L. striatus	2N = 44	RCI	Tranier, Dosso et Gautun, unpublished
L. striatus	2N = 44, NFa = 58	Adiopodoumé, Dabou, Lamto, Mopoyem RCI	Van der Straeten & Verheyen 1978
L. striatus	2N = 44, NFa = 58	Lamto, RCI	Ducroz (1998)
L. striatus	2N = 43, 44	Banfora, Burkina Faso	Gautun et al. 1985
L. striatus	2N = 44, NFa = 68	Benin	Castiglia et al. 2002
L. striatus	2N = 44, NFa = 58	Naso, Burkina Faso	Van der Straeten & Verheyen 1985
L. striatus	2N = 44, NFa = 66	Yerende, Tanganya, Bantou Guinea	Denys et al. 2009, this study
L. striatus	2N = 44, NFa = 72-74	Atcherigbé, Tanougou Avakpa, Benin	Capanna et al. 1997
L. linulus	2N = 56, NFa = 64	Baffing, Mts. Mandingues Mali	Granjon & Duplantier 2009
L. linulus	2N = 54, NFa = 58	Bouna, RCI	Mathey 1954 under *L. griselda*
L. linulus	2N = 56, NFa = 66	Bantou, Tanganya, Guinea	This study
L. zebra	2N = 54, NFa = 58	La Tapoa, Niger	Dobigny et al. 2002
L. zebra	2N = 54, NF = 58	RCI	Matthey 1954
L. zebra	2N = 54, NFa = 58	N. Cameroon, Chad	Dobigny et al. 2011
L. macculus	2N = 56, NFa = 60	CAR, Ethiopia	Matthey unpublished, Ducroz et al. 2001, Bulatova et al. 2002

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Molecular analyses

Total genomic DNA was extracted following the CTAB method as described in Winnepenninckx et al. (1993). For the 28 new specimens sequenced, a large part of the cytochrome *b* gene (cyt*b*) was amplified using PCR primers L7 (5′-ACCAATGACATGAAAAATCATCGTT-3′) and H14896 (5′-TAGTTGTCGGGGTCTCCTA-3′) or H15915 (5′-TCTCCATTTCTGGTTTACAAGAC-3′). The PCR consisted of an initial denaturation for 3 min at 94 °C, followed by 38 cycles: 30 s at 94 °C, 40 s at 52-55 °C and 90 s at 72 °C. The reaction was completed by a final extension for 10 min at 72 °C. PCR Products were purified and commercially Sanger-sequenced at EUROFINS (by Automatic Sequenceur ABI 3730).

Numerous cyt*b* sequences are available in GenBank for *L. striatus*. Nicolas et al. (2008) showed a strong phylogeographic structure for this species with only one lineage (IV-1) present in Guinea. We included in the present study all specimens from Guinea available in GenBank. For other lineages we retained only one specimen per lineage. For other *Lemniscomys* species all sequences available in GenBank were included in our study, as well as several newly sequenced specimens, giving a total of 62 individuals (Table S1).

For phylogenetic analyses, we retained a fragment on 846 bp available for most specimens. Evolutionary relationships among sequences were estimated by constructing a phylogenetic tree using Bayesian inference. We used several Arvicanthini to root our tree: *Lamottemys okuensis*, *Desmomys harringtoni*, *Rhabdomys pumilio*, *Mylomys dybowski*, *Pelomys campanae*, *Dasymys incomtus* and *Arvicanthis niloticus*. The computer program MRMODELTEST ver. 2 (Nylander et al. 2004) was used to evaluate the fit of 24 nested models of nucleotide substitution in the data. The model chosen by MRMODELTEST according to the Akaike information criterion (GTR + I + G) was subsequently used for Bayesian analysis. Bayesian inference was performed with MRBAYES ver. 3.2.5 (Ronquist et al. 2012) using 5 million generations (burnin = 25%), sampling every 1000 steps. Convergence between chains was checked by manual inspection using the 'sump' command and by using the mean SD of split frequencies, which was below 0.01 in our runs, as an indicator of convergence.

Cytogenetics

Standard karyotype analysis of eight individuals (four multi-striped specimens and four single-striped individuals) from two localities (Tanganya and Bantou) was performed under field conditions using the colchicine method of Lee & Elder (1980) detailed in Denys & Aniskin (2012) (Table S1).

External and skull morphometry

Morphological observations of skulls were performed using microscopy. Molars were drawn with the use of a camera lucida and skulls photographed with a Canon EOS reflex camera. The dental nomenclature follows Monadjem et al. (2015). A classical morphometrics analysis was performed using new specimens and comparisons with holotypes from the NHM London, the MRAC Tervuren, the ZFMK Bonn, the SMNS Stuttgart and previously karyotyped individuals of the MNHN Paris collections (Table S1). Skull measurements were taken with a MITUTOYO calliper using the protocol of Denys et al. (2012). Following a repeatability test, 10 skull and three mandibular measurements were retained: LGT (greatest length of the skull), WNAS (width of nasals across the points where maxillofrontal sutures contact nasals), LNAS (maximal length of nasals), CIO (inter-orbital constriction width), WZYG (bizygomatic width), WPAR (maximal posterior width of the skull at the level of the interparietal), LPAL (length of incisor foramen), OCCPAL (post-palatal length), LS13 (upper tooth row length), LBT (tympanic bulla length), HMDB (maximal height of the mandible), LMDB (length of the mandible) and LI13 (lower tooth row length). Molars are abbreviated as follows: M1/, M2/, M3/ upper M123, M/1, M/2, M/3 lower M123.

Univariate and multivariate morphometric analyses were performed using external and skull measurements with XLSTAT version 10.1 software (Addinsoft). T-tests were employed to compare distributions of each variable for each species. We used discriminant function analysis (DFA) on log-transformed external measurements and skull distances based only on genetically-typed specimens and holotypes and topotypes in good condition (Table S1). Because not all specimens are integrally preserved (broken tails, broken skull bones, etc.) there was some variability in the number of individuals (N) for each variable. In total we observed the skins and measured the skulls of 31 *L. linulus*, including the holotype and a paratype, 58 *L. striatus* including the holotypes of *L. s. venustus* and *L. s. pulchella*, 14 *L. bellieri* including the holotype, five paratypes and five topotypes. We performed comparisons with *L. zebra* and *L. macculus* holotypes.

