Phylogenetic position of the endemic Mount Oku rat, *Lamottemys okuensis* (Rodentia: Muridae), based on molecular and morphological data

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Lamottemys okuensis Petter, 1986, is restricted to the Mount Oku montane forest in the central-northern part of the Cameroon Volcanic Line (CVL; Central West Africa). It is endangered and has a decreasing population trend. The genus is monotypic and little is known about its phylogeny and evolutionary history. Using both molecular and morphological evidence, we tested two competing systematic hypotheses involving *Lamottemys*: whether it is more closely related to *Desmomys* or to *Oenomys*. We also discuss *Lamottemys*' biogeographical origin. Molecular phylogenies indicated a sister-group relationship with the Ethiopian montane forest endemic genus *Desmomys*. This reinforces the hypothesis of recurrent connections over time between West and East African mountains, probably facilitated by climate changes that led to expansions and contractions of montane environments. Our molecular dating, consistent with a period of intense volcanic activity in Central East Africa and the CVL, suggests that the geological history of East and Central Africa also contributed to promoting the isolation of *Lamottemys* in the CVL. Moreover, this study provides the most comprehensive phylogenetic analysis for the whole tribe Arvicanthini, sampling 17 of the 18 member genera. In this rodent group, stephanodonty probably appeared independently with grasses expansion. These habitat changes probably promoted the evolution of specialist rodents able to feed on abrasive vegetal matter by a dental adaptation.

INTRODUCTION

Montane forests of tropical Africa, East Africa, and the Cameroon Volcanic Line (CVL) are considered as terrestrial islands in which different evolutionary processes probably led to the development of several lineages (Zimkus & Gvoždík, 2013). Several phylogeographical studies that have examined intrageneric or intraspecific diversification in birds and small mammals have suggested that these are linked to periodic fragmentation of montane forests resulting from climatic oscillations in the Pleistocene (Bowie *et al*., 2006; Huhndorf, Kerbis Peterhans & Loew, 2007; Missoup *et al*., 2012; Nicolas *et al*., 2012a; Bryja *et al*., 2014; Demos *et al*., 2014). Several small mammals endemic to the CVL have their closest relatives confined to the mountains of East Africa (e.g. *Lophuromys*: Verheyen *et al*., 2002; *Otomys*: Dieterlen & Van der Straeten, 1992; Taylor *et al*., 2014), a pattern that

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suggests ancient connections between these habitats. The evolutionary scenarios that have led to the high species richness and endemism of small mammals in the montane forests of East and Central Africa need to be better elucidated.

Reaching about 3011 m a.s.l., Mount Oku belongs to the West Central African Archipelago, the so-called CVL, which is a unique geological feature in Africa. The CVL is of tectonic and volcanic origin, with an unclear chronological history (Marzoli *et al*., 2000; Montigny, Ngounouno & Deruelle, 2004; Deruelle, Ngounounou & Demaiffe, 2007; Koch *et al*., 2012; Milelli, Fourel & Jaupart, 2012). The oldest mountains are probably in the northern parts, with a trend of decreasing age of volcanic activity in the southern direction (Marzoli *et al*., 2000). Mount Oku is located in the north-central part of the CVL, within the Bamenda-Banso Highlands, which was probably uplifted during the Cenozoic (Oligocene to Miocene). The CVL supports exceptional endemism of montane vertebrate taxa (Herrmann *et al*., 2004, 2005a,b, 2007; Graham, Smith & Languy, 2005; Gonwouo *et al*., 2006; Blackburn, 2008a,b; Zimkus, 2009; Missoup *et al*., 2012; Zimkus & Gvoždík, 2013; Denys *et al*., 2014). It is considered as a distinct ecoregion within the Guineo-Congolian biome and one of the most important biodiversity hotspots in Africa (Burgess *et al*., 2004).

Lamottemys okuensis, the Mount Oku rat, is a CVL-endemic rodent that was originally described by Petter (1986) based on two specimens collected in 1970 at about 2000 m a.s.l. in montane forest close to Lake Oku. This montane forest-dwelling species, the single member of the genus, is known from a restricted geographical area, being found only on Mount Oku at elevations of 2100 to 2900 m a.s.l. The Mount Oku montane forest, about 100 km^2 in area (Oates, Bergl & Linder, 2004), is one of the most important hotspots for African small mammal diversity (Denys *et al*., 2014) and represents the largest remaining montane forest in West and Central Africa. It is threatened by grazing, wood harvesting, burning, debarking of *Prunus africana* and over-exploitation of small mammals as bushmeat (Smith *et al*., 2000). As a result, the Mount Oku rat is listed as Endangered in the IUCN Red List of Threatened Species with a trend of decreasing population size (Dieterlen, 2008). To date, there are no conservation measures for either this particular endemic species or for the montane forest of Oku.

Since the description of *Lamottemys*, little has become known about its phylogenetic position and evolutionary history, probably because it has for so long remained poorly represented in natural history museums, with two specimens documented in the Muséum National d'Histoire Naturelle, Paris (MNHN, Petter, 1986) and five specimens in the Zoologisches Forschungsmuseum Alexander Koenig, Bonn (Dieterlen

& Van der Straeten, 1988; Fülling, 1992). More recently, Denys *et al*. (2014), based on 53 recently trapped specimens of *L. okuensis*, provided the third description of the genus, describing skull and dental characters and their morphological variability, but without any discussion of its phylogenetic relationships. Based on external morphology and cranial and dental patterns, the genus was suggested to belong to the murine tribe Arvicanthini (Ducroz, Volobouev & Granjon, 2001; Michaux, Libois & Filippucci, 2005; Lecompte *et al*., 2008), but its closest relatives are doubtful: (1) based on eco-ethological and morphological characters, Petter (1986) underlined its affinity with *Desmomys*, an Ethiopian endemic, whereas, (2) based on dental characters, Dieterlen & Van der Straeten (1988) underlined its affinity with *Oenomys*, which is widespread in sub-Saharan Africa. Clarifying the phylogenetic position of *Lamottemys* is important for systematics, but also to better understand its evolutionary and biogeographical origin. To test the two proposed phylogenetic hypotheses (*Lamottemys* as sister clade to *Desmomys* or to *Oenomys*), we gathered both molecular and morphological evidence.

Taxon sampling has a strong influence on the accuracy of phylogenetic reconstruction, the distribution of branching times and phylogenetic tree imbalance (Heath *et al*., 2008). The Arvicanthini currently include 18 genera, most of them African, except *Golunda*, which is the only Asian representative (Lecompte *et al*., 2008). The taxonomic composition of the tribe has varied enormously since its creation by Misonne (1969). The monophyly of Arvicanthini has been repeatedly recognized (Ducroz *et al*., 2001; Steppan, Adkins & Anderson, 2004; Lavrenchenko & Verheyen, 2005; Steppan *et al*., 2005; Michaux, Chevret & Renaud, 2007; Lecompte *et al*., 2008; Rowe *et al*., 2008; Schenk, Rowe & Steppan, 2013), although no single molecular study has integrated all the taxa of the tribe. The most complete work, based on one mitochondrial and two nuclear markers, included 14 of the 18 genera allocated to the tribe, omitting *Dephomys*, *Thallomys*, *Thamnomys*, and *Lamottemys* (Lecompte *et al*., 2008). In the present study, we used mitochondrial and nuclear markers from 17 of the 18 recognized genera of the tribe (*Thamnomys* was missing). These molecular data, combined with a morphological cladistic analysis, allowed us to test the phylogenetic relationships and biogeographical origin of the enigmatic Mount Oku rat.

MATERIAL AND METHODS

MOLECULAR PHYLOGENY

Gene and taxon sampling

Following Lecompte *et al*. (2008), we selected one mitochondrial (*cytochrome b, cyt b*) and two nuclear

[exon 1 of *IRBP* (interphotoreceptor retinoid binding protein) and exon 10 of *GHR* (growth hormone receptor)] genes for this study. Sequences from 16 arvicanthine species, representing 14 genera, were extracted from the GenBank database. To these, we added 19 new sequences from six species, all housed in the MNHN, as follows (museum voucher or field numbers in parentheses): a *GHR* sequence for *Aethomys chrysophilus* (1999-165); six sequences, two of each gene, for *Dephomys defua* (2015-1257, 2015-1256); an *IRBP* sequence for *Hybomys univittatus* (2015-734); one *IRBP* and one *GHR* sequence for *Pelomys fallax* (C003); three sequences, one for each gene, for *Thallomys nigricauda* (SED001); and six sequences, two of each gene, for *Lamottemys okuensis* (2011-946, 2011-957). Compared with the previous phylogeny of Lecompte *et al.* (2008), we were thus able to add three genera (*Dephomys*, *Thallomys*, and *Lamottemys*) from Arvicanthini. To test the monophyly of this tribe, we also analysed specimens from nine other murine tribes recognized by Lecompte *et al.* (2008): Apodemyini (three species), Hydromyini (three species), Malacomyini (two species), Millardini (three species), Murini (one species), Otomyini (two species), Phloeomyini (two species), Praomyini (four species), and Rattini (one species). To root trees, we used two species as outgroups: one deomyine (*Lophuromys flavopunctatus*) and one gerbilline (*Gerbilliscus robustus*). GenBank accession numbers of all the taxa included in our analyses are available in Table 1.

DNA amplification and sequencing
Genomic DNA was extracted following the CTAB (cetylmethylammonium bromide) method (Winnepenninckx, Backeljau & de Wachter, 1993). Sequences were amplified via PCR using the following primers: L14723 (Kocher *et al.*, 1989), L14749 (Nicolas *et al.*, 2012b), H15915 (Ducroz *et al.*, 2001), and H14896 (Kouassi *et al.*, 2008) for the *cyt b* gene; I1, I2 (Poux & Douzery, 2004), F1, F2, and R1 (Missoup *et al.*, 2012) for the first exon of the *IRBP* gene; and GHR1, GHR 2 (Adkins *et al.*, 2001), GHR7, and GHR8 (Lecompte *et al.*, 2008) for exon 10 of the *GHR* gene. PCR consisted of an initial denaturation for 3 min at 94 °C, followed by 35 cycles of denaturation for 1 min at 94 °C, primer annealing for 1 min at 51 to 55 °C for the *cyt b* gene, 53 to 57 °C for the *IRBP* gene and 60 °C for the *GHR* gene, and a primer extension for 1 min 30 s at 72 °C. Reactions were completed by a final extension for 10 min at 72 °C. Double-stranded amplified products were visualized by electrophoresis on a 1.5% agarose gel [TBE (Tris borate ethylenediaminetetraacetic acid) buffer] and stained with ethidium bromide. The double-stranded PCR product was purified and run using an Automatic Sequencer ABI 3730 (ABI, Ramsey, Minnesota, USA). Sequencing was conducted under BigDye

terminator cycling conditions. Newly sequenced specimens were assigned GenBank numbers JQ639317 to JQ639328 and JQ694057 to JQ694063.

