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A giant among dwarfs: a new species of galago (Primates: Galagidae) from Angola

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ABSTRACT

Objectives: Based on vocalization recordings of an unknown galago species, our main objectives were to compare morphology and call structure with known closely-related taxa and describe a new species of galago.

Materials and Methods: We conducted field surveys in three forest habitats along the escarpment region in western Angola (Kumbira Forest, Bimbe Area and Northern Scarp Forest), and examined galago specimens from museums worldwide. We digitized and analyzed calls using Avisoft SASLab Pro software. We also compared museum specimens from Angola with other *Galago* and *Galagoides* specimens, and conducted comparative analyses (ANOVA and between group principle component analysis) based on a set of twelve linear measurements of skulls and teeth.

Results: We describe the new species to which we give the name Angolan dwarf galago, *Galagoides kumbirensis* sp. nov. The new species has a loud and characteristic crescendo call, used by other *Galagoides* spp. (*sensu stricto*) in West Africa to attract companions and repel rivals. However, this call shows species-typical differences from its closest relatives. *Galagoides kumbirensis* sp. nov. is also distinguished by differences in the skull morphology, pelage color and facial markings, as well as a larger body size, similar to that of *Galago moholi*, which is not known to be sympatric.

Conclusion: This discovery points to the importance of Angolan forests as refuges for endemic biodiversity. These forests are under severe threat from over-exploitation, and there is an urgent need to establish conservation measures and designate protected areas.

Previously unrecognized species of terrestrial mammals are being discovered at an ever-increasing rate as researchers expand their activities into new areas of forests and woodlands, and conduct extensive surveys (Ceballos and Ehrlich, 2009; Wilson and Mittermeier, 2011; Mittermeier et al., 2013). Some of these discoveries are made because of a change in views of what a species is, i.e. dependent on which species concept is adopted (Isaac et al., 2004; Groves and Grubb, 2011; Cotterill et al., 2014) and owing to the use of different technologies, including molecular analysis, to recognize species diversity within cryptic taxa (i.e. species that are very similar morphologically even though they are reproductively isolated: Bickford et al., 2007). In the field crucial information on the presence of cryptic taxa is often gathered with the aid of new methodologies such as camera trapping and remote recording (Hart et al., 2012; Li et al., 2015). In an era when many new species descriptions rely heavily on genetic evidence, it has become atypical to distinguish new taxa based on morphology and vocalizations alone. However, in groups such as molluscs (Alvim and Pimenta, 2013), crustaceans (Vonk and Jaume, 2014), insects (Gibbs, 2010; Hertach et al., 2015), birds (Ng et al., 2016), and nocturnal mammals (Helgen et al., 2010; Munds et al., 2013; Reeder et al., 2013), new taxa continue to be described in the absence of molecular data. The delimitation of these taxa using molecular data have repeatedly confirmed separations based on morphology and vocalizations (Wollscheid-Lengeling et al., 2001; Nekaris and Bearder, 2011; Mittermeier et al., 2013; Pozzi et al., 2014; Pozzi et al., 2015).

The well-studied Order Primates is a case in point: most new primate species recognized in the 21st century are the result of the taxonomic elevation of previously known subspecies to species (Groves, 2001; *Macaca* spp.: Kitchener and Groves, 2002; *Aotus* spp.: Defler and Bueno, 2007; *Nomascus* spp.: Thinh et al., 2010; *Microcebus* spp.: Hotaling et al., 2016). Taxa wholly new to science, however, are also being described (e.g. *Rungwecebus* *kipunji*: Jones et al., 2005; Davenport et al., 2006; *Tarsius tumpara*: Shekelle et al., 2008; *Rhinopithecus strykeri*: Geissmann et al., 2010; *Nycticebus kayan:* Munds et al., 2013).