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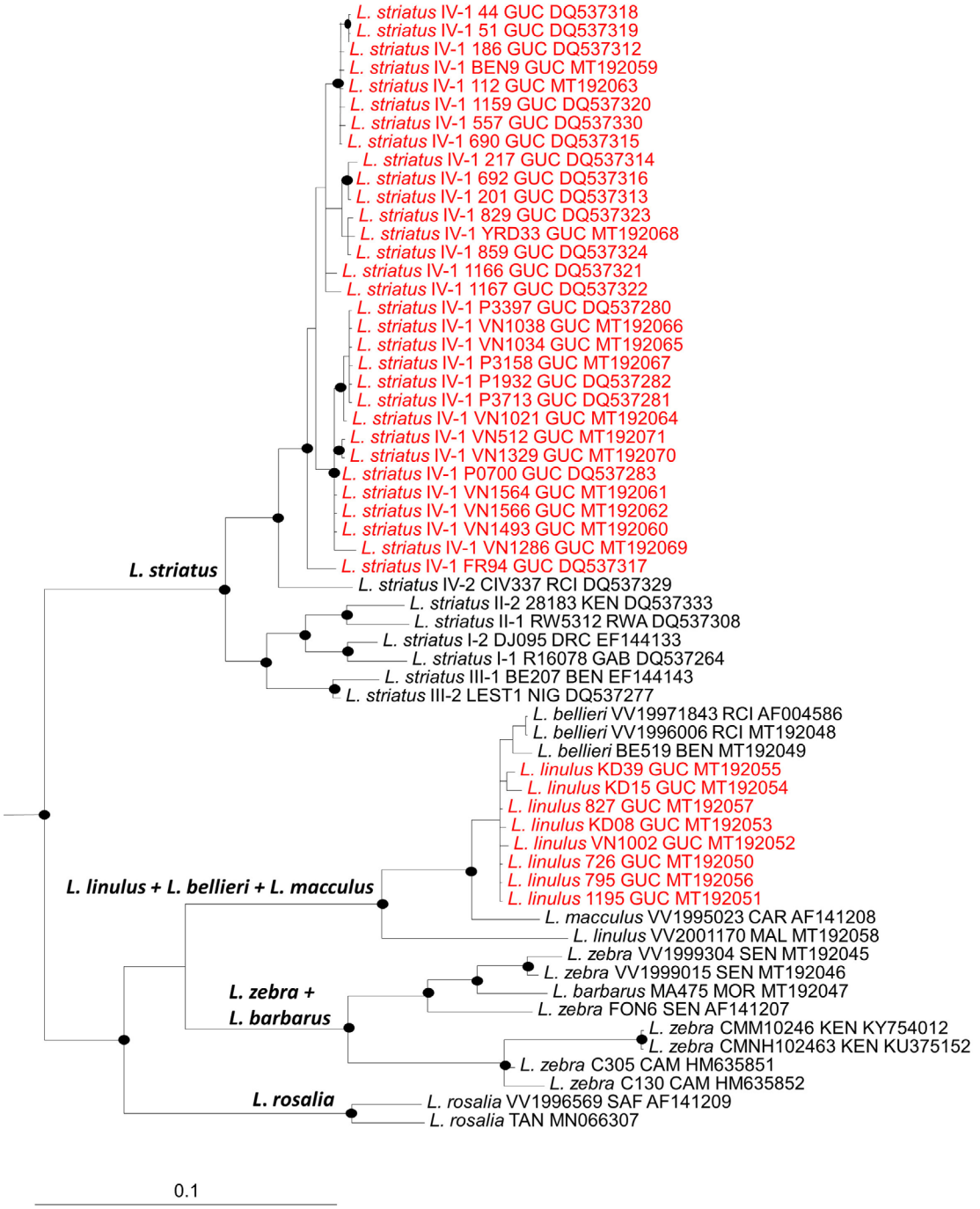


Fig. 2. Cytochrome *b* phylogeny of *Lemniscomys* individuals recovered by Bayesian analysis (GTR + I + G model). To improve clarity outgroup taxa were removed. Nodes with posterior probabilities greater than 0.96 are indicated with a black dot. Specimens from Guinea are in red. For *L. striatus*, Roman numbers indicate the genetic lineage following Nicolas et al. (2008). For newly sequenced specimens only field numbers are indicated. For sequences retrieved from GenBank both field numbers (when known) and GenBank numbers are indicated. Three-letter codes indicate country of origin: BEN = Benin, CAM = Cameroon, CAR = Central African Republic, DRC = Democratic Republic of Congo, GAB = Gabon, GUC = Guinea, KEN = Kenya, MAL = Mali, MOR = Morocco, NIG = Nigeria, RCI = Ivory Coast, RWA = Rwanda, SEN = Senegal, TAN = Tanzania, SAF = South Africa.

Results

We collected 97 *Lemniscomys* specimens from 25 localities in Guinea (Fig. 1). *Lemniscomys* were never the most abundant species in our field trapping campaigns, and the genus represents only 1.45 % of all captures (7441 specimens in total).

Mitochondrial phylogeny

Specimens from Guinea fit within two mitochondrial clades (Fig. 2): the first clade includes *L. striatus* specimens from Franfina, Tanganya, Bamba, Bantou, Benti, Bowé, Gania, Gayebombo, Gbaolé, Kaali, Samedou, Yerende, Ziama and Zogota, and corresponds to the clade IV-1 of Nicolas et al. (2008).

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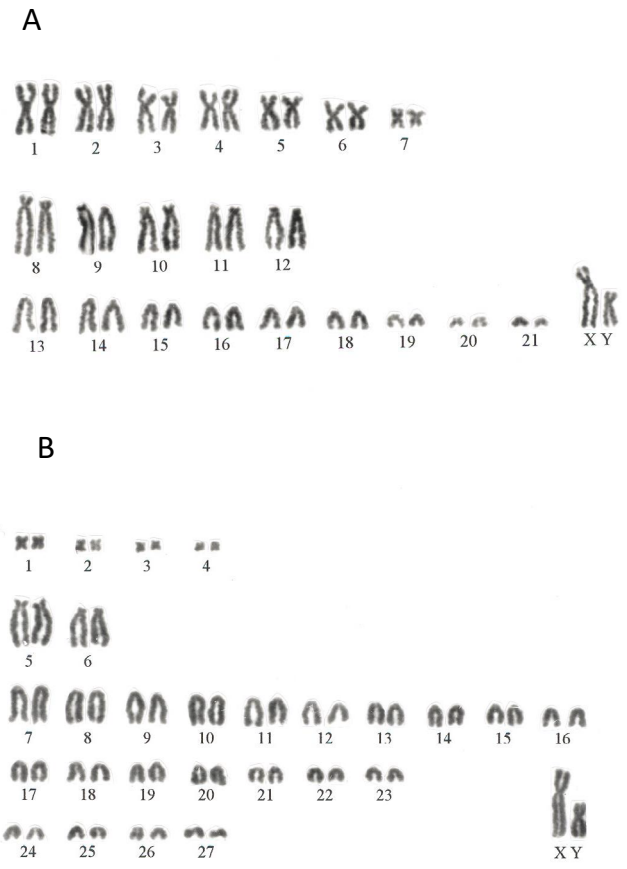


Fig. 3. Standard karyotype of new Guinean specimens of *Lemniscomys*. A) *Lemniscomys striatus* with 2n = 44, FNa = 66 (MNHN-ZM-2008-8), B) *Lemniscomys linulus* with 2n = 56, FNa = 66 (MNHN-ZM-2012-1028).

The second clade includes those specimens from Guinea morphologically identified as *L. linulus* and derived from Fressoudou, Kodoko, Bantou and Tanganya. This second clade also includes one specimen of *L. linulus* from Mali, specimens of *L. bellieri* from RCI and Benin, and one sequence of *L. macculus* from the Central African Republic (CAR).

Cytogenetic analysis

Among the eight new karyotyped specimens, we found only two discrete karyotypes. The first was obtained from specimens associated with the first molecular clade. It corresponds well with the standard *L. striatus* karyotype. It is characterized by 2N = 44, NFa = 66 and comprises seven metacentric, nine acrocentric and five subtelocentric autosomes. Two females and two males from central Guinea (localities of Tanganya and Bantou) display this karyotype (MNHN-ZM-2008-7, MNHN-ZM-2008-8, MNHN-ZM-2008-9 and MNHN-ZM-2008-10; Fig. 3A). The second karyotype was obtained in specimens associated with the second molecular clade. The karyotype is 2N = 56, NFa = 66 (Fig. 3B). It is characterized by 4 metacentric, 21 acrocentric and 2 telocentric autosomes. One female and three males from Tanganya and Bantou show this karyotype (MNHN-ZM-2012-1026, MNHN-ZM-2012-1030, MNHN-ZM-2012-1028



Fig. 4. Dorsal pelage of *Lemniscomys* holotypes. 1) *L. linulus* NHM Holotype NHM 11.6.10.89 Gamon, Senegal; 2) *L. venustus* Holotype NHM 11.3.24.13 Panyam, northern Nigeria; 3) *L. macculus* Holotype NHM 6.12.4.57 Mokia, SE Ruwenzori, Uganda; 4) *L. oweni* Holotype NHM 11.6.10.61 Gemenjulla, Senegal; 5) *L. bellieri* Holotype RMNH 75-74-M-1 1446 Lamto, RCI Credit Royal Museum for Central Africa; 6) *L. zebra* Holotype S.M.N.S. 5422-1100 Bongo, Sudan, credit H. Turni/SMNS.