MOLECULAR PHYLOGENETIC ANALYSES
Sequences were aligned in BioEdit (Hall, 1999) with the software ClustalW (Thompson, Higgins & Gibson, 1994) and further checked by eye. Phylogenetic reconstructions were first performed on the single mitochondrial gene and on the two nuclear genes separately in order to evaluate each signal and to detect any incongruence. As no well-supported conflict was observed between the different topologies, the two data sets were finally combined in a single matrix. Relationships were explored using Bayesian inference (BI) and maximum likelihood (ML). The MrBayes v. 3.1 (Ronquist & Huelsenbeck, 2003) program's default priors for parameters of the Bayesian Markov-chain Monte Carlo (MCMC) was performed for the BI. Analyses were conducted with two runs and four chains (three hot and one cold), each of 20 000 000 generations, with trees sampled every 1000 generations. Stationarity was assessed by examining the average SD of split frequencies. As the two runs converged onto the stationary distribution, we expected the average SD of split frequencies to approach zero, reflecting the fact that the two tree samples become increasingly similar (Ronquist, Huelsenbeck & Van der Mark, 2005). The potential scale reduction factor will approach 1 as the runs converge. After a visual inspection, the first 25% of iterations was excluded as burn-in time and the resulting trees were combined in a majority rule consensus tree to obtain posterior probabilities (PP). ML analyses were run in RAxML v. 7.26 (Stamatakis, 2006) using the rapid Bootstrapping algorithm. Nodal support was estimated with 1000 bootstrap (BP) replicates. BI and ML analyses were conducted under three partition models (one for each gene). Each gene data set was tested for the most appropriate model of sequence evolution using the Akaike information criterion (Akaike, 1973) test as implemented in MrModeltest v. 3.7 (Posada & Crandall, 2001) using MrMTgui (available from http://genedrift.org/software/mrmtgui.html). The GTR + I + G, SYM + I + I, and HKY + I + G models were chosen respectively for *cyt b*, *IRBP*, and *GHR*. When the model chosen was not available in MrBayes or RAxML, the next most complex one was used in the software.

ESTIMATION OF DIVERGENCE DATES
Estimates of times to the most recent common ancestor (TMRCA), in Mya, and their credibility intervals were inferred using a Bayesian analysis implemented in BEAST v. 1.4.7 (Drummond & Rambaut, 2007). We used an uncorrelated lognormal relaxed clock, which

Table 1. GenBank accession numbers of taxa used in molecular analyses

| Subfamily | Tribe | Genus | Species | GenBank accession number | | |
				cyt b	*IRBP*	*GHR*
Murinae	Arvicanthini	*Aethomys*	*A. chrysophilus*	AJ604515	AY326075	JQ694059*
		Arvicanthis	*A. niloticus*	AF004569	DQ022386	AM910944
			A. somalicus	AF004573	–	AY294918
		Dasymys	*D. incomtus*	AF141217	EU292143	AM910950
		Dephomys	*D. defua* 1	JQ639324*	JQ639317*	JQ694057*
			D. defua 2	JQ639325*	JQ639318*	JQ694058*
		Desmomys	*D. harringtoni*	AF141206	EU292144	–
		Golunda	*G. ellioti*	AM408338	AM408332	AM910951
		Grammomys	*G. macmillani*	AM408345	AM408329	AM910980
			Grammomys sp.	AF141218	DQ022389	AM910952
		Hybomys	*H. univittatus*	AF141219	JQ639319*	DQ019059
		Lamottemys	*L. okuensis* 1	JQ639327*	JQ639320*	JQ694061*
			L. okuensis 2	JQ639326*	JQ639321*	JQ694060*
		Lemniscomys	*L. striatus*	AF141210	AM408321	AM910956
		Micaelamys	*M. namaquensis*	AF141215	AM408330	AY294914
		Mylomys	*M. dibowskii*	AF141212	EU292146	AM910965
		Oenomys	*O. hypoxanthus*	AM408342	AM408324	AM910970
		Pelomys	*P. fallax*	DQ022382	JQ639322*	JQ694062*
		Rhabdomys	*R. pumilio*	AF141214	AY326106	AY294913
		Stochomys	*S. longicaudatus*	EU292149	EU292147	DQ019076
		Thallomys	*T. nigricauda*	JQ639328*	JQ639323*	JQ694063*
	Apodemini	*Apodemus*	*A. flavicollis*	AB032853	AB032860	AM910943
			A. mystacinus	AF159394	AJ311158	AM910942
			A. sylvaticus	AB033695	AB032863	–
	Hydromyini	*Conilurus*	*C. penicillatus*	AM910935	AM910938	AM910949
		Hydromys	*H. chrysogaster*	AM408339	AM408319	AM910954
		Rhynchomys	*R. isarogensis*	AY324462	AY326108	DQ019075
	Malacomyini	*Malacomys*	*M. edwardsi*	DQ022379	DQ022392	AM910958
			M. longipes	AM408341	DQ022393	AM910957
	Millardini	*Cremnomys*	*C. cutchicus*	DQ022381	DQ022384	–
		Millardia	*M. kathleenae*	EU292148	EU292145	AM910963
			M. meltada	AF141221	AM408322	AM910962
	Murini	*Mus*	*M. musculus*	V00711	AB033711	AY271378
	Otomyini	*Otomys*	*O. angoniensis*	AM408343	AM408325	AM910971
		Parotomys	*Parotomys* sp.	EU349773	–	AY294912
	Phloeomyini	*Batomys*	*B. granti*	AY324459	DQ191496	AY294917
		Phloeomys	*P. cumingi*	DQ191484	AY326103	–
	Praomyini	*Hylomyscus*	*H. parvus*	AF518330	DQ022399	DQ019060
		Mastomys	*M. erythroleucus*	AF518338	AM408335	AM910959
		Myomyscus	*M. verreauxii*	AF518355	DQ022408	AM910967
		Praomys	*P. tullbergi*	AF518365	AM408327	AM910974
	Rattini	*Rattus*	*R. rattus*	AB033702	AM408328	AM910976
Deomyinae		*Lophuromys*	*L. flavopunctatus*	AY828236	AY326091	AY326091
Gerbillinae		*Gerbilliscus*	*G. robustus*	AJ875234	AY326113	AY294920

*new sequence; –, missing data; *cyt b*, *cytochrome b*; *GHR*, growth hormone receptor; *IRBP*, interphotoreceptor retinoid binding protein.

allows independent rates of nucleotide substitution on different branches. Two independent runs, each of 20 000 000 generations, were performed under the Yule speciation model. For each, the first 10% of trees was discarded, and a 50% consensus tree was constructed from the remaining trees. The two runs were combined in TRACER v. 1.4 (Rambaut & Drummond, 2007), which also provides options for examining effective

sample size values and frequency plots in order to check that mixing of the MCMC chain was adequate. Analyses were conducted on the combined data set, under three partition models (one for each gene), and following the best-fitting models chosen by MrModeltest, as above. Three priors based on fossil records were specified to calibrate our molecular clock: (i) following Steppan *et al*. (2004) and Rowe *et al*. (2011), the divergence time of 12.1 Mya (±2.0 SD) for the transition from *Antemus* to *Progonomys* (Jacobs & Downs, 1994) was used to calibrate the split of Phloeomyini (*Phloeomys* + *Batomys*) from other Murinae; (ii) the calibration point of 11 Mya (±2.0 SD, Rowe *et al*., 2011) for the oldest fossils of *Apodemus* (Martin Suarez & Mein, 1998; Vangengeim, Lungu & Tesakov, 2006) was defined for the split between Apodemyini (*Apodemus mystacinus*, *Apodemus sylvaticus*, *Apodemus flavicollis*), Murini (*Mus musculus*), Malacomyini (*Malacomys edwardsi*, *Malacomys longipes*) and Praomyini (*Myomys verreauxii*, *Mastomys erythroleucus*, *Praomys tullbergi*, *Hylomyscus parvus*); (iii) the date of 6.5 Mya (±1 SD)

as the calibration prior for the Arvicanthini–Otomyini split (Winkler, 2002; Rowe *et al*., 2008; Taylor *et al*., 2014).

MORPHOLOGICAL PHYLOGENY

Following our molecular results, the morphological cladistic analysis was restricted to Arvicanthini, along with two representatives (*Otomys irroratus* and *Otomys typus*) of its closest tribal relative (Otomyini) in order to check the monophyly of the tribe. All genera of Arvicanthini were included in the morphological analyses, except *Thamnomys*. For a given genus, a related species was selected when the species used in the molecular analysis was not available. To root trees, three species from three other murine tribes, *sensu* Lecompte *et al*. (2008), were added as outgroups: Malacomyini, *Malacomys longipes*; Praomyini, *Praomys jacksoni*; and Rattini, *Rattus exulans*. Museum voucher numbers of all specimens included in our analysis are given in Table 2. To build our data matrix (Table 3), we used

Table 2. Origin and museum voucher numbers of specimens used in the morphological cladistic analysis

Species	Hosting museum	Country of origin	Voucher numbers
Aethomys chrysophilus	MNHN	Zimbabwe	1990-297, 1990-312, 1990-318, 1990-328
Arvicanthis niloticus	MNHN	Senegal	1992-1189, 1992-1160
Arvicanthis somalicus	MNHN	Ethiopia	1973-197, 1973-336
Dasymys rufulus	MNHN	Ivory Coast	1999-800, 1999-867, 1999-875
Dephomys eburnea	MNHN	Ivory Coast	1997-2184, 1997-2191
Desmomys harringtoni	BMNH	Ethiopia	72–467, 72–751
Golunda ellioti	MNHN	India	1957-590, 1957-592
Grammomys dolichurus	MNHN	Zimbabwe	1990-289, 1990-289
Grammomys macmillani	MNHN	Central African Republic	1991-1094, 1991-1095
Grammomys poensis	MNHN	Central African Republic	1991 – 846, 1991-2115
Hybomys univittatus	MNHN	Gabon	1996-1227, 1996-1334
Lamottemys okuensis	MNHN	Cameroon	1984-493 (holotype), 1984-494 (paratype), 2011-946 to 2011-966, 2013-49 to 2013-80
Lemniscomys striatus	MNHN	Ivory Coast	1979-157, 1979-158,1979-430
Micaelamys namaquensis	MNHN	South African Republic	1964-57, 1996-570, 1996-571
Mylomys dybowskii	MNHN	Ivory Coast	1992-829
Oenomys hypoxanthus	MNHN	Gabon	1995-2941, 1995-3009, 1995-3017
Pelomys campanae	MNHN	Democratic Republic of Congo	1966-117, 1966-118
Stochomys longicaudatus	MNHN	Gabon	1996-501, 1996-502, 1996-1998, 1996-2100
Thallomys loringi	MNHN	South African Republic; Angola	1962-1123 1960-379
Thallomys paedulcus	MNHN	Somalia	1997-23, 1997-24
Otomys irroratus	MNHN	South African Republic	1964-294, 1996-562
Otomys typus	MNHN	Ethiopia	1792-220, 1972-225
Malacomys longipes	MNHN	Gabon	1995-2552, 1995-2718, 1995-2811
Praomys jacksoni	MNHN	Central African Republic	1963– 583, 1963-584, 1965-243
Rattus exulans	MNHN	Unknown	1970-174

BMNH, British Museum of Natural History of London; MNHN, Muséum National d'Histoire Naturelle.