Both morphological and genetic evidence suggest that a far greater number of cryptic species may yet be revealed within the galagos (Family Galagidae, also known as bushbabies; Grubb et al., 2003; Pimley, 2009; Oates, 2011; Nekaris, 2013; Pozzi et al., 2014; Pozzi et al., 2015). The galagos of the African mainland consist of 18 named and described species, although their taxonomy remains debated, with various arrangements of described species and sub-species being proposed (Nekaris and Bearder, 2011; Butynski, Kingdon and Kalina, 2013; Nekaris, 2013; Masters and Couette, 2015). We here follow the taxonomy of Nekaris (2013), which is largely identical to that of Butynski et al. (2013) but differs from Groves (2001) in that it recognizes the genera *Galagoides* and *Sciurocheirus*, which Groves subsumed under the genus *Galago*. In addition, we recognize the recently proposed genus *Paragalago*, for the eastern dwarf galagos, which includes the taxa *Gd. rondoensis*, *Gd. zanzibaricus, Gd. orinus, Gd. cocos* and *Gd. granti* (Masters et al., 2017).

Galagos are a monophyletic taxon originating in the Late Eocene that comprises six distinct radiations, (Pozzi et al., 2014, 2015; Pozzi, 2016). Dwarf galagos occur over much of Africa, with *Galagoides thomasi* and *Gd. demidovii* (also referred to as *Gd. demidoff*, Olson, 1979; Jenkins, 1987; Groves, 2001; Masters and Couette, 2015) occurring as far west as Senegal and Guinea Bissau, and *Paragalago granti* occurring as far east as the shores of Mozambique, with some species and subspecies being endemic to montane complexes (*P. orinus*) and offshore islands (*P. zanzibaricus zanzibaricus* and *Gd. demidovii poensis*) (Nekaris, 2013).

The nocturnal galagos fit the cryptic pattern in that they recognize each other and communicate via vocal, chemical and subtle morphological differences that may be cryptic to humans, rather than adopting the colorful pelages and sexually dimorphic features of diurnal primates (Masters, 1993; Pozzi et al., 2015). In the field, researchers have relied particularly on vocalizations and behavior to distinguish otherwise morphologically similar and difficult to distinguish species (Zimmermann, 1990; Bearder and Svoboda, 2013; Nash et al., 2013). In multiple classical studies it has been shown that it is possible to differentiate between species by observing their locomotion, behavior and habitats (Charles-Dominique and Bearder, 1979; Harcourt and Nash, 1986; Crompton et al., 1987; Weisenseel et al., 1993; Ambrose, 1999). All galagos produce advertising calls that are used to maintain contact between dispersed individuals, indicating spatial position and movement (Bearder et al., 1995). Galago species can be categorized into eight different vocal groups: click callers (*Euoticus* spp.), croak callers (*Sciurocheirus* spp.), repetitive callers (*G. senegalensis*, *G. moholi* and *G. matschiei*), trailing callers (*Otolemur* spp.), rolling callers (*P. rondoensis* and *P. zanzibaricus*), scaling callers (*P. orinus*), incremental callers (*P. cocos* and *P. granti*) and crescendo callers (*Gd. thomasi* and *Gd. demidovii*) (Grubb et al., 2003). Advertising calls exhibit marked specific variations, which make them particularly suitable for species discrimination (Masters, 1993; Bearder et al., 1995). In addition, complex vocal repertoires are often species-unique. For example, after being considered the same species for over 50 years, lesser galagos *G. moholi* and *G. senegalensis* were eventually classified as separate species due to substantially different vocal repertoires (Zimmermann et al., 1988; Zimmermann, 1990). This separation of the *G. senegalensis* and *G. moholi* was also suggested based on differences in adult body mass and reproductive parameters (Izard and Nash, 1988).

Other features used to distinguish galago species include pelage characteristics, facial markings, reproductive anatomy and other morphological attributes. Anderson (1999; 2001) and Anderson et al. (2000) used the cuticle scales of hairs and the arrangement of friction pads on the hands and feet to help distinguish between *G. senegalensis* and *G. moholi*, and between greater galagos *Otolemur crassicaudatus* and *O. garnetti*. Ambrose (2003; 2013) described a new species of squirrel galago (*Sciurocheirus makandensis)* based on facial markings, vocalization and pelage coloration. The eastern dwarf galagos (*P. orinus, P. rondoensis, P. granti, P. cocos* and *P. zanzibaricus*) can all be classified as distinct species on the basis of correlated differences in vocalizations and penile morphology (Anderson, 1999; Perkin, 2007; Masters et al., 2017). Although differences in skull morphology are more subtle in cryptic species, Masters and Bragg (2000) found that *O. crassicaudatus* and *O. garnettii* could be discriminated using ear and palate length, and *Gd. demidovii* and *Gd. thomasi* using ear and skull length.