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Fig. 5. Dorsal pelage of Guinean specimens collected in this study. 1) *L. linulus* (MNHN-ZM-2012-1029, Tanganya); 2) *L. striatus* (MNHN-ZM-2012-1040, Bantou).

and MNHN-ZM-2012-1031). This karyotype is novel for the genus based on data from the literature (Table 1).

Morphology

Pelage colouration of types and Guinean specimens

Lemniscomys linulus is characterized by a single black median stripe and no other light stripes while *L. striatus*, *L. bellieri*, *L. macculus* and *L. zebra* display supplementary stripes in addition to the median stripe. Compared to the holotype of *L. bellieri* and *L. macculus*, the *L. linulus* holotype is characterized by the absence of punctuated lines and by a browner colouration, including the belly (Fig. 4). In *L. bellieri* there is one thin median black stripe bounded by two thin lines of white-cream spots. The punctuated line of white-cream spots increase in size towards the flanks and five lines are visible on each side of the dorsal region, separated by light grey-brown pelage. This pattern differs clearly from the *L. macculus* holotype, which displays one large black line, bordered on each side by four nearly continuous rows of small white-cream spots alternating with four dark or brown zones that do not form clear lines, on its dorsal pelage. It was not possible to see the Linnaeus holotype of *L. striatus*, but we compared our specimens with other west central African type specimens, which were considered junior synonyms, such as *L. venustus* and *L. pulchella*. *L. venustus* was re-described in detail by Van der Straeten (1981) who noticed slight differences with *L. striatus* but considered it as a valid sub-species of *striatus*. The holotype of *L. striatus*, re-described by Carleton & Van der Straeten (1997), corresponds to an immature juvenile. It bears seven pairs of dark and light punctuated stripes and a median brown dorsal line (not illustrated here). In *L. venustus* there are three dark brown bands on each side of the black median dorsal line and 3 to 4 yellow-cream lines of spots. The same number of dark lines is observed in *L. pulchella* and the yellow-cream spots are organized in more continuous and visible lines than in *L. venustus*. In the *L. zebra* holotype and in *L. oweni* (a junior synonym of *L. zebra*) 3 to 4 continuous yellow-white-cream lines and 3 to 4 brown lines can be seen on both sides of the black median line (Fig. 4).

We found two different types of dorsal pelage in our *Lemniscomys* from Guinea. 78 specimens display the typical *L. striatus* dorsal colour pattern, while in 19 specimens only one dorsal stripe was visible (Fig. 5). Because, only one species with a single dark line and no yellow lines is known to occur in West Africa, *L. linulus*, we attributed to the specimens displaying this morphological characteristic. Like the holotype of *L. linulus*, a clear median-dorsal black stripe and no lateral yellow stripes or punctuated lines was visible in our specimens. The pelage is brown with some yellow hairs and spots visible on the flanks, but not organized geometrically (Fig. 5). Our Guinean specimens appear to have slight differences compared with the holotype of *L. linulus*, including a slightly larger black median stripe that is framed by two conspicuous thin and nearly continuous yellow lines of spots. Several supplementary specimens from the Guinean locality of Dinguiraye (not genotyped) display the same pattern and were consequently attributed to *L. linulus*. We did

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Table 2. Standard measurements of West African *Lemniscomys* species using Types, MNHN karyotyped and new genotyped Guinean specimens. *after Tranier & Gautun's work. **measured on wet and dry mounted specimens by S.M. ***after Carleton & Van der Straeten (1997).

Species		Weight g	HB mm	TL mm	HF mm	E mm	TL/ HB%
L. linulus Guinea	Mean	31.9	109.3	127.2	25.4	16.5	116
This study (N = 19)	Min-Max	13-42	98-120	112-143	23-27	15-17	105-132
L. linulus South	Mean	34.9	108.3	116	24.1	16.9	107
Mali (N = 8)	Min-Max	30-45	100-119	104-135	21-26	16-18	98-128
L. linulus RCI (Bouna) (N = 2)	Min-Max		95-102	102	23-24	15-17	100
L. linulus holotype & paratype							
BMNH 11.6.10.69			94	115	23	15	122
BMNH 11.6.10.70			101	135	27	17	134
L. striatus Guinea	Mean	37.7	111.5	118	25.5	15.2	107
Genotyped (N = 18)	Min-Max	13-67	65-131	61-149	19-29	11-18	82-121
L. striatus holotype NHRS A53.2048***			49.1	34.5	13.4	NA	70
L. striatus RCI karyotyped	Mean		118.1	114.1	26		96.7
MNHN*	Min-Max		117-126	125-131	27-29	15	105.5
L. venustus holotype BMNH 11.3.24.13			119	140			118
L. bellieri paratypes	Mean	45	110.8	102	25.6	15.9	99.9
RCI, Lamto, MNHN (N = 5)	Min-Max		105-113	89-115	24-27	15-18	96-104
L. bellieri holotype RMCA 75.074-M-0001			105	106	24	15	101
L. bellieri type series	Mean		109	112	25.4	15.9	
(after Van der Straeten 1975)	Min-Max		91-127	94-134	23-27	13-19	
L. bellieri Guinea	Mean	36	110.3	117.7	25.3	16	106.5
ZFMK (N = 3)	Min-Max	27-45	101-120	108-134	24-27	14-19	101-112
L. macculus holotype NHM 6.12.4.57			105	111	22	17	106
L. zebra RCI, Burkina Faso	Mean	42	101.8	94.5	25	15.5	
(N = 4), MNHN	Min-Max		95-107	73-116	24-26	15-16	108
L. zebra Sudan lectotype							
& paralectotype			96	90	21.5		94
**SMNS1100			82	65+	23	13	NA
**SMNS1100b							
L. oweni holotype NHM 11.6.10.61			105	114	22	14	109

not observe any variability in this dorsal pelage pattern among our new Guinean specimens. The new specimens attributed to *L. striatus* (following the molecular work of Nicolas et al. 2008) have one median black line with 3-4 lateral lines on each flank, which corresponds to the original description. In our specimens, the upper stripes are organized in eight nearly continuous lines of spots and the lateral ones are less continuous (Fig. 5). The median black stripe is relatively large. The new Guinean specimens attributed here to *L. striatus* differ from specimens of *L. zebra* by not having continuous lines on both sides of the median black line (Fig. 5). They have four lateral lines of brown and yellow-white spots on both sides of a median black line like in *L. striatus.*

Specimens attributed to *L. bellieri* by Ziegler et al. (2002) from Faranah (Guinea) housed at the ZFMK were examined. The dorsal skin displays a narrow black median line surrounded by two cream-white thin lines of nearly continuous spots. From each side of the thin white spot lines four dark-brown-grey lines alternating with four white cream spots lines are visible. This pattern is similar to the holotype of *L. bellieri*.