Table 3. Morphological data matrix. Unknown conditions indicated by '?'

	Character states							
Taxon	10	20	30	40	50	60	70	79
Malacomys longipes	0000012112001001020110110001010102010010111002311?1?1000010020010001010010122 0
Praomys jacksoni	1010000102011001020011011001101000201101101101001031?000001002001000101011011 20
Praomys tullbergi	1010010102011101021011111?01101012001101101101031031?00000100200100010101101 120
Rattus exulans	1211000002011000100001111002101110201101110010310001?10000100200100010010010 1220
Otomys irroratus	10201210111011?001211?0010001120102101001102222220 21?10122121?2010101100110001 0
Otomys typus	102012101110100012111001100011101021010011022222220 21?10122121?201011111011000 10
Golunda ellioti	10210001121011101210010001111102101001012000010 01?000110002011011111101011 210
Lamottemys okuensis	1011001000?0101?1000101001121101000211000101011011001100100210021?100010000 1110
Desmomys harringtoni	101111210210100020001111121110102201101101000 1?0111?01011000230101111000010?2 0
Grammomys dolichurus	101100010201100110011011001101000020?001001001101000012200000002000110110110 1022
Grammomys macmillani	00110001020111111200110110011010102000010010010010001020000002100011001011011 022
Grammomys poensis	101100010201110112001100100110100021101101101110000010000000020000110000110 1022
Pelomys campanae	1021000110101110121001011001111100010100003100000200000020000211010000000 210
Thallomys paedulcus	10111001120010??120?00001002111100210111101001100010102000000200001100101??11 22
Thallomys damarensis	10101001120011101200000010021010002101111012011010101000010002000011000?1??112 2
Dasymys rufulus	12201210111011011110010110011110001101111002000311?1?10010021?2010100010010010 1
Dephomys eburnea	1000000002001101121011001001101010210101101001201011?000100000011010000?0?1210 22
Micaelamys namaquensis	101000011101010100101011002101000210101110000310 01?0001002 0?00001101101121120
Aethomys chrysophilus	101000012101010120101001002101000001011010000310 01?00000100200101101101121120
Lemniscomys striatus	0020000121011110120001011002111102101011002000031001?02010100200111101100011200
Oenomys hypoxanthus	101000011200110010101101100111101021010110101111101020100000020110100111110141 0
Rhabdomys pumilio	1021000021011101200110110011111000101101001001011?000000002000111010001212 10
Stochomys longicaudatus	10000001121010011210110010111110102001111100010310 01?0001000000110101110110112 0
Arvicanthis niloticus	12200001021010101001010010021111002001111012000310 31?000111202?2110110100111011 1
Arvicanthis somalicus	12200001210101010010100211110000011110020013100 1?00111000?00101101001110111
Mylomys dybowskii	1010100121011001210110010021111002101001011001310 01?20111100201101101100010?10
Hybomys univittatus	1011011000111?0002001100111101102201101101111000011?0000101000011001000011102

(i) 22 characters defined by Lecompte, Granjon & Denys (2002) for Praomyini; (ii) three characters set by Taylor, Denys & Mukerjee (2004) for Otomyini; and (iii) 52 newly defined characters. Finally, a total of 77 characters was selected as follows: 37 cranial (including 17 new characters), 26 dental (24 new), and 14 external (11 new). To this, we added two other characters, one ecological and one ethological (following the previous works of Rosevear, 1969; Skinner & Smithers, 1990; Nowak, 1991), giving a final matrix of 79 characters. In order to exclude potential variability related to age, only specimens with erupted functional molars were used for the definition of characters. For a given genus, the type species was primarily examined and intraspecific variability was taken into account by examining as many specimens as possible based on material housed in the MNHN. Craniodental characters of *L. okuensis* were selected according to the recent description of the species, based on the 53 newly trapped specimens from Mount Oku (Denys *et al*., 2014). Of the 79 characters used for analyses, 47 were coded as binary (0/1) and the rest as multistate characters as follows: 27 in three (0/1/2), four in four (0/1/2/3), and one in five (0/1/2/3/4) states. The listing of characters and character states are presented in the Appendix. Phylogenetic relationships were inferred from maximum parsimo-

ny (MP) using PAUP v. 3.1 (Swofford, 1993). Heuristic searches were performed using stepwise-addition branch-swapping (ten random additions) and TBR swapping algorithm. Ambiguous characters (not observed or not applicable) were coded with a '?' that has been optimized to not generate additional steps. The optimization was carried out under the option 'accelerated transformation', which favours reversions by increasing the number of synapomorphies on the internal branches. All characters were weighted equally. Node robustness was estimated by the values of the decay index (DI) computed for each cladogram (Bremer, 1988).

RESULTS

MOLECULAR PHYLOGENY

Our final combined data set included 44 taxa and consisted of 3264 characters, representing 1140, 1202, and 922 bp for the *cyt b*, *IRBP*, and *GHR* genes, respectively. Both the BI and ML analyses produced highly concordant topologies (Fig. 1) that strongly supported the monophyly of Arvicanthini (PP = 1.00, BP = 95) and the position of Otomyini (represented by *Otomys angoniensis* and *Parotomys* sp.) as its sister clade

(PP = 1.00, BP = 100). The hypothesis of a close relationship between *Lamottemys* and *Oenomys* is refuted; instead *Oenomys hypoxanthus* and *Golunda ellioti* have basal positions within Arvicanthini. *Lamottemys* clustered with all other taxa in a moderately supported monophyletic group (PP = 1.00, BP = 68). Within this group, a polytomic relationship was recovered between *Micaelamys* and three moderately supported subclades: the first one (PP = 0.89, BP = 65) included *Dasymys* and a highly supported group (PP = 1.00, BP = 100) consisting of seven other genera (*Rhabdomys*, *Desmomys*, *Lamottemys*, *Lemniscomys*, *Arvicanthis*, *Mylomys*, and *Pelomys*); the second subclade (PP = 1.00, BP = 74) was

restricted to four genera (*Aethomys*, *Hybomys*, *Stochomys*, and *Dephomys*); and the third (PP = 0.76, BP < 50) was represented by *Thallomys* and *Grammomys*. In the first subclade, a close relationship between *Lamottemys* and *Desmomys* was found in both analyses, but this group was only well supported in the BI analysis (PP = 0.95, BP = 51).

DIVERGENCE TIMES

Our phyletic reconstruction indicates that arvicanthine representatives last shared a common ancestor around
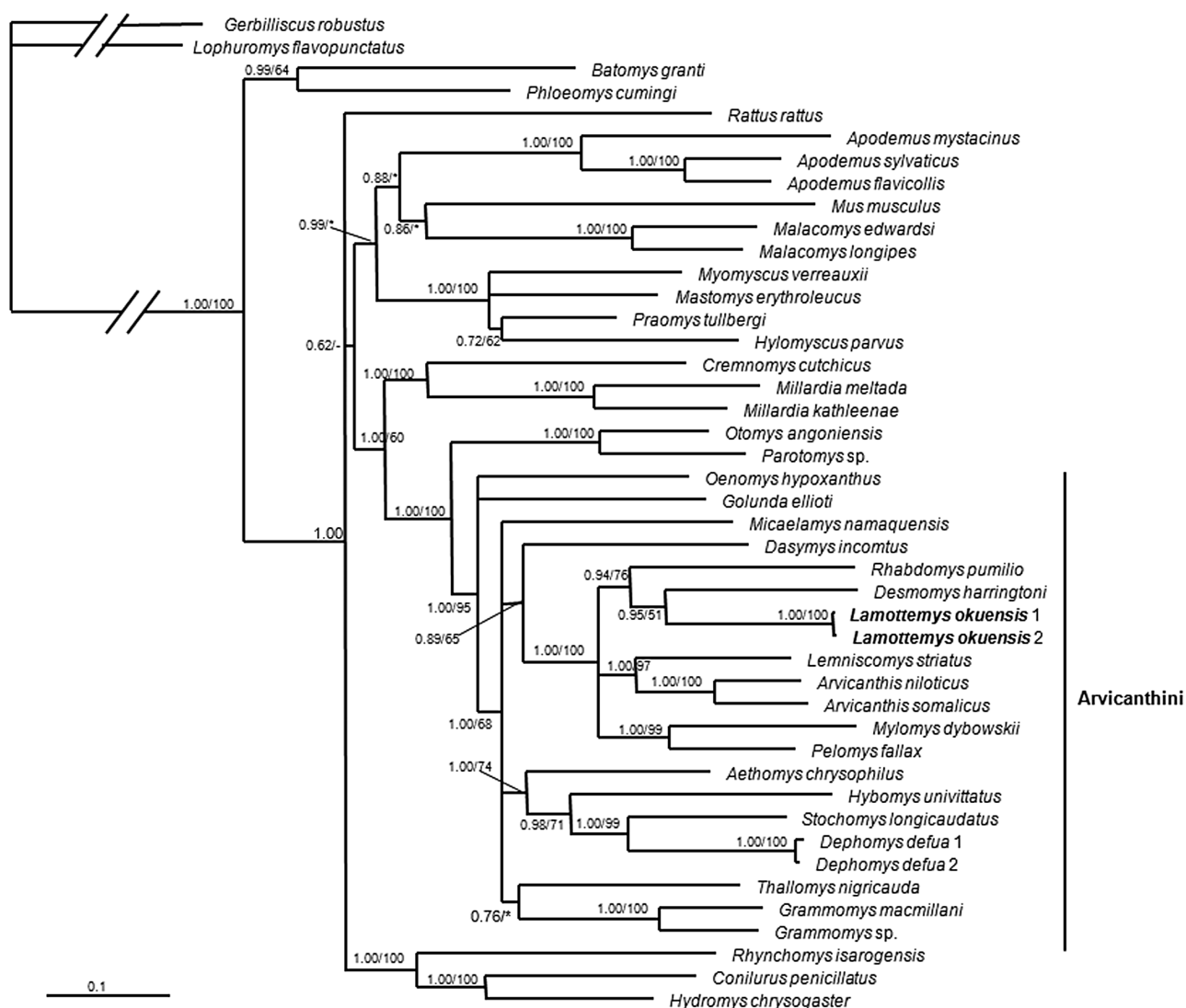

Figure 1. Molecular phylogenetic tree inferred using Bayesian inference for the concatenated data set [*cytochrome b*: 1140 bp, *IRBP* (interphotoreceptor retinoid binding protein): 1202 bp, *GHR* (growth hormone receptor): 922 bp]. The average Bayesian posterior probabilities (left) of two runs, and bootstrap values (>50%, right) calculated for 1000 bootstrap replicates are indicated for each node.