Here we report on a new species of dwarf galago from Angola that has a unique combination of traits, and several features that are diagnostically different from other galagos. In terms of pelage coloration, skull shape and vocal behavior this species resembles other western dwarf galagos (*Galagoides* spp.), but their body size is like that of lesser galagos (*Galago* spp.). Three galagid species have been reported to occur in Angola, i.e. *O. crassicaudatus monteiri*, *G. moholi*, and *Gd. demidovii phasma*, whereas the occurrence of a fourth species, *Gd. thomasi* in the country is based solely on museum specimens (Nekaris, 2013; Bersacola et al., 2015). Machado (1969) reported *Gd. demidovii* to occur only in parts of the Lunda Norte Province, situated in the far north-east of the country, and in the north-western Angolan provinces of Zaire and Uige.

A Perkin and JC Masters examined the collections of the Field Museum of Natural History in Chicago (FMNH) in 2007 and considered three specimens labelled as '*Galago*' collected in the escarpment area of Angola to be distinct due to their large body size, and noted that they possessed a *Galagoides* type skull rather than a *Galago* one. Masters and Couette (2015) identified these skulls using multivariate morphometrics as *Gd. thomasi*. Based on museum specimens, Nash et al. (1989) tentatively listed *Gd. thomasi* as present in northern Angola, including the Angolan Escarpment (termed ‘Luanda highlands’ by Nash et al., 1989). Reviewing geographic variation of *Gd. thomasi*, Kingdon (2015) was of the opinion that distinct populations, possibly even a new subspecies or species, occurred on the Angolan Escarpment and in the Katanga Province of the Democratic Republic of Congo (DRC). In contrast, neither Groves (2001), based on studies of museum specimens, nor Bersacola et al. (2015), based on field surveys, found evidence of *Gd. thomasi* in Angola.

In 2005 vocal recordings of a dwarf galago were made by MSL Mills along the central Angolan Escarpment and sent for identification to the Nocturnal Primate Research Group (NPRG) at Oxford Brookes University. These calls were compared with those from the NPRG’s extensive sound library of all known galagos (Bearder et al., 1996). The vocalizations recorded from Angola were crescendo calls, identifying them as having been emitted by a *Galagoides* species, but different enough to lead to speculation that they belong to a previously undescribed species. Following *in situ* surveys and examination of museum specimens, in this paper we describe the new species, compare it to other sympatric and allopatric taxa, assess its conservation status, and outline an agenda for future work.

MATERIALS AND METHODS

Study area

Four biomes represent the land ecosystems in Angola, namely the Zambezian biome (covering 85% of the country), Guinea-Congolese biome (10.7%), the Karoo-Namib biome (2.6%) and the Afro-Upstream biome (0.5%) (Kuedikuenda and Xavier, 2009). Within Angola these biomes include 15 different ecoregions, including desert, savannah woodlands, grasslands, dry forests, montane forest-grassland mosaics, forest-savannah mosaic, miombo woodlands and mangroves (Olson et al., 2001). The Angolan Escarpment is located in the western part of the country, and stretches for 1000 km from north to south, forming part of the Great Escarpment of southern Africa (hereafter “Great Escarpment”) (Clark et al., 2011). Several ecological regions meet at the Angolan Escarpment, making it a complex area where topographical features have led to significant levels of endemism and floristic diversity (Hall, 1960; Figueiredo, 2010; Clark et al., 2011; Romeiras et al., 2014). Angola is believed to support more vertebrate species endemic to the Great Escarpment than any other country, except South Africa (Clark et al., 2011). Between the early 1970s and 2002, surveys in Angola were limited due to the protracted civil war, and subsequently the expense and logistical difficulties of operating in the country prevented much biological exploration. Now that systematic biological surveys are resumed, researchers expect that further endemic species will be discovered in this region (Vetter, 2003; Clark et al., 2011). We visited four study sites in north-western Angola: Kumbira forest (sub-montane/dry Congo basin forest); Bimbe (dry thicket islands in tall grass savannah with stream beds); Northern Scarp Forest (moist forest) and Calandula (miombo woodland/gallery forest).