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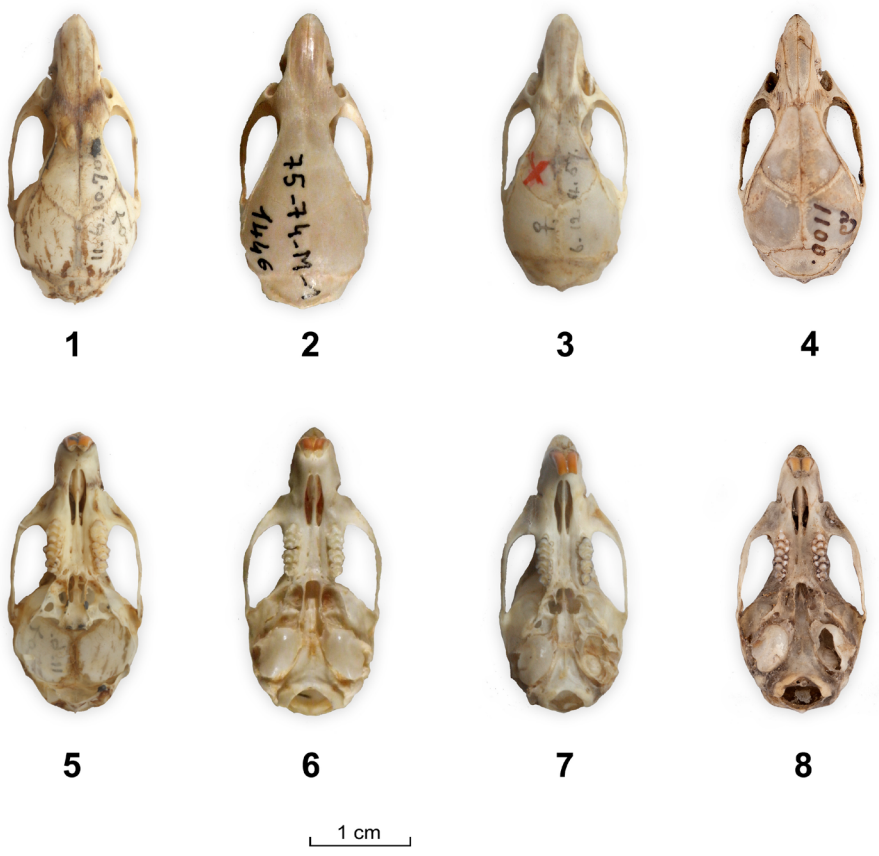


Fig. 6. Skulls of *Lemniscomys* type specimens. 1-4: dorsal view, 5-8: ventral view. 1 & 5: *L. linulus* paratype NHM 11.6.10.70; 2 & 6: *L. bellieri* Holotype RMNH 75-74-M-1 1446, Credit Royal Museum for Central Africa 3 & 7: *L. macculus* Holotype NHM 6.12.67.57; 4 & 8: *L. zebra* Holotype S.M.N.S. 5422-1100, credit C. Leidenroth/SMNS.



Fig. 7. Dorsal and ventral skulls of *L. striatus* – 2 & 4 (MNHN-ZM-2012-1044) and *L. linulus* – 1 & 3 (MNHN-ZM-2012-1031) from Tanganya, Guinea.

Some West African specimens housed at the MNHN, and already karyotyped by several authors, were re-examined here (not illustrated). The striped South Mali specimens from Balamansala and Tombane (Table S1), already attributed to *L. linulus*, display the same dorsal pattern as the holotype with a relatively thin median black line, brown pelage and yellow-brown hairs on the hind feet and tail. The tail length is equal or smaller to the head and body length. On several specimens the pelage is speckled, with yellow and cream spots, but never organized into a continuous line. Two RCI specimens from Bouna are deposited in the MNHN collection as *L. griselda*. These specimens were karyotyped by Matthey (1954) under this specific name but are clearly similar to *L. linulus* and display the same dorsal pattern and colouration. Thus, we re-attribute them to the species *L. linulus*. In these two specimens the tail length is equal to the head and body length.

Variability in external measurements

Standard statistics for external morphological measurements show large overlap among *Lemniscomys* species from West Africa (Table 2),

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Table 3. Skull measurements of Guinean *Lemniscomys* and surrounding countries (southern Mali, Senegal, and RCI). In bold: highest mean value. In italic lowest mean value. Min-max = minimum and maximum values.

Species/ Country	Values	LTC	WZYG	CIO	LNAS	WNAS	WOCC	FO	FOPAL	LS13	LBT	LMDB	HMDB	LI13
L. linulus														
Guinea	Mean	27.4	*12.8*	4.8	*9.7*	*4.2*	*11.5*	*5.1*	*9.9*	5.1	5.1	17.9	8.4	4.9
(N = 15)	Min-max	27.2-30.1	12-13.7	4.5-5.6	7.6-11.3	3.9-4.4	10.3-12.2	4.6-5.5	9.3-10.5	4.7-5.3	4.1-5.5	16.7-18.8	7.6-9.2	4.6-5.3
L. linulus														
Holotype		NA	NA	4.5	8.9	4	NA	5.02	NA	4.67	NA	NA	8.9	4.64
Paratype		29	*13*	4.8	10.1	4.2	NA	5.86	NA	5.57	NA	18.27	8.55	5.42
L. linulus														
RCI (N = 2)	Min-max	27.2-28.8	12.9-13	4.5-5.2	10.8-9.4	4.4-4.6	11.3-11.9	5.5	9.3-9.6	5.1-5.2	5.5-5.7	17.5-17.7	8.3-8.9	4.7-5.1
L. linulus	Mean	28.39	13.43	4.92	9.85	*4.20*	11.64	5.40	10.07	**5.16**	*4.94*	18.19	**8.54**	**5.04**
Mali (N = 11)	Min-max	26.9-29.9	12.7-14.1	4.3-5.8	8.4-11	3.7-4.6	10.9-12.2	4.8-6.5	9.4-10.5	4.3-5.9	4.3-5.3	17.2-19.3	7.9-9.6	4.7-5.4
L. striatus														
Guinea	Mean	29.07	13.27	4.86	10.38	**4.34**	11.86	**5.55**	10.19	4.97	5.03	17.92	*8.15*	4.80
(N = 52)	Min-max	23.5-33.1	10.7-15	3.9-5.9	8.3-12.9	3.7-5	10.3-12.9	4.5-6.4	8.3-12	4.5-5.4	4.5-5.9	14.2-20.2	6.4-9.4	4.1-5.2
L. striatus	Mean	**30.00**	**13.61**	**5.15**	**10.92**	4.25	**12.33**	5.29	**11.36**	4.89	5.19	**18.38**	8.48	4.80
RCI (N = 5)	Min-max	28.8-32	12.4-14.6	4.9-5.5	10.2-11.9	3.7-4.6	11.7-13	4.1-6.3	10.4-12.4	4.6-5.1	4.8-5.7	17.5-19.5	8.1-8.9	4.7-5.1
L. bellieri														
Holotype		27.12	12.6	4.31	10.57	5.03		4.78	9.68	4.75	4.8	16.32	7.93	4.34
L. bellieri	Mean	*28.21*	13.11	*4.65*	10.23	4.21	11.59	5.19	10.15	*4.88*	**5.27**	*17.39*	8.19	*4.79*
RCI (N = 7)	Min-max	27-28.8	12.8-13.5	4.4-5	9.8-10.6	3.7-4.5	11.1-12.3	4.9-5.7	9.7-10.6	4.7-5	4.8-5.9	16.3-18.2	7.7-8.7	4.2-5.1
L. bellieri	Mean	28.6	13.1	4.8	10.5	3.9	12.01	5.3	10	4.9	5.5	17.7	7.7	4.7
Guinea (N = 6)	Min-max	27.3-30.1	12.4-14.3	4.4-5.2	9.5-11.4	3.6-4.3	11.7-12.6	4.8-6	9.3-11.3	4.7-5.1	5.3-5.8	16.8-18.6	7.4-8.3	4.6-4.9
L.macculus														
Holotype		27.54	12.16	4.5	8.84	4.11	11.17	4.87	10.19	4.76	10.19	16.86	7.7	4.55
L. oweni														
Holotype		26.96	12.5	4.31	9.8	4.22	10.35	5.22	9.39	4.72	5.19	16.75	8	4.27