6.87 Mya (95% range: 8.29–5.50 Mya), in the Upper Miocene (Fig. 2). When the two cladistically basal taxa of the tribe (*Oenomys* and *Golunda*) are excluded, the TMRCA of the remaining taxa was estimated in the same epoch, at about 6.43 Mya (7.76–5.10 Mya). The TMRCA of the subclade including the genera *Rhabdomys*, *Desmomys*, *Lamottemys*, *Lemniscomys*, *Arvicanthis*, *Mylomys*, and *Pelomys* was dated at 4.95 Mya (6.07–3.86 Mya). The TMRCA of the clade grouping *Lamottemys* and *Desmomys* was estimated at about 3.53 Mya (4.57–2.56 Mya).

MORPHOLOGICAL PHYLOGENETIC ANALYSIS

The MP analysis of 26 taxa produced 22 equally parsimonious trees of a total length of 353 steps (consistency index = 0.317 and retention index = 0.682). Seventy-four of the 79 characters included in our data matrix (Table 3) are parsimony informative, one is constant, and four are non-informative. The strict consensus tree (Fig. 3) did not recover the monophyly of Arvicanthini. The clade including the Otomyini and Arvicanthini was well supported (DI = 2), as was the relationship between the two otomyine representatives and *Dasymys* (DI > 3). As in our molecular results, morphological cladistics also refuted the hypothesis of

a close relationship between *Oenomys* and *Lamottemys*. A well-supported clade (DI = 2) grouped *Lamottemys* and the genera *Desmomys* and *Hybomys*, but the relationship was polytomic amongst the three taxa. Six synapomorphies supported this grouping: a lower position of the sphenopalatine foramen relative to the palatal bone (character 14); a long and clearly visible carotidial canal (character 23); a small and soft basioccipital crest (character 26); a mentale foramen at a different level to the masseteric crest (character 36); a slightly bent dental crest relative to the mandibular corpus (character 37); and a mammary formula of 0 + 2 (character 77).

DISCUSSION

PHYLOGENETIC RELATIONSHIPS AND ORIGIN OF *LAMOTTEMYS*

We confirm for the first time, based on our molecular data, the inclusion of *Lamottemys* within the tribe Arvicanthini. The monophyly of Arvicanthini was not recovered by our morphological cladistic analysis, but *Lamottemys* was included in the clade encompassing both Arvicanthini and Otomyini. Our molecular and morphological data clearly refute the hypothesis of Dieterlen & Van der Straeten (1988), who proposed a
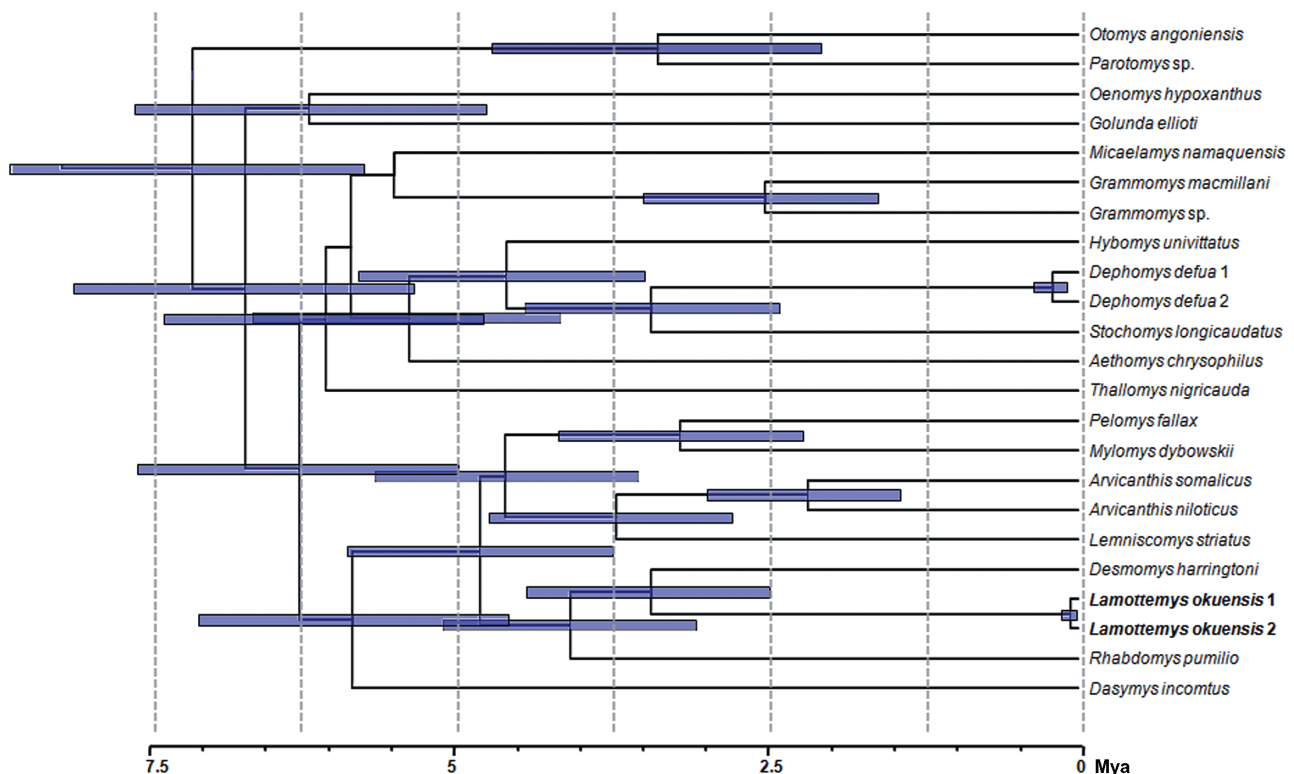

Figure 2. Simplified maximum clade credibility chronogram obtained from BEAST with 95% highest posterior density intervals.
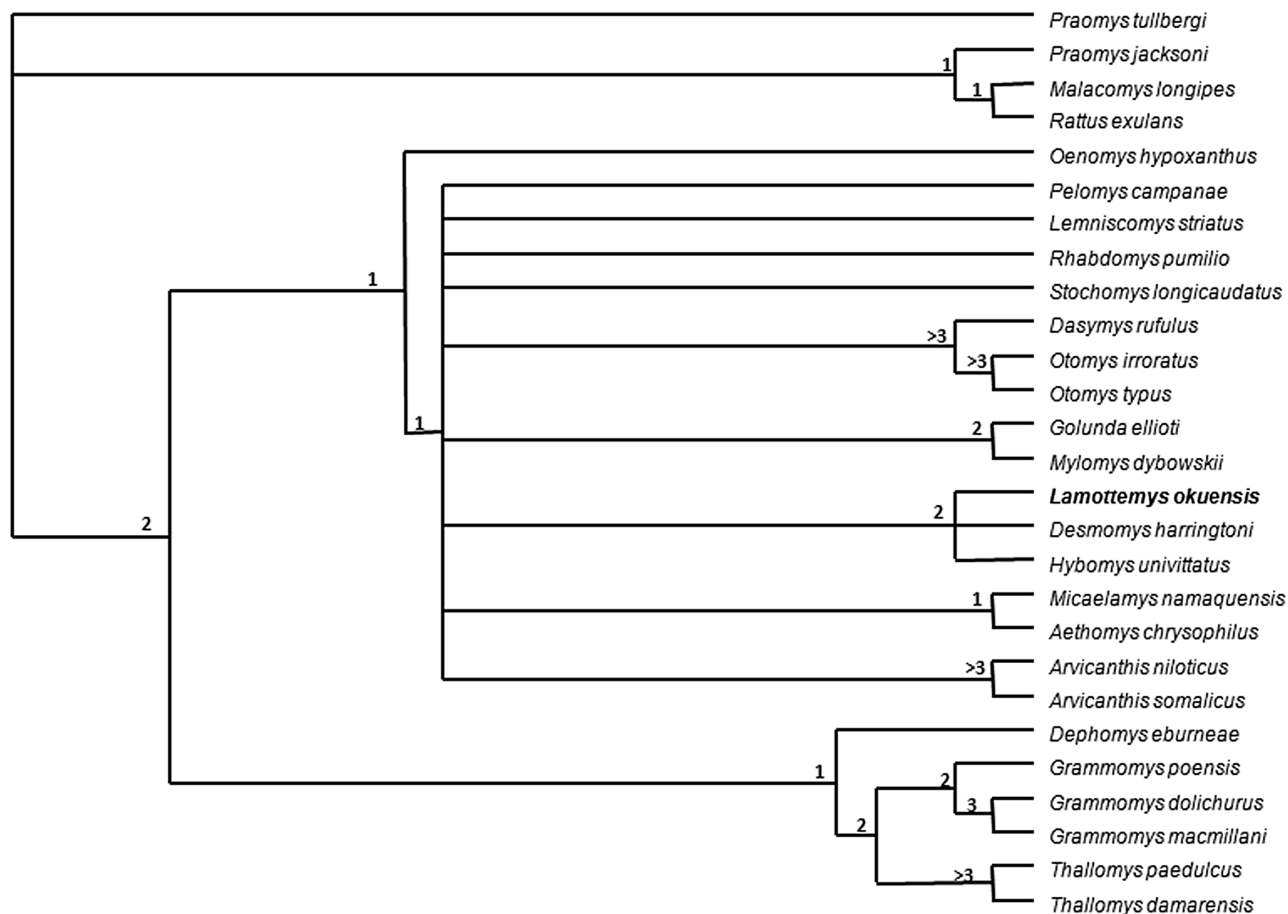
Figure 3. Morphological strict consensus cladogram inferred from PAUP. Decay index values are indicated for each node.