Data acquisition

MS Svensson, E Bersacola, MSL Mills and SK Bearder conducted nocturnal surveys in Angola between 5 and 19 September 2013. The surveys lasted for 39 hours, walking on small roads and established paths and recording the habitat use and height in the canopy for each animal observed (for a more detailed description of the survey method see Bersacola et al., 2015). Nocturnal animals were photographed with a Canon EOS 600D camera, with Canon 70-200mm EF Zoom lens and Canon Speedlight 430EX II flash.

Vocalizations

At each survey site we recorded calls of galagos before sunrise (04:30 - 05:30) and after sunset (18:00-22:00). We remained stationary at recording sites throughout recording sessions. We made recordings using a Fostex Field Recorder equipped with a Sennheiser K6-ME67 directional microphone. We digitized calls using Avisoft SASLab Pro software (R. Specht, Berlin; version 5.2). We compared our results with vocalizations of the *Galagoides* taxa (*Gd. demidovii* and *Gd. thomasi*), as these are the only other crescendo callers, and with *G. moholi* as the only other small galago found in Angola (a repetitive caller, Bearder et al., 1995). Recordings were converted into spectrograms with a frequency resolution of 48 kHz (FFT length 512; 50% overlap; Hamming window). We focused on fundamental frequency (first harmonic, measured in kHz), crescendo unit length (the basic element of the crescendo phrase, measured in s), twitter unit length (the basic element of the twitter phrase, measured in s) and formant (dominant frequency, measured in kHz). We used a one-way ANOVA to test for differences among the four species followed by Tukey's HSD post-hoc test for pairwise differences between species.

Morphology

During visits to the FMNH in Chicago in 2011, A Perkin and JC Masters examined the skulls and skins of three distinct types of small galago collected in Angola: *G. moholi, Gd. demidovii* and specimens whose taxonomic identity remained inconclusive but were tentatively named *Gd. thomasi*. Knowing that Angolan specimens existed at FMNH in 2015 RA Munds revisited the anomalous specimens (FMNH 81755, 81756 and 81758).

In order to assess the taxonomic status of the three specimens from Angola we ran a multivariate analysis based on a set of twelve linear measurements of skulls and teeth. JC Masters measured the frontal, suppraoccipital, snout, premaxilla, toothcomb and skull lengths, the cranial height, the first lower molar, mastoid and palate widths, and the widths of the interorbital and temporal constrictions (for description and schematic illustration see Masters and Couette, 2015 Table 1 and Fig. 1). The dataset was composed of 50 specimens of *Gd. demidovii*, 50 specimens of *Gd. thomasi* and 50 specimens of *G. moholi*, plus the three specimens from Angola. JC Masters collected measurements in several institutions around the world [American Museum of Natural History, New York, USA (AMNH); Museum of Comparative Zoology, Cambridge, USA (MCZ); Field Museum of Natural History, Chicago, USA (FMNH); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Natural History Museum, London, UK (NHM); National Museum of Kenya, Nairobi, Kenya (NMK); Royal Museum of Central Africa, Tervuren, Belgium (RMCA) and National Museum of Zimbabwe, Bulawayo, Zimbabwe (NMZ)] and measured specimens using digital calipers according to the procedure described in Masters and Couette (2015). JC Masters measured 40 specimens twice and estimated the percentage of intra-observer measurement error using the method proposed by Bailey and Byrnes (1990). Error represented 2.4% of total variation in our sample and can be considered as insignificant.

The morphometric procedures were conducted by S Couette, who applied a size correction to the raw data using the Burnaby (1966) procedure that proposes to compute an isometric vector from all linear measurements and back project these measurements in a space orthogonal to this vector. Shape and size were analyzed separately. The raw data were logged prior to the size correction. The Geometric Mean (GM), considered as a proxy of the overall size, is the matrix product without units of the isometric vector and the raw data. All the statistical analyses were conducted using R 3.0.2. software (R Core Team, 2013) and the package MASS (Venables and Ripley, 2002). No body weights were available for specimens FMNH 81755, 81756 and 81758.