as noted by Rosevear (1969). *Lemniscomys striatus* looks slightly larger than *L. linulus*, *L. bellieri* and *L. zebra*, and seems to have a proportionally smaller hind foot. The tail is longer than the head and body length for all species (Table 2). A comparison of genotyped *L. bellieri* versus *L. linulus*, shows only a significant difference in tail length, while between *L. linulus* and *L. striatus* only ear length is significantly different. Between *L. bellieri* and *L. striatus* all the external measurements showed no significant differences. The holotype of *L. striatus*, re-described by Carleton & Van der Straeten (1997), has a tail shorter than head and body length. The *L. linulus* from Guinea and Mali have similar external measurements to the holotype and topotype specimens. The tail length is equal or slightly longer than the head and body length in all the specimens examined here (Table 2).

Skull characters

The skulls of *L. striatus* and *L. linulus* display short and wide nasals, a wide interorbital constriction, large braincase, long incisor foramen, large molars and small tympanic bullae. The holotype of *L. linulus* (not illustrated) is old and with posterior damage, but it displays a short and wide nasal whose anterior end is oblique on both sides of the median suture, with well-marked fronto-parietal crests. This conformation is also observed on the *L. linulus* paratype (Fig. 6).

The holotype of *L. striatus* is a juvenile and its skull has never been illustrated (Carleton & Van der Straeten 1997). The holotypes of *L. venustus* and *L. pulchella* (syn. *L. striatus*) are damaged and few morphological skull characters are visible. On the *L. bellieri*, *L. macculus* and *L. zebra* holotypes the nasals are short and narrow and with a round anterior end on both sides of the median suture. It is more oblique in *L. zebra* and *L. macculus* than in *L. bellieri* (Fig. 6).

In ventral view (Fig. 6), the incisor foramen of *L. linulus* looks slightly longer and narrower at its distal part compared to those of *L. striatus*; it stops at the level of the t1 of the upper M1/ in *L. linulus* while in our *L. striatus* and the *L. pulchellus* holotype it stops before the t1. In *L. bellieri* the incisor foramen is rectilinear and relatively large, ending at the level of the pre-lobe of the upper M1/. In *L. pulchella*, despite its poor state of preservation, the incisor foramen stops at the level of the pre-lobe of the M1/. In *L. zebra* and *L. macculus* the incisor foramen is also narrower at its distal end and stops before the t1 of the upper M1/. The pterygoid fossae looks larger in *L. striatus* than in *L. linulus*, the foramen magnum is wider and more open ventrally in *L. striatus* than in *L. linulus*. In lateral view (not illustrated), the incisors are orthodont in *L. linulus* and opistodont in *L. striatus*. The mastoid processes in *L. linulus* is well developed. The mandible is high and short in *L. linulus* and the angular process less developed than in *L. striatus*.

In dorsal view, our Guinean specimens assigned to *L. striatus* also display short nasals, narrower than in *L. linulus* and ending with a round anterior end on both sides of the median suture (Fig. 7). Our Guinean *L. linulus* specimens show the anterior ends of the nasals to be oblique, like in the type specimen, and well-marked fronto-parietal crests. In ventral view, our new specimens show either a short large incisor foramen ending at the level of the M1/ prelobe (like *L. striatus* or *L. bellieri*) or a longer one that is narrower at its distal part, ending at the level of the t1 of the M1/, like in *L. linulus*. The new specimens attributed to *L. linulus* also show orthodont incisors and a well-developed mastoid process (not illustrated).

L. linulus has similar skull dimensions to specimens attributed to *L. striatus* but differs in having significantly longer molar rows and smaller tympanic bullae (Table 3). There were significant differences between *L. bellieri* and *L. linulus* in WNAS, LMDB, HMDB, LS13 and LI13. Between *L. bellieri* and *L. striatus* the mean values of CIO width, WNAS and LBT differ significantly.

Dental morphology

The upper molars of west African *Lemniscomys* all display the typical Arvicanthini dental pattern with large molars and well-aligned transversal, bunodont cusps t2 and t3. On the holotype of *L. linulus*, there is a small t9 on the M1/ and the M2/. The t3 and the t4 of the M1/ displays a small trace of stephanodont crest. The upper M3/ has a large t1 and no t3, two lophs and the second lobe of the M3/ displays one cusp. The lower M/1 does not show a supplementary median anterior cusp (tma) nor a posterior cingulum or labial Cv5. The antero-labial cusp of the prelobe is smaller than the antero-lingual cusp and the prelobe is fused to the first lobe by a longitudinal crest, the latter also visible on the second lobe whose cusps are oblique and of equal size. On the M/2 there is a small Cp and a round antero-labial cusp. The M/3 is smaller than the M/2 and has two lobes of

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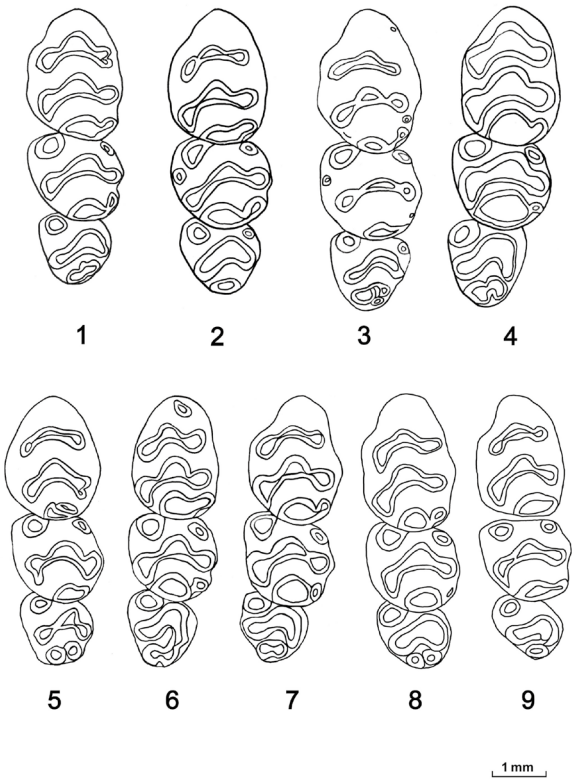


Fig. 8. Upper molar rows of several West African *Lemniscomys*. 1-4: *L. linulus* (MNHN-ZM-2012-1030 Tanganya, Guinea, 2 – MNHN-ZM-2011-615 Kodoko, Guinea, 3 – MNHN-ZM-2013-2778 Dinguiraye, Guinea, 4 – MNHN-ZM-MO-2004-728 Tombané, Mali); 5-6: *L. striatus* (5 – MNHN-ZM-2008-10 Tanganya, Guinea, 6 – 207 = MNHN-ZM-2011-619 Bantou, Guinea); 7: *L. bellieri* (MNHN-ZM-1979-156 Lamto, RCI); 8: *L. zebra* (MNHN-ZM-1971-756, Foro RCI); 9: *L. macculus* (MNHN-ZM-1992-1542, Bossangoa, CAR).