close relationship between *Lamottemys* and *Oenomys* based on the size of the skull and the molar pattern. These authors reported the similar shapes and organization plan of the cusps of the molars (the third upper molar particularly) in *Lamottemys* and *Oenomys*. In his description of *Lamottemys*, Petter (1986) underlined several similarities amongst *Lamottemys*, *Desmomys*, and *Oenomys*. Based on external morphology, ecology, and dental patterns, however, he concluded that *Lamottemys* and *Desmomys* are more closely related. Petter (1986) highlighted the presence of a nail on digit V in *Lamottemys* and *Desmomys* (digit V with claw in *Oenomys*), underscored their similar coloration pattern, emphasized their terrestrial behaviour and preference for montane forest habitat, and underlined the similar structure of the upper incisors (slightly fluted) and occlusal plan of the upper molar cusps. Our morphological cladistic analysis allowed us to assess the importance of these different characters in a phylogenetic context. None of the diagnostic characters of Petter (1986) was found to be useful to resolve the phylogenetic position of *Lamottemys*. Indeed, most of the morphological homologies that determine the cladistic position (Fig. 3) of *Lamottemys* concern skull characters (position of the sphenopalatine foramen relative to the palatal bone, pattern of the carotidial canal, shape of the basioccipital crest, position of the mentale foramen relative to the masseteric crest, shape of bent dental crest relative to the mandibular corpus). Only one was related to external morphology (the mammary formula). The sharing of states of these six characters anchored the node formed by *Lamottemys*, *Desmomys*, and *Hybomys* in our morphological cladistic tree. This may explain why specimens of *Lamottemys* in the Zoologisches Forschungsmuseum Alexander Koenig, Bonn, reported by Dieterlen & Van der Straeten (1988) were misidentified as *Hybomys*. In a recent canonical analysis of 12 skull measurements, Denys *et al.* (2014) clearly discriminated samples of these three genera. However, according to the position of the two representatives of *Desmomys* in their principal components analysis graph, they suggested the possibility of a close relationship between *Lamottemys* and *Desmomys*.

Although caution should be taken (weak ML support), our molecular data indicate a close phylogenetic relationship between *Lamottemys*, a rodent endemic to Mount Oku, and *Desmomys*, an endemic of Ethiopian montane forests. A scenario to explain *Lamottemys*' peculiar distribution and this close relationship is needed. For rodents, such relationships between CVL endemics and East African taxa have been reported before. For example, based on craniometric analyses, *Lophuromys dieterleni* (endemic to the montane forest of Mount Oku) and *Lophuromys eisentrauti* (endemic to Mount Lefo) were suggested to be closely related to the Ethiopian montane forest endemic *Lophuromys chrysopus* (Verheyen *et al.*, 2002). Dieterlen & Van der Straeten (1992), based on dental pattern, proposed a close relationship between the Bamenda Highland endemic *Otomys occidentalis* and the two species *Otomys barbouri* and *Otomys lacustris*, respectively from Mount Elgon (Uganda and Kenya) and the Southern Highlands and Eastern Arc Mountains of Tanzania. Although this hypothesis was recently refuted by molecular data, the two CVL-endemic species (*Otomys occidentalis* and *Otomys burtoni*) are still considered to be closely related to two *Otomys* species complexes from the mountain ranges comprising the East African 'Montane circle' and Ethiopian Highlands (Taylor *et al.*, 2014). This similar biogeographical pattern (CVL – East Africa), observed in taxa living in different environments (montane forest and montane grasslands), may reflect recurrent connections between West and East African archipelagos, probably favoured during climatic fluctuations that led to subsequent expansions and contractions of montane environments (deMenocal, 2004; Plana, 2004; Feakins & deMenocal, 2010).

Today, *L. okuensis* is restricted to an area (Mount Oku) within the Bamenda Highlands. A recent dispersal-vicariance analysis of puddle frogs (*Phrynobatrachus*) suggested that this CVL subregion contains more than half of puddle-frog diversity and was probably an ancestral distribution area of the genus (Zimkus & Gvoždík, 2013). The Bamenda Highlands were formed in the Early Miocene, whereas the southern part of the CVL is more recent (probably of Pleistocene age; Marzoli *et al.*, 2000). For puddle frogs, molecular dating suggested an Early Miocene speciation event during a time of prolific volcanic activity, but the majority of intraspecific diversification events seem to have occurred during the Pliocene and Pleistocene. Our molecular dating placed the origin of *Lamottemys* after 3.53 Mya, in the Late Pliocene. This was probably favoured by Plio-Pleistocene climatic changes that led to the isolation of *Lamottemys* on Mount Oku as major climate changes occurred in Africa at the end of the warm Pliocene phase (Feakins & deMenocal, 2010). Subsequent development of periodically cooler and drier African conditions commenced during the late Plio-

cene, and this overall drying trend was punctuated with humid phases. During xeric phases, both lowland and montane forest cover was significantly reduced across tropical Africa with peak periods of aridifications at 2.8, 1.7, and 1.0 Mya (deMenocal, 2004; Feakins & deMenocal, 2010). In addition, the intensification of Pliocene volcanic activities in Central East Africa, which led to the formation of the Rift Valley (Baker, Mohr & Williams, 1972; Logatchev, Belossov & Milanovsky, 1972), and in the CVL (Wright *et al.*, 1985), inhibited exchange between the CVL and Ethiopian mountains and thus promoted the differentiation of *Lamottemys* following the montane forest refuge model (Rietkerk, Ketner & de Wilde, 1996; Robbrecht, 1996; Plana, 2004). Our divergence time estimate is congruent with the pulse of morphospecies diversification observed at about 4.1 Mya for the Afroalpine fossorial rodent *Tachyoryctes* in the Ethiopian Plateau (López-Antonanzasa, Flynn & Knoll, 2013). Pliocene palaeontological data from Central Africa are needed for a better understanding of the evolutionary scenarios that promoted the diversification of CVL endemics. On the basis of the available data (Blackburn, 2008a, b; Missoup *et al.*, 2012; Nicolas *et al.*, 2012a; Zimkus & Gvoždík, 2013; Taylor *et al.*, 2014), both the complex tectonic and volcanic history of the CVL and the palaeoclimatic history of the region seem to have promoted the diversification of the CVL fauna.

NEW INSIGHTS ON SYSTEMATICS AND EVOLUTION OF ARVICANTHINE RODENTS

With 17 of the 18 genera currently included within the tribe, this study is the most comprehensive for Arvicanthini to date. Even with the inclusion of previously unrepresented taxa (*Dephomys*, *Thallomys*, and *Lamottemys*), the monophyly of Arvicanthini was still recovered with molecular data. The low coherence index (IC = 0.317) and the high proportion of homoplasic characters (51 out of the 79 tested characters have an IC ≤ 0.333) suggested by our morphological cladistic analysis may explain the position of the two otomyine representatives that are known to be closely related to Arvicanthini based on molecular data (Ducroz *et al.*, 2001; Lecompte *et al.*, 2008; Rowe *et al.*, 2008; Schenk *et al.*, 2013; this study). Our morphological results also indicate the difficulties in defining morphological synapomorphies for arvicanthine rodents. None of the characters evoked before (dorsal striping, shape of the foot, size of digit V, morphology of nasal bones, shape and pattern of molar teeth, striations on upper incisors, dominant living mode, Ducroz *et al.*, 2001) can be used to define the tribe.

Our comprehensive phylogenetic analysis of Arvicanthini allowed us to examine several results from previous works. First, our molecular data support a

basal cladistic position for both *Golunda* and *Oenomys*. Schenk *et al.* (2013) proposed a basal position for *Oenomys*, followed by the divergence of *Golunda*. Second, we have reaffirmed the validity of the clade grouping *Arvicanthis*, *Desmomys*, *Lemniscomys*, *Mylomys*, *Pelomys*, and *Rhabdomys* (Ducroz *et al.*, 2001; Lecompte *et al.*, 2008). Moreover, we have shown that this clade includes the genus *Lamottemys*. Within this clade, a sister-group relationship between *Desmomys* and *Lamottemys*, both closely related to *Rhabdomys*, was recovered, complementing previous results that grouped *Desmomys* and *Rhabdomys* (Ducroz *et al.*, 2001; Lavrenchenko & Verheyen, 2005; Lecompte *et al.*, 2008). Third, we have shown a close relationship amongst *Aethomys, Stochomys*, *Hybomys*, and *Dephomys*. Within this clade, the highly supported group made up of *Hybomys* and *Dephomys* confirms earlier findings based on dental and cranial characters (Misonne, 1969; Van der Straeten, 1984). This result is also consistent with the *Hybomys* division of Musser & Carleton (2005) formed by *Dephomys*, *Stochomys*, and *Hybomys*. Fourth, our data confirm previous molecular evidence for sister-group relationships between *Arvicanthis* and *Lemniscomys* (Michaux *et al.*, 2007; Lecompte *et al.*, 2008; Schenk *et al.*, 2013) and between *Mylomys* and *Pelomys* (Ducroz *et al.*, 2001; Lecompte *et al.*, 2008).

Our divergence time analyses showed that Arvicanthini and Otomyini last shared a common ancestor around 7.32 Mya (8.82–5.93 Mya). According to palaeontological data, the Middle Miocene was characterized by faunal exchanges between Africa and Asia that persisted in the northern part of the East African rift system in the Upper Miocene and Pliocene (Denys, Chorowicz & Jaeger, 1985). Our estimate of tribal divergence corresponds to this epoch and is consistent with the presence of an Asian representative (*Golunda*) as a primitive member within the Arvicanthini. Furthermore, an extinct arvicanthine genus (*Saidomys*) is known to have occurred in both Africa and Asia within that time frame: the Upper Miocene of East Africa (Winkler, 1997, 2002); Early Pliocene of Pakistan and Afghanistan (Brandy, Sabatier & Jaeger, 1980; Sen, 1983); and Late Pliocene of Thailand (Chaimanee, 1988). The Upper Miocene also corresponds to an aridification episode and the spread of C4 grasses into East Africa (Cerling *et al.*, 1997). Our results suggest that the main lineages within Arvicanthini diversified at that time (e.g. split between all Arvicanthini, excluding *Golunda* and *Oenomys*, *c*. 6.43 Mya; split between *Aethomys* and *Stochomys*, *Hybomys* and *Dephomys*, *c*. 5.52 Mya; see Fig. 2). According to Renaud *et al.* (2005), the expansion of C4 grasses probably created new ecological opportunities and could have favoured the evolution of specialist rodents able to feed on abrasive vegetal matter rather than on seeds because of a dental adaptation. Both generalist and specialist species would have been able to cope with deteriorating environmental conditions and stephanodonty (found in *Grammomys*, *Thamnomys*, *Thallomys*, *Aethomys*, *Hybomys*, *Lamottemys*, *Oenomys*, and *Rhabdomys*) probably appeared independently within the tribe. Indeed, by increasing the enamel crests of the molar cusps, stephanodonty favours a more anteroposterior component of mastication and increases the ability of rodents to consume harder and more fibrous vegetal matter (Denys, 1994; Rodriguez *et al.*, 2013). The development of stephanodont crests is known to be variable amongst different rodent species and is not homologous from one genus to another. Rodriguez *et al.* (2013) have shown that the initial and parallel appearance of stephanodonty may have been facilitated by developmental processes. In otomyine rodents, the unique pattern of lamellar molars has been suggested to be related to an increase in the grazing component of the diet (Sénégas, 2001). For Arvicanthini, complementary ecological, behavioural, and trophic data are needed to improve our understanding of the evolution of such morphological traits.