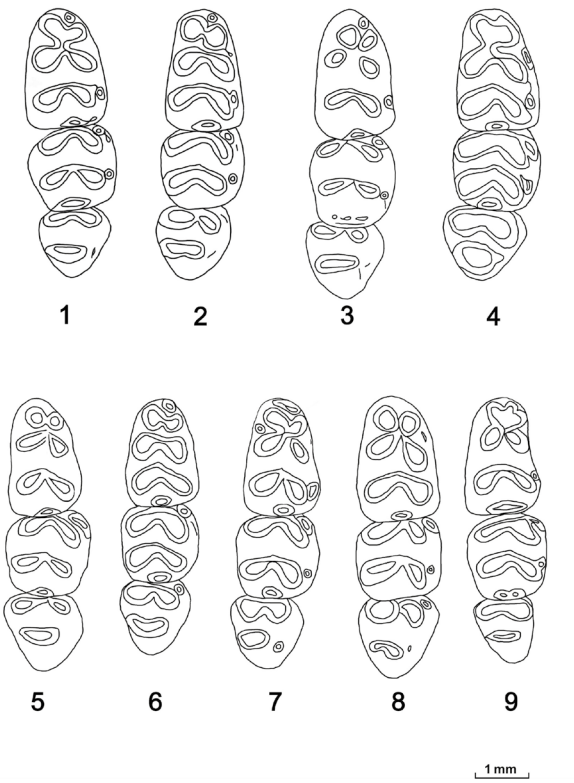


Fig. 9. Lower molar rows of several West African *Lemniscomys*. 1-4: *L. linulus* (1 – MNHN-ZM-2012-1030 Tanganya, Guinea, 2 – MNHN-ZM-2011-615 Kodoko, Guinea, 3 – MNHN-ZM-2013-2778 Dinguiraye, Guinea, 4 – MNHN-ZM-2004-728 Tombané, Mali), 5-6: *L. striatus* (5 – MNHN-ZM-2008-10 Tanganya, Guinea, 6 – MNHN-ZM-2011-619 Bantou, Guinea), 7: *L. bellieri* (MNHN-ZM-1979-156 Lamto RCI), 8: *L. zebra* (MNHN-ZM-1971-756, Foro, RCI), 9: *L. macculus* (MNHN-ZM-1992-1542, Bossangoa, CAR).

two cusps (not illustrated). In the paratypes and type of *L. bellieri* a similar disposition of the molar cusps can be seen to that in *L. linulus* except for the prelobe of the lower M/1 (Fig. 8). The two anterior cusps are approximately equal in size and nearly longitudinal in their orientation, which differs from *L. linulus* where the two anterior cusps of the prelobe of M/1 have a more transverse orientation, with the labial cusp smaller than the lingual. The holotype of *L. zebra* corresponds to a stage 3 specimen and displays bunodont cusps. The t9 is small. On the upper M3 only one small cusp on the second lobe is visible. On the lower M/1 the two anterior cusps of the prelobe are small, of similar size and oblique with a 90° angle between them. There are no stephanodont crests, and the molars do not display any cingular supplementary cusps. The posterior cingulum is small on M/1 and slightly larger on M/2. The M/3 display one large cusp and a tiny external cingular cusp.

On our Guinean *L. linulus* specimens a similar organisation of the cusps to those in the holotype can be seen, accompanied by some variability in the numbers of accessory tubercles. The t3 of the upper M1/ display a small t3 bis. The upper M3/ has two small cusps on its second lobe. On the lower molars a tma, Cp, Cv1, cv5 are visible on the lower M/1. Cusps are oblique and the prelobe is fused with the first lobe. The same orientation and smaller size of the antero-labial cusp as in the holotype can be seen at all stages of wear. The lower M/3 has one cusp on the second lobe (Figs. 8, 9).

In our Guinean *L. striatus* material, the cusps are more bunodont and less fused than in *L. linulus*. A small stephanodont crest is seen on the t4. The t9 is small. On the upper M3/ there is always a trace of two cusps on the second lobe. On the lower M/1 the cusps of the prelobe and the first lobe are well separated until an advanced stage of wear, the two anterior cusps are about equal size and nearly aligned transversally. A tma and a cv5, as well as a small Cp are present on the M/1. The second lobe of the M/1 display a transverse lamina with well aligned cusps (Figs. 8, 9).

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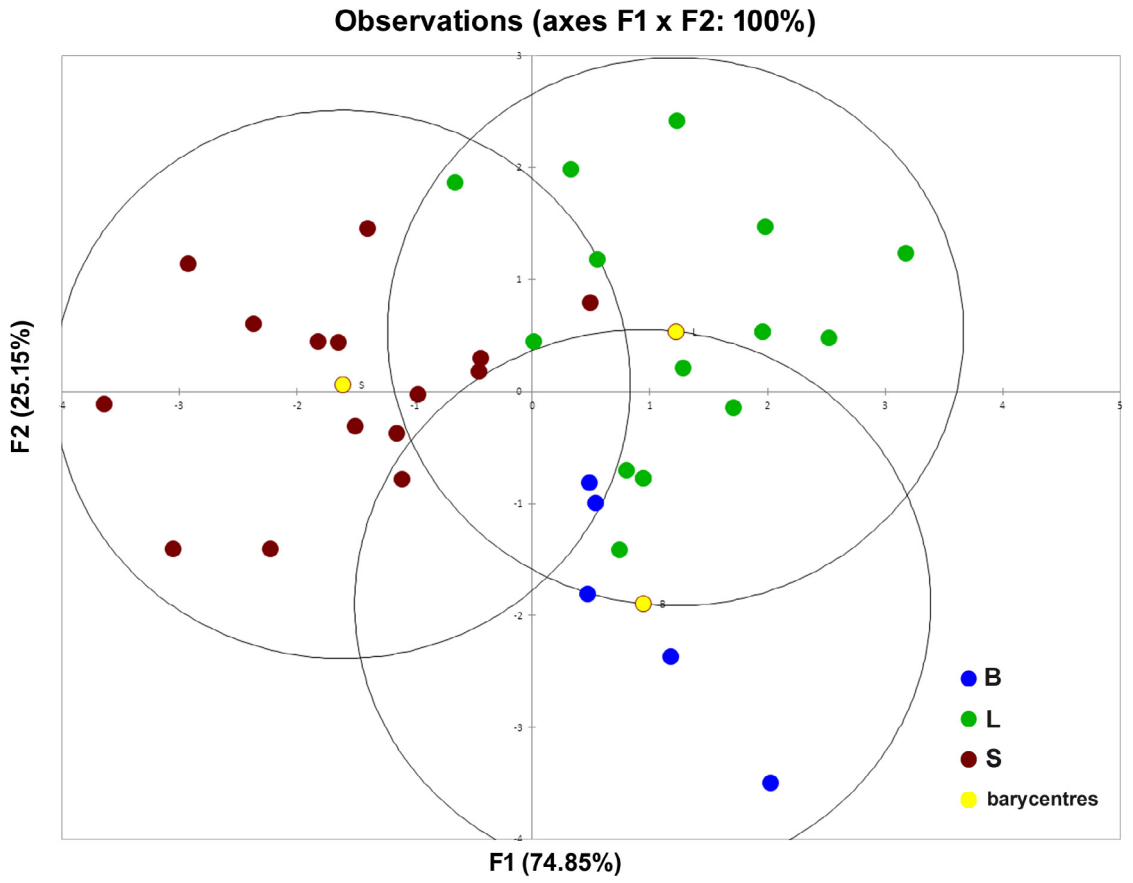


Fig. 10. Discriminant function analysis on 13 skull distances of 36 genetically typed Guinean and Malian specimens of *L. linulus* (L), Guinean *L. striatus* (S), and karyotyped *L. bellieri* from the type locality of Lamto in Ivory Coast (B). Circles represent 95% confidence ellipses and yellow points barycentres of each species.

Malian and karyotyped RCI *L. linulus* display the same slightly stephanodont upper molars, the well-fused cusps of the prelobe and first lobe of the M/1 with the labial anterior cusp smaller than the lingual in comparison with the holotype. The upper M3/ has a large t1 and no t3, the second lobe of the upper M3/ displays two cusps on the second lobe of the M3/ in two Malian specimens and only one cusp on the RCI in specimens from the locality of Bouna (Fig. 8). The MNHN karyotyped specimen attributed to *L. macculus* from CAR (locality of Bossangoa) have bunodont cusps, a small upper M3/ with one cusp on the second lobe, slightly stephanodont t4 on M12/, well fused cusps on the pre-lobe of M/1, a cv5 and a tma (Figs. 8, 9).

Multivariate morphometric analyses

The discriminant function analysis performed on four external measurements of 47 genetically typed specimens (not shown) indicates that there is substantial overlap among species and high intra-specific variability. With the exception of ear length, no other variable is well correlated with the two first discriminant axes. As a result, only 64% of the specimens are reliably classified.

A second discriminant function analysis performed on the 13 skull measurements for 36 genetically typed specimens (Fig. 10) allowed a better discrimination among species, with an 86% correct classification. On the 1-2 axis plane there is still overlap among the three species. The variable which best explained the separation between *L. linulus* and *L. bellieri* compared to *L. striatus* are LI13, LS13, HMDB (positively correlated with axis 1), CIO, FO, WOCC and LGT (negatively correlated with axis 1). LBT and WNAS separate *L. linulus* from *L. bellieri* along axis 2. The best classification score in this case is obtained for *L. striatus* (93%), then *L. linulus* (87%) and finally *L. bellieri* (60%). The two specimens incorrectly classified as *L. bellieri* were reattributed to *L. linulus* and not to *L. striatus*.

Discussion

Number of species of *Lemniscomys* in Guinea

Based on published data, there are potentially four species of *Lemniscomys* in Guinea: *L. striatus*, *L. linulus*, *L. bellieri* and *L. zebra.* Our integrative study shows that the new Guinean specimens

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belong to two different mitochondrial clades: one assigned to *L. striatus* clade IV-1 by Nicolas et al. (2008), and the other corresponding with the *L. linulus-bellieri-macculus* clade. Our specimens also cluster in two morphological groups (multi-striped and mono-striped pelage, respectively) and with two different karyotypes (2N = 44 and NFa = 66, *vs.* 2N = 56 and NFa = 66, respectively), reinforcing the hypothesis that our sample comprises two species. However, assigning specific attributes to our specimens requires further analyses especially in the case of the second clade.

In our phylogenetic tree, *L. linulus* and *L. bellieri* are not recovered as monophyletic, and the genetic distance is higher between specimens of *L. linulus* from Guinea and Mali, than between specimens of *L. linulus* from Guinea and *L. bellieri*. Only one specimen of *L. macculus* was sequenced and its cyt*b* sequence is closer to sequences of *L. linulus* from Guinea and *L. bellieri* than to those of *L. linulus* from Mali. In the Arvicanthini molecular phylogeny based on three mitochondrial genes (cyt*b*, 16S, 12S), Ducroz et al. (2001) also found a robust clade including *L. bellieri* + *L. macculus*, and suggested that these two taxa are conspecific. Further studies including nuclear markers at the genome scale may better clarify the number of species in this complex (de la Harpe et al. 2017, Pedraza-Marrón et al. 2019). It is important to note that within the *L. linulus-bellieri-macculus* clade, different karyotypic formulae were recorded. Van der Straeten & Verheyen (1978) described a karyotype for *L. bellieri* from RCI of 2N = 56 and NF = 78, while in the type locality of Lamto a different karyotype (2N = 56, NFa = 60) was found (Volobouev et al. unpublished data, Table 1). The single known karyotype of *L. linulus* comes from south Mali (Mandingue Mountains, Baffing, 2N = 56, NFa = 64, Granjon & Duplantier 2009) and is slightly different from that observed in our study at two localities (Tanganya, Bantou: 2N = 56, NFa = 66). For *L. macculus* a specimen from CAR (Bossangoa) and others from Ethiopia displayed a karyotype of 2N = 56 and NFa = 64 (Ducroz et al. 2001, Bulatova et al. 2002). According to Ducroz (1998), *L. bellieri* and *L. macculus* differ only by one pericentric inversion. More detailed cytogenetic analyses are needed to draw conclusions on the biological consequences of these differences, particularly whether they represent karyotypically distinct sibling species or intraspecific polymorphism. Our discriminant analyses on skull distances showed poor discrimination between *L. bellieri* and *L. linulus*. For sibling species, it is recognised that rates of reliable classification are often relatively low. For example, for sibling species of the African murid genus *Mastomys*, the discrimination rate varies between 75 and 92 % (Denys et al. 2012). Even if these two species cannot be readily discriminated based on skull measurements they can be distinguished on external and skull morphology: the dorsal pelage has only one black stripe and no yellow lines in *L. linulus* while it has eight bands of dark brown/grey alternating with obvious yellow spot lines in *L. bellieri.* The incisor foramen is narrower posteriorly in *L. linulus* while it is of equal width posteriorly and anteriorly in *L. bellieri.* Given these morphological differences between the two species we will consider them as distinct species and confirm the presence of *L. linulus* and *L. striatus* in Guinea.

The Faranah specimens attributed to *L. bellieri* by Ziegler et al. (2002) were not genetically typed but their skin, skull characters and dimensions fit well with the *L. bellieri* type specimen. This observation implies the presence of a third species of *Lemniscomys* in Guinea. Despite previous reports, we failed to collect *L. zebra* in savannah regions of Guinea during this study but it remains possible that the species is present in the north of the country.

Patterns of variability in West African *Lemniscomys*

Like for other African murid rodents, the west African *Lemniscomys* may present a complex of cryptic species that arises from complex biogeographical and historical patterns (Taylor 2000, Dobigny et al. 2002a, Castiglia 2013). Rosevear (1969) hypothesised that multi-striped species are derived compared to mono-striped taxa. In our phylogenetic tree the mono-stripe pattern may appear in different lineages (clade *L. linulus-bellieri-macculus* and clade *L. rosalia*), a conclusion also supported by Castiglia et al. (2002).

High cytogenetic variability appears to be a feature of *L. striatus* in West Africa (Table 1). If in Guinea all specimens display the 2n = 44 and NFa = 66 karyotype (Denys et al. 2009, this study), the fundamental number of autosomes can vary for this species from 58 in RCI and Burkina Faso (Van der Straeten & Verheyen 1978, 1985, Ducroz 1998) to 72-74 or 68 in Benin (Capanna et al. 1997, Castiglia et al. 2002). Such polymorphism may reflect geographical structuring in this species accompanied by gene flow restrictions among

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populations, as already proposed based on cyt*b* sequencing results by Nicolas et al. (2008).

Based upon our morphological and morphometrical study, we observe that *Lemniscomys* in West Africa is characterized by substantial variability in skull and dental morphology. However, in Guinea it appears that *L. striatus* has a larger skull and smaller molars compared to *L. linulus*. In his description of *L. bellieri*, Van der Straeten (1975) mentioned its large tympanic bulla and small size compared to *L. striatus*. These differences were not recovered in our measurements of the paratypes of *L. bellieri* or the karyotyped specimens from RCI. We found a large overlap in both external and skull measurements between the two species. In *L. bellieri* the tympanic bullae length varied between 4.8-5.9 mm against 4.5-5.9 mm in Guinean *L. striatus*. We did not identify any diagnostic characters for *L. bellieri*, such as a smaller hindfoot length and the Sm (or tma) on M/1. Thus, we cannot confirm here Van der Straeten & Verheyen's (1978) conclusion that *L. striatus* has a larger skull, on average, than *L. linulus* and *L. bellieri*.