REFERENCES

Adkins RM, Gelke EL, Rowe D, Honeycutt RL. 2001. Molecular phylogeny and divergence time estimates for major rodent groups: evidence from multiple genes. *Molecular Biology and Evolution* **18:** 777–791.

Akaike H. 1973. Information theory as an extension of the maximum likelihood principle. In: Petrov BN, Csaki F, eds. *Second International Symposium on Information Theory*. Budapest: Akademiai Kiado, 267–281.

Baker BH, Mohr PA, Williams LAJ. 1972. Geology of the eastern rift system of Africa. *Geological Society of America* **136:** 1–67.

Blackburn DC. 2008a. A new species of *Cardioglossa* (Amphibia: Anura: Arthroleptidae) endemic to Mount Manenguba in the Republic of Cameroon, with an analysis of morphological diversity in the genus. *Zoological Journal of the Linnean Society* **154:** 611–630.

Blackburn DC. 2008b. Biogeography and evolution of body size and life history of African frogs: phylogeny of squeakers (*Arthroleptis*) and long-fingered frogs (*Cardioglossa*) estimated from mitochondrial data. *Molecular Phylogenetics and Evolution* **46:** 806–826.

Bowie RCK, Fjeldsa J, Hackett SJ, Bates JM, Crowe TM. 2006. Coalescent models reveal the relative roles of ancestral polymorphism, vicariance, and dispersal shaping phylogeographic structure of an African montane forest robin. *Molecular Phylogenetics and Evolution* **38:** 171–188.

Brandy LD, Sabatier M, Jaeger JJ. 1980. Implications phylogénétiques et biogéographiques des dernières découvertes de Muridae en Afganistan, au Pakistan et en Ethiopie. *Geobios* **13:** 639–643.

Bremer K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* **42:** 795–803.

Bryja J, Mikula O, Patzenhauerov H, Oguge NO, Sumbera R, Verheyen E. 2014. The role of dispersal and vicariance in the Pleistocene history of an East African mountain rodent, *Praomys delectorum*. *Journal of Biogeography* **41:** 196–208.

Burgess N, Hales JD, Underwood E, Dinerstein E, Olson D, Itoua I, Schipper J, Ricketts T, Newman K. 2004. *Terrestrial ecoregions of Africa and Madagascar.* Washington, DC: Island Press.

Cerling TE, Harris JM, MacFadden BJ, Leakey MG, Quade J, Eisenmann V, Ehleringer JR. 1997. Global vegetation change trough the Miocene/Pliocene boundary. *Nature* **389:** 153–158.

Chaimanee Y. 1988. Plio-Pleistocene rodents of Thailand. *Thai Studies in Biodiversity* **3:** 1–303.

Demos TC, Kerbis Peterhans JC, Agwanda B, Hickerson MJ. 2014. Uncovering cryptic diversity and refugial persistence among small mammal lineages across the Eastern Afromontane biodiversity hotspot. *Molecular Phylogenetics and Evolution* **71:** 41–54.

Denys C. 1994. Diet and dental morphology of two coexisting *Aethomys* species (Rodentia) in Mozambique. Implications for diet reconstruction in related extinct species from South Africa. *Acta Theriologica* **39:** 357–364.

Denys C, Chorowicz J, Jaeger J-J. 1985. Tectogenèse et évolution des faunes de rongeurs et autres mammifères du rift est-africain au Mio-Pliocène. Mise en évidence de corrélations. *Bulletin de la Société Geologique France* **8:** 381–389.

Denys C, Missoup AD, Nicolas V, Fülling O, Delapré A, Bilong Bilong CF, Taylor PJJ, Hutterer R. 2014. African highlands as mammal diversity hotspots: new records of *Lamottemys okuensis* (Rodentia: Muridae) and other endemic rodents from Mount Oku, Cameroon. *Zoosystema* **36:** 647–690.

Deruelle B, Ngounounou I, Demaiffe D. 2007. The 'Cameroon Hot Line' (CHL): a unique example of active alkaline intraplate structure in both oceanic and continental lithospheres. *Comptes Rendus Geosciences* **339:** 589–600.

Dieterlen F 2008. *Lamottemys okuensis* IUCN 2012. IUCN Red List of Threatened Species. Version 2014.3. Available at: http://www.iucnredlist.org Downloaded 04 December 2014.

Dieterlen F, Van der Straeten E. 1988. Deux nouveaux spécimens de *Lamottemys okuensis* Petter, 1986 du Cameroun (Muridae: Rodentia). *Mammalia* **52:** 379–385.

Dieterlen F, Van der Straeten E. 1992. Species of the genus *Otomys* from Cameroon and Nigeria and their relationship to East African forms. *Bonner Zoologische Beitrage* **43:** 383–392.

Drummond AJ, Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by 861 sampling trees. *BMC Evolutionary Biology* **7:** 214.

Ducroz J-F, Volobouev V, Granjon L. 2001. An assessment of systematics of arvicanthine rodents using mitochondrial DNA sequences: evolutionary and biogeographical implications. *Journal of Mammalian Evolution* **8:** 173–206.

Feakins SJ, deMenocal PB. 2010. Global and African regional climate during the Cenozoic. In: Werdelin L, Sanders WJ, eds. *Cenozoic mammals of Africa.* Berkeley, CA: University of California Press, 45–55.

Fülling O. 1992. Ergänzende Angaben über Gaumenfaltenmuster von Nagetieren (Mammalia: Rodentia) aus Kamerun. *Bonner Zoologische Beiträge* **43:** 415–421.

Gonwouo NL, LeBreton M, Wild C, Chirio L, Ngassam P, Tchamba NM. 2006. Geographic and ecological distribution of the endemic montane chameleons along the Cameroon mountain range. *Salamandra* **42:** 209–226.

Graham CH, Smith TB, Languy M. 2005. Current and historical factors influencing patterns of species richness and turnover of birds in the Gulf of Guinea highlands. *Journal of Biogeography* **32:** 1371–1384.

Hall TA. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41:** 95–98.

Heath TA, Zwickl DJ, Kim J, Hillis DM. 2008. Taxon sampling affects inferences of macroevolutionary processes from phylogenetic trees. *Systematic Biology* **57:** 160–166.

Herrmann H-W, Bohme W, Euskirchen O, Herrmann PA, Schmitz A. 2005a. African biodiversity hotspots: the reptiles of Mt. Nlonako, *Cameroon. Revue Suisse de Zoologie* **112:** 1045–1069.

Herrmann H-W, Bohme W, Herrmann PA, Plath M, Schmitz A, Solbach M. 2005b. African biodiversity hotspots: the amphibians of Mt. Nlonako, Cameroon. *Salamandra* **41:** 61–81.

Herrmann H-W, Bohme W, Herrmann PA, Plath M, Schmitz A, Solbach M. 2007. Amphibians and reptiles of the Tchabal Mbabo Mountains, Adamaoua Plateau, Cameroon. *Bonner Zoologische Beiträge* **55:** 27–35.

Herrmann H-W, Herrmann PA, Schmitz A, Bohme W. 2004. A new frog species of the genus *Cardioglossa* from the Tchabal Mbabo Mtns, Cameroon (Anura: Arthroleptidae). *Herpetozoa* **17:** 119–125.

Huhndorf MH, Kerbis Peterhans JC, Loew SS. 2007. Comparative phylogeography of three endemic rodents from the Albertine Rift, east central Africa. *Molecular Ecology* **16:** 663–674.

Jacobs LL, Downs WR. 1994. The evolution of murine rodents in Asia. In: Tomida Y, Li CK, Setoguchi T, eds. *Rodent and lagomorph families of Asian origins and diversification*. Tokyo: National Science Museum Monographs, 149–156.

Koch FA, Wiens DA, Nyblade AA, Shore PJ, Tibi R, Ateba B, Tabod CT, Nnange JM. 2012. Upper-mantle anisotropy beneath the Cameroon Volcanic Line and Congo Craton from shear wave splitting measurements. *Geophysical Journal International* **190:** 75–86.

Kocher TD, Thomas WK, Meyer A, Edwards SV, Pääbo S, Villablanca FX, Wilson AC. 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences, USA* **86:** 6196–6200.

Kouassi KS, Nicolas V, Aniskine V, Lalis A, Cruaud C, Couloux A, Colyn M, Dosso M, Koivogui L, Akoua-Koffi C, Denys C. 2008. Taxonomy and biogeography of the African pigmy mice, subgenus *Nannomys* (Rodentia, Murinae, *Mus*). *Mammalia* **72:** 223–228.

Lavrenchenko LA, Verheyen E. 2005. An assessment of the systematics of the genus *Desmomys* Thomas, 1910 (Rodentia: Muridae) using mitochondrial DNA sequences. In: Hubert BA, Sinclair BJ, Lampe K-A, eds. *African biodiversity. Molecules, organisms, ecosystems*. Bonn, Germany: Springer, 363–369.

Lecompte E, Aplin K, Denys C, Catzeflis F, Chades M, Chevret P. 2008. Phylogeny and biogeography of African Murinae based on mitochondrial and nuclear gene sequences, with a tribal classification of the subfamily. *BMC Evolutionary Biology* **8:** 1–21.

Lecompte E, Granjon L, Denys C. 2002. The phylogeny of the *Praomys* complex (Rodentia: Muridae) and its phylogeographic implications. *Journal of Zoological Systematics and Evolutionary Research* **40:** 8–25.

Logatchev NA, Belossov VV, Milanovsky EE. 1972. East African rift development. *Tectonophysics* **15:** 72–81.

López-Antonanzasa R, Flynn LJ, Knoll F. 2013. A comprehensive phylogeny of extinct and extant Rhizomyinae (Rodentia): evidence for multiple intercontinental dispersals. *Cladistics: The International Journal of the Willi Hennig Society* **29:** 247–273.

Martin Suarez E, Mein P. 1998. Revision of the genera *Parapodemus*, *Apodemus*, *Rhagamys* and *Rhagapodemus* (Rodentia, Mammalia). *Geobiosciences* **31:** 87–97.

Marzoli A, Piccirillo EM, Renne PR, Bellieni G, Iacumin M, Nyobe JB, Tongwa AT. 2000. The Cameroon Volcanic Line revisited: petrogenesis of continental basaltic magmas from lithospheric and asthenospheric mantle sources. *Journal of Petrology* **41:** 87–109.

deMenocal PB. 2004. African climate change and faunal evolution during the Pliocene-Pleistocene. *Earth and Planetary Science Letters* **220:** 3–24.

Michaux J, Chevret P, Renaud S. 2007. Morphological diversity of Old World rats and mice (Rodentia, Muridae) mandible in relation with phylogeny and adaptation. *Journal of Zoological Systematics and Evolutionary Research* **45:** 263–279.

Michaux JR, Libois R, Filippucci MG. 2005. So close and so different: comparative phylogeography of two small mammal species, the yellow-necked fieldmouse (*Apodemus flavicollis*) and the woodmouse (*Apodemus sylvaticus*) in the Western Palearctic region. *Heredity* **94:** 52–63.

Milelli L, Fourel L, Jaupart C. 2012. A lithospheric instability origin for the Cameroon Volcanic Line. *Earth and Planetary Science Letters* **335–336:** 80–87.

Misonne X. 1969. African and Indo-Australian Muridae. Evolutionary trends. *Musée Royal l'Afrique Centrale, Zoologie Tervuren* **172:** 1–219.

Missoup AD, Nicolas V, Wendelen W, Keming E, Bilong Bilong CF, Couloux A, Atanga E, Hutterer R, Denys C. 2012. Systematics and diversification of *Praomys* species (Muridae: Murinae) endemic to the Cameroon Volcanic Line (West Central Africa). *Zoologica Scripta* **41:** 327–345.

Montigny R, Ngounouno I, Deruelle B. 2004. Ages K–Ar des roches magmatiques du fossé de Garoua (Cameroun): leur place dans le cadre de la «ligne du Cameroun». *Comptes Rendus Geoscience* **336:** 1463–1471.

Musser GG, Carleton MD. 2005. Superfamily Muroidea. In: Wilson DE, Reeder DM, eds. *Mammal species of the world: a taxonomic and geographic reference*, 3rd edn. Baltimore, MD: The Johns Hopkins University Press, 894–1531.

Nicolas V, Missoup AD, Colyn M, Cruaud C, Denys C. 2012a. West-Central African Pleistocene lowland forest evolution revealed by the phylogeography of Misonne's soft-furred mouse. *African Zoology* **47:** 100–112.

Nicolas V, Schaeffer B, Missoup AD, Kennis J, Colyn M, Denys C, Tatard C, Cruaud C, Laredo C. 2012b. Assessment of three mitochondrial genes (16S, Cytb, CO1) for identifying species in the Praomyini tribe (Rodentia: Muridae). *PLoS ONE* **7:** e36586.

Nowak RM. 1991. *Walker's mammals of the world. Vol II.* 5th edn. Baltimore & London: Johns Hopkins University Press.

Oates JF, Bergl RA, Linder JM. 2004. *Africa's Gulf of Guinea forests: biodiversity patterns and conservation priorities*. Advances in Applied Biodiversity Science, number 6. Washington, DC: Conservation International.

Petter F. 1986. Un rongeur nouveau du mont Oku (Cameroun): *Lamottemys okuensis*, gen. sp. nov. (Rodentia, Muridae). *Cimbebasia Serie A* **8:** 97–105.

Plana V. 2004. Mechanisms and tempo of evolution in the African Guineo-Congolian rainforest. *Philosophical Transactions of the Royal Society of London B* **359:** 1585–1594.

Posada D, Crandall K. 2001. A comparison of different strategies for selecting models of DNA substitution. *Systematic Biology* **50:** 580–601.

Poux C, Douzery EJP. 2004. Primate phylogeny, evolutionary rate variations, and divergence times: a contribution from

the nuclear gene IRBP. *American Journal Physician Anthropology* **124:** 1–16.

Rambaut A, Drummond AJ 2007. Tracer version 1.4. Available at: http://beast.bio.ed.ac.uk/Tracer

Renaud S, Michaux J, Schmidt DN, Aguilar JP, Mein P, Auffray JC. 2005. Morphological evolution, ecological diversification and climate change in rodents. *Proceeding of the Royal Society of London B* **272:** 609–617.

Rietkerk M, Ketner P, de Wilde JJFE. 1996. Caesalpinioideae and the study of forest refuges in central Africa. In: Van der Maesen LJG, Van der Burgt XM, Van Medenbach de Rooy JM, eds. *The biodiversity of African plants*. Dordrecht: Kluwer, 618–623.

Robbrecht E. 1996. Geography of African Rubiaceae with reference to glacial rain forest refuges. In: Van der Maesen LJG, Van der Burgt XM, Van Medenbach de Rooy JM, eds. *The biodiversity of African plants*. Dordrecht: Kluwer, 564–581.

Rodriguez HG, Renaud S, Charles C, Le Poul Y, Solé F, Aguilar JP, Michaux J, Tafforeau P, Headon D, Jernvall J, Viriot L. 2013. Roles of dental development and adaptation in rodent evolution. *Nature Communications* **4:** 2504. doi: 10.1038/ncomms3504

Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics (Oxford, England)* **19:** 1572–1574.

Ronquist F, Huelsenbeck JP, Van der Mark P 2005. *MrBayes 3.1 manual*, 69 p. Available at: http://www.cs.mcgill.ca/~birch/birchhomedir/dat/GDE/GDEHELP-linux-x86_64/doc/BIRCH/doc/mrbayes/mb3.1_manual.pdf

Rosevear DR. 1969. *The rodents of West Africa*. London: Trustees of the British Museum (Natural History).

Rowe KC, Aplin KP, Baverstock PR, Moritz C. 2011. Recent and rapid speciation with limited morphological disparity in the genus *Rattus*. *Systematic Biology* **60:** 188–203.

Rowe KC, Reno ML, Richmond DM, Adkins RM, Steppan SJ. 2008. Pliocene colonization and adaptive radiations in Australia and New Guinea (Sahul): multilocus systematics of the old endemic rodents (Muroidea: Murinae). *Molecular Phylogenetics and Evolution* **47:** 84–101.

Schenk JJ, Rowe KC, Steppan S. 2013. Ecological opportunity and incumbency in the diversification of repeated continental colonizations by muroid rodents. *Systematic Biology* **0:** 1–28.

Sénégas F. 2001. Interpretation of the dental pattern of the South African fossil *Euryotomys* (Rodentia, Murinae) and origin of otomyine dental morphology. In: Denys C, Granjon L, Poulet A, eds. *African small mammals*. Paris: Institut de Recherche pour le Développement, 151–160.

Sen S. 1983. Rongeurs et Lagomorphes du gisement Pliocène de Pul-e Charki, bassin de Kabul, Afghanistan. *Bulletin of Museum of Natural History* **5:** 33–74.

Skinner JD, Smithers RHN. 1990. *The mammals of the Southern Africa subregion*. 2nd edn. Cape Town: University of Pretoria.

Smith TB, Holder K, Girman D, O'Keefe K, Larison B, Chan Y. 2000. Comparative avian phylogeography of Cameroon and Equatorial Guinea mountains: implications for conservation. *Molecular Ecology* **9:** 1505–1516.

Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics (Oxford, England)* **22:** 2688–2690.

Steppan SJ, Adkins RM, Anderson J. 2004. Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. *Systematic Biology* **53:** 533–553.

Steppan SJ, Adkins RM, Spinks PQ, Hale C. 2005. Multigene phylogeny of the Old World mice, Murinae, reveals distinct geographic lineages and the declining utility of mitochondrial genes compared to nuclear genes. *Molecular Phylogenetics and Evolution* **37:** 370–388.

Swofford DL. 1993. *PAUP – phylogenetic analysis using parsimony, version 3.1*. Champaign: Illinois Natural History Survey.

Taylor P, Denys C, Mukerjee M. 2004. Phylogeny of the African murid tribe Otomyini (Rodentia), based on morphological and allozyme evidence. *Zoologica Scripta* **33:** 389–402.

Taylor PJ, Maree S, Cotterill FPD, Missoup AD, Nicolas V, Denys C. 2014. Molecular and morphological evidence for a Pleistocene radiation of laminate-toothed rats (*Otomys*: Rodentia) across a volcanic archipelago in equatorial Africa. *Biological Journal of the Linnean Society* **113:** 320–344.

Thompson JD, Higgins DG, Gibson TJ. 1994. Clustal W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research* **22:** 4673–4680.

Van der Straeten E. 1984. Etude biométrique des genres *Dephomys* et *Stochomys* avec quelques notes taxonomiques (Mammalia, Muridae). *Revue de Zoologie Africaine* **98:** 771–798.

Vangegeim EA, Lungu AN, Tesakov AS. 2006. Age of Vallesian lower boundary (continental Miocene of Europe). *Stratigraphy and Geological Correlation* **14:** 655–667.

Verheyen W, Hulselmans LJ, Dierckx T, Verheyen E. 2002. The *Lophuromys flavopunctatus* Thomas, 1888 *s.l.* species complex: a craniometric study, with the description and genetic characterization of two new species (Rodentia-Miridae-Africa). *Bulletin de l'Institut Royal des Sciences de Belgique, Biologie* **72:** 141–182.

Winkler AJ. 1997. Systematics, paleobiogeography, and paleoenvironmental significance of rodents from the Ibole Member, Manonga valley, Tanzania. In: Harrison T, ed. *Neogene paleontology of the Manonga Valley, Tanzania*. New York: Plenum Press, 311–332.

Winkler AJ. 2002. Neogene paleobiogeography and East African paleoenvironments: contributions from the Tugen Hills rodents and lagomorphs. *Journal of Human Evolution* **42:** 237–256.

Winnepenninckx B, Backeljau T, de Wachter R. 1993. Extraction of high molecular weight DNA from molluscs. *Trends in Genetics* **9:** 407.

Wright JB, Hastings DA, Jones WB, Williams HR. 1985. *Geology and mineral resources of West Africa*. London: George Allen and Unwin Publishers.

Zimkus BM. 2009. Biogeographical analysis of Cameroonian puddle frogs and description of a new species of

Phrynobatrachus (Anura: Phrynobatrachidae) endemic to Mount Oku, Cameroon. *Zoological Journal of the Linnean Society* **157:** 795–813.

Zimkus BM, Gvoždík V. 2013. Sky Islands of the Cameroon Volcanic Line: a diversification hot spot for puddle frogs (Phrynobatrachidae: *Phrynobatrachus*). *Zoologica Scripta* **42:** 59–611.