West African *Lemniscomys* – diagnosis and identification key

Using new data from the present study, we provide a revised diagnosis of the poorly known *L. linulus* and confirm the extension of its distribution to Guinea. This new information allows us to present a new identification key for the West African species of the genus.

Following the initial description of Thomas (1910), we confirm his diagnosis of the species' external characters of: "grizzled greyish – buff general colour of the dorsal pelage becoming ochraceous posteriorly. Under surface is white, edge on each side with a pinkish-buff line. The fur is coarse, hairs of back have about 7 mm length. The ears and a spot above and below each eye are ochraceous buff. Dorsal black line commencing between the ears and running to the root of the tail. Hairs on each side of it lighter than the general colour. Hands and feet light pinkish buff. Tail dark above dull ochraceous laterally, dull buffy below".

To this description we can add an amended diagnosis: tail equal or slightly longer than HB (%TL/HB: 98-132, N = 31, Mean: 114, Sd = 10.4). Nasals short and large ending obliquely from the median suture. Fronto-parietal crests well developed and rectilinear. Large braincase. Incisor foramen long and narrower posteriorly than anteriorly, ending between the t1 of the upper M1/. Lower M/1 with the antero-labial cusps small and transverse.

Identification key for West African *Lemniscomys* species:

1. Dorsal pelage with clear yellow spots more or less aligned in parallel lines..... 2
Dorsal pelage with only one black stripe and no yellow lines, skull length equal or below 30 mm, end of nasals oblique on each side of the median suture, long incisor foramen narrower posteriorly, large tooth rows .....*L. linulus*
2. Yellow or cream lines comprising independent spots, especially at the posterior end, incisor foramen of equal width posteriorly and anteriorly, ending at the level of the pre-lobe of the upper M1/ 3
Yellow lines continuous (no spots).....*L. zebra*
3. Brown colour of the pelage, yellow-white spots, eight bands of brown spots alternating with yellow-cream spots, greatest length of the skull more than 29 mm for adults, end of nasal bones rectilinear on each side of the median suture.....*L. striatus*
Cream spots and grey-brown colour of the pelage, eight bands of dark brown-grey alternating with lines of cream spots, greatest length of the skull less than 30 mm LBT = 16-20% of GLS ..... *L. bellieri*

Distribution and ecology of the Guinean *Lemniscomys* species

Based on molecular, cytogenetic and morphological analysis, we have been able to identify the specimens of *Lemniscomys* collected in Guinea. Table S1 provides specimen identifications for the Guinean localities we sampled between 2003 and 2011. We found *L. linulus* in six localities and *L. striatus* in 25 localities (Fig. 1). There are only three localities where both species were found together (Bantou, Ganya and Tanganya). Ganya and Tanganya are two localities situated in the Faranah region close to the location were Ziegler et al. (2002) recovered *L. bellieri* (Fig. 1).

Lemniscomys striatus was the only species present in the coastal lowland Guineo-Congolian forest block of Guinea and in upland deciduous forest and grassland regions. It was also trapped in bush and secondary forest enclosing grasslands in the Guinean savannah region. It can occur at an elevation of 1000 m on Mount Ziama and Nimba. According to Granjon & Duplantier (2009), this species occupies Guinean savannah, which we

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confirm here. We also encountered it in degraded forest habitats and anthropogenic habitats (cultivated areas), and the margins of enclosed grassland (Denys et al. 2009). It was collected by Ziegler et al. (2002) in Samaria grassland at the edge of the Mafu forest and on the eastern bank of the River Niger, corresponding with a Guinean savannah-type environment.

Lemniscomys linulus was the only species of the genus found in north Guinea in Sudanian savannah or at the ecotone between Sudanian and Guinean savannah at around 500 m altitude (Kodoko, Dinguiraye, Fressoudou; Fig. 1). We encountered it in Sudanian savannah and in cultivated areas close to villages. We did not collect it close to Senegal in the Guinean Niokolo-Koba buffer zone, which is the closest region to the type locality. According to Granjon & Duplantier (2011), *L. linulus* is also known in south Mali (Mandingues Mountains, Bafing) in the same type of habitat as in Guinea.

In central Guinea, *L. linulus* and *L. striatus* occurred in sympatry at three localities at about 500 m altitude in the transition zone between Guinean and Sudanian savannah (Fig. 1). It is in the same region (Faranah) that Ziegler et al. (2002) also found *L. bellieri* in sympatry with *L. striatus*. Despite regular ecological surveys in that region, we have been unable to trap *L. bellieri*. We unsuccessfully investigated essentially anthropogenic habitats but did encounter *L. bellieri* in the High Niger National Park, which supports more native vegetation and mosaic environments that are preferred habitats. The recent discovery of *L. linulus* in north Guinea may reflect a lack of previous studies in that region, though it is also possible that *L. linulus* has only recently arrived in central Guinea. As in the Sahelo-Sudanian countries of West Africa, global change (aridification) and deforestation may have caused a southward contraction of the Sudanian, Guinean and evergreen forest zones. No data are available for Guinea, but such changes in the biogeographic vegetation zones of west Africa has already been reported in Senegal (Bâ et al. 2006) and appear rapid. Rodents may represent informative indicators for monitoring these changes, especially in West Africa.

Conclusion

To conclude, the presence of *L. striatus* and *L. linulus* in Guinea is confirmed, and these species can be readily identified based on pelage colouration, cyt*b* molecular analyses, cytogenetic data and several skull characters. Because we observed several external, skull and cytogenetic differences between *L. linulus* and *L. bellieri*, we retain them as valid species, despite the low genetic distance observed in the cyt*b* analysis and pending further revision of the complex. Ziegler et al. (2002) identified *L. bellieri* in one locality close to our field collections in Faranah, and we consider this observation as valid.

During this work we karyotyped *L. linulus* and described its habitat and its co-occurrence with other rodents of the same genus in Guinea. We confirm the existence of three species in Guinea: *L. linulus*, *L. striatus* and *L. bellieri*, though further research will be needed to confirm the geographic distribution of the *L. bellieri-macculus-linulus* species complex and its validity. Further field work is also necessary to confirm the presence of *L. zebra* in the northern parts of the country and precise western distribution of *L. linulus*. *Lemniscomys linulus* did not occur frequently during our sampling (0.25 % of captures) but seems to have a wide distribution from at least Senegal to RCI in the western Sudanian savannah regions of Africa and, thus, may not be endangered. Despite intensive trapping we were not able to collect *L. bellieri* in Guinea. This result could indicate that populations are decreasing, or may reflect a trapping bias (i.e. preferred habitat not sampled). *Lemniscomys bellieri* is considered as a species of least concern by the IUCN due to its wide geographical range, but appears quite a rare species, at least in Guinea.

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Supplementary online material

Table S1. List of specimens used in this study for morphometric and/or genetic analysis. Status: designation of the specimen as Holotype (HT), Paratype (PT), Topotype (TT). (GPS, specimen preparation data available on request through database consultation via Collhelper (http://colhelper.mnhn.fr/) for MNHN specimens). (https://www.ivb.cz/wp-content/uploads/JVB-vol.-69-2-2020-Denys-et-al.TableS1.docx)

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