APPENDIX

Description of characters used for the morphological cladistic analysis. The letter T represent the characters taken from Taylor *et al*. (2004) and L those previously used by Lecompte *et al*. (2002). Newly defined characters are in bold. Abbreviations: VD, dorsal view; VV, ventral view; VL, lateral view.

SKULL CHARACTERS

1. Nasal – VD
   (0) Anterior part as wide as posterior one
   (1) Anterior part enlarged
2. Nasal – VL – L
   (0) Long, stops anteriorly to the level of the incisors
   (1) Short, does not reach the level of the incisors
   (2) Same level as the incisors
3. Nasal curvature – VL
   (0) Rectilinear
   (1) Curve starting at middle point of nasal
   (2) Curve starting at beginning of nasal
4. Nasofrontal suture – VD – L
   (0) Backwards extension, nasofrontal is far beyond the maxillary-frontal-lacrymal suture
   (1) Short extension, nasofrontal suture not reaching the middle of maxillary-frontal-lacrymal suture
5. Frontal: interorbital constriction – VD – L
   (0) Poorly marked
   (1) Marked and narrow
6. Frontal: maximal interorbital constriction point – VD – L
   (0) Situated anteriorly to the frontal bone
   (1) In the centre of the frontal bone
   (2) No stable position, the edges of frontal makes two parallel lines
7. Frontoparietal crests: shape of the anterior frontal part – VD
   (0) Parallel
   (1) Divergent
   (2) Convergent
8. Frontoparietal crests: shape of the posterior part – VD
   (0) Curved
   (1) Linear

9. Frontoparietal crests – VD
   (0) Aligned on the braincase
   (1) Not aligned
10. Zygomatic arches: posterior part of zygomatic plate – VL
    (0) Forms a hook backwards
    (1) Forms a hook frontwards
    (2) Forms a vertical crest
11. Zygomatic arch: anterior edge of the zygomatic plate – VL – L
    (0) Anterior edge of the zygomatic plate straight, almost vertical
    (1) Anterior edge of the zygomatic plate well projected forward
12. Zygomatic arch: malar process and zygomatic bone – VL – L
    (0) Very thin zygomatic bone (half the breadth of malar process)
    (1) Zygomatic bone and malar process of same breadth
13. Zygomatic arch: position of squamosal root – VL – L
    (0) Same level as the dorsal border of periotic capsula
    (1) Above the dorsal border of periotic capsula
14. Sphenopalatine foramen relative to palatal bone – VL
    (0) Lower than palatal bone
    (1) Higher than sphenoid bone
15. Optic foramen – VL – T
    (0) Small
    (1) Large
16. Postglenoid fossa: general shape – VL
    (0) Crescentiform, elongated
    (1) Round or oval shape
17. Parietosquamosal suture and interparieto-occipital suture – VL – L
    (0) The two sutures are face-to-face
    (1) The parietosquamosal suture is placed more dorsally than the interparieto-occipital suture
18. Mastoid process: orientation compared to tympanic bulla – VL
    (0) Oblique forwards
    (1) Oblique backwards
    (2) Vertical
19. Tympanic hook – VL – L
    (0) Short
    (1) Long
    (2) Wide and flat lamina
20. Disposition of the auditory meatus – VL
    (0) Vertical
    (1) Backwards
21. Auditory meatus: size compared to the tympanic bulla – VL – L
    (0) Small
    (1) Large

22. Periotic capsula – VV
    (0) Large
    (1) Small
23. Tympanic bulla: carotidial canal – VV – L
    (0) Long and well visible
    (1) Small, hardly visible or absent
24. Ovale foramen width – VV – T – L
    (0) Small, width less than half of the pterygoid fossa or absent
    (1) Large, half of the pterygoid fossa, round to egg-shaped
25. Ovale foramen length – VV – T
    (0) Does not pass through the pterygoid bone
    (1) Passes through the pterygoid bone
26. Basioccipital crest – VV – L
    (0) Strong, salient
    (1) Small, soft
27. Anterior lacerate foramen – VV
    (0) Medium length, stops in the middle of tympanic bullae
    (1) Short, stops before the tympanic bullae
    (2) Long, reaches the posterior part of tympanic bullae
28. Posterior limit of the incisor foramen – VV – L
    (0) Short, not reaching the first root of upper M1/
    (1) Reaching the first root of M1/
    (2) Reaching the second root of M1/
29. Incisor foramen: shape of central septum – VV
    (0) Narrow
    (1) Enlarged anteriorly
30. Intermolar rows' shape – VV – T
    (0) Parallel (equal anterior and posterior width)
    (1) Narrow anteriorly, wider distally (diverging posteriorly)
    (2) Narrow posteriorly, wider anteriorly (converging anteriorly)
31. Anterior palatal foramen – VV
    (0) Absent
    (1) Short
    (2) Long
32. Supraoccipital crests – VD/VL
    (0) Thin and short
    (1) Long, reaching the upper part of mastoid hook

MANDIBLE

33. Size and shape of the interval between coronoid and condyloid processes – VL
    (0) Short and curved
    (1) Long and rectilinear
34. Relative heights of coronoid and condyloid processes – VL
    (0) Coronoid process higher
    (1) Condyloid process higher
    (2) Equal heights

35. Capsular process – exterior VL – L
    (0) Prominent, at the level of or anterior to the coronoid crest
    (1) Prominent, posterior to the coronoid crest
    (2) Not prominent, smooth, poorly marked
36. Foramen mentale – VL ext
    (0) At a different level from the masseteric crest
    (1) In front of the masseteric crest
37. Internal face of the mandible: dental crest of the mandibular corpus – interior VL – L
    (0) Crest strongly bent
    (1) Crest slightly bent

TEETH

38. Molar proportions. Ratio between upper tooth row length and maximum skull length – VV – L
    (0) < 0.15, microdontia
    (1) > 0.15, macrodontia
39. Incisors – VL – L
    (0) Opisthodont
    (1) Orthodont
    (2) Proodont
40. Grooves on the upper incisors
    (0) Present
    (1) Absent
41. Grooves on the lower incisors
    (0) Present
    (1) Absent
42. Molar cusps appearance
    (0) Independent (both on young and old individuals)
    (1) Linked
43. Molar cusps alignment
    (0) Aligned transversally
    (1) Not aligned
44. Relative size of M3 compared with M1 and M2
    (0) Normal
    (1) Reduced strongly
    (2) Enlarged

UPPER MOLARS

45. Cusp t1 of M1
    (0) Round
    (1) With a crest
    (2) Crest slightly distinguishable
46. Cusp t3 of M1
    (0) Round
    (1) With a crest
    (2) Crest slightly distinguishable
47. General shape of cusp t4 of M1
    (0) Round
    (1) With a stephanodont crest
    (2) Crest slightly distinguishable

48. Shape and length of cusp of t4
    (0) Crestiform, elongated until t8
    (1) Round and individualized on one crest
    (2) Not visible
    (3) No stephanodont crest
49. Cusp t7 of M1
    (0) Crestiform
    (1) Round, in the form of a cusp
    (2) Absent
    (3) Slightly differentiated
50. Presence of cusp t9 of M1
    (0) Present
    (1) Absent
51. Shape of cusp t9 of M1
    (0) Well individualized
    (1) In the form of a crest, linked to cusp t6
    (2) Not visible
    (3) Poorly individualized, not linked to t6
52. Presence of posterior cingulum of the upper molars
    (0) Present on at least one molar
    (1) Absent on all three molars
53. Frequence of posterior cingulum of the upper molars
    (0) Present on one molar
    (1) Present on two molars
    (2) Present on three molars
54. Anterolabial cingular cusp of M2
    (0) Well marked cusp
    (1) Absent
    (2) Crestiform
55. Cusp t3 of M3
    (0) Absent
    (1) Well marked
    (2) Slightly differentiated

Note: Characters 45, 46, 47, 49, 50, and 54 allow to characterize the stephanodonty degree in regard to the increasing number of present crests.

LOWER MOLARS

56. Labial cingulum
    (0) Present at least on one molar
    (1) Absent
57. Stephanodont crests on the first and second lobe of the first lower molar (m1)
    (0) Present
    (1) Absent
    (2) Poorly visible
58. Transverse link between anterolabial and anterolingual cusps
    (0) Present
    (1) Absent
    (2) Poorly visible
59. Presence of a accessory anterior cusp on m1
    (0) Present
    (1) Absent

60. Posterior cingulum on m1
    (0) Small
    (1) Large
    (2) Absent
61. Presence of the posterior cingulum on m1
    (0) Present
    (1) Absent
62. Shape of the posterior cingulum on m1
    (0) Larger than the posterior cingulum (Cp) of m1
    (1) Smaller than the Cp of m2
    (2) Equal size on both molars
63. Second lobe of m3
    (0) One cusp
    (1) Two large cusps of equal size
    (2) Undifferentiated cusps fused into a single lamina
    (3) Two cusps of unequal size

EXTERNAL CHARACTERS

64. Length of dorsal and lateral hairs
    (0) Equal length on back and flanks
    (1) Some longer, bristle-like hairs on the back
65. Colour of the ventral part of pelage – L
    (0) White base of the hairs
    (1) Dark or coloured base of the hairs
66. Pelage dorsal striations
    (0) Present
    (1) Absent
67. Colour of the dorsal coat
    (0) The coat has two distinct colours
    (1) The coat has more than two colours
68. Tail
    (0) Naked or few hairs
    (1) Hairy
69. Terminal tuft on the tail
    (0) Present
    (1) Absent
70. Tail: colour of dorsal and ventral parts
    (0) Identical
    (1) Bicoloured tail, paler on ventral side
71. Ears
    (0) Small (smaller than the head length)
    (1) Large (longer than the head length)
72. Nose: red colour
    (0) Present
    (1) Absent
73. Hindfoot: principal plantar pad number – L
    (0) Four to five
    (1) Six
74. Hindfoot: size of digit V
    (0) Vestigial
    (1) Not reduced
75. Hindfoot: relative size of digits I and V
    (0) Digit V is the smallest one
    (1) Digits I and V equal
    (2) Digit I is the smallest

76. Relative length of head and body length (HB) vs. tail length (TL)
    (0) HB > TL
    (1) HB < TL
77. Mammary formula (pectoral + unguinal pairs number) – L
    (0) 0 + 2
    (1) 1 + 2
    (2) 2 + 2
    (3) 0 + 2 or 1 + 2
    (4) More than four mammae

ECO-ETHOLOGICAL CHARACTERS
(FROM LITERATURE DATA)

78. Nycthemeral rhythm
    (0) Diurnal
    (1) Semidiurnal
    (2) Nocturnal
79. Dominant mode of life
    (0) Terrestrial
    (1) Fossorial
    (2) Arboreal