Table 1. Comparison of characteristics of *Gd. kumbirensis* sp. nov. and similar species with which it could be confused

Variables		***Gd. kumbirensis* sp. nov.**	***Gd. demidovii***	***Gd. thomasi***	***G. moholi***
Morphology*	**Head-body length (mm)**	♀♂ **159** (149-171) n=3	♀♂ **129** (73-155) n=200	♀♂ **146** (123-166) n=47	♀♂ **150** (88-205) n=826
	Tail (mm)	♀♂ **195** (179-208) n=3	♀♂ **179** (110-215) =199	♀♂ **195** (150-223) n=46	♀♂ **225** (200-258) n=82
	Greatest length of skull (mm)	♀♂ **40** (40-41) n=3	♀♂ **37** (32-41) n=100	♀♂ **38** (35-42) n=66	♀♂ **39** (36-42) n=150
	Ear height (mm)	♀♂ **31** (29-33) n=3	♀♂ **24** (14-35) n=180	♀♂ **29** (23-33) n=46	♀♂ **37** (31-41) n=85
	Hind foot (mm)	♀♂ **52** (50-53) n=3	♀♂ **46** (35-60) n=191	♀♂ **52** (39-58) n=46	♀♂ **57** (51-62) n=91
	Muzzle	Upturned muzzle	Upturned muzzle	Long pointed muzzle	Short slanted muzzle
	Tail	Dark long-haired tail	Long non-bushy	Non-bushy, same colour as dorsum	Long, dark, thin
Facial Markings	**Circumocular markings**	Dark, round	Dark, round	Indistinct	Dark, diamond-shaped
	Muzzle	Dark, merges into eye rings	Dark, merges into eye rings	Dark, disconnected from eye rings	Light
	Nose tip	Dark	Light	Dark	Dark
	Face shade	Dark	Dark	Medium	Medium
	Light nose stripe	Short, broad	Short	Long, stripe broadens on forehead	Long, broad
	Inside ear color	Light	Light	Light	Graded
Vocalisation	**Advertisement calls**	Crescendo-twitter	Crescendo	Multiple crescendo	Bark
	Crescendo unit length (s)	0.269 ± 0.044, n=14	0.086 ± 0.020, n=32	0.095 ± 0.033, n=10	N/A
	Twitter unit length (s)	0.068 ± 0.015, n=14	N/A	N/A	N/A
	Fundamental frequency (kHz)	1039 ± 311, n=14	889 ± 219, n=32	2188 ± 1824, n=10	691 ± 74, n=5
	Formant (kHz)	3721 ± 1713, n=14	1629 ± 1405, n=32	5141 ± 1818, n=10	1009 ± 199, n=5
	Pitch at end of crescendo	Decreasing	Decreasing	Increasing	N/A
	No of calls in each crescendo sequence	1	1	Multiple	N/A
Ecology	**Strata use**	Mid-high	Low	Mid-high	All
	Known sympatry with *Gd. kumbirensis* sp. nov.		Yes	No	No
	Habitat use	Moist forest, primary and secondary	Rainforest, evergreen, deciduous, gallery, riparian strips, edge vegetation, tree falls	Rainforest, evergreen, deciduous, gallery	Acacia woodland-savanna, semi-arid habitats, riparian strips

*All measurements taken from Butynski, Kingdon & Kalina (2013) except the ones for *Galagoides kumbirensis* sp. nov.

RESULTS

During nocturnal surveys in September 2013 36 live individuals of the new species of dwarf galago were observed in north-western Angola, i.e. on 17 occasions in Kumbira, one in Bimbe and on 18 occasions in the Northern Scarp Forest (Fig. 1). Where possible we took photographs. All observations were made within 3-10 m of the animals using red light, so that we were able to observe and identify the species clearly without the animals being blinded or disturbed by our lights (Svensson and Bearder, 2013). We recorded 37 vocalizations of the new species at all three sites: Kumbira (n = 15), Bimbe (n = 3) and Northern Scarp Forest (n = 19), 14 of which were crescendo-twitter calls of high enough quality to be analyzed (see below). The location where, in 2005, MSL Mills had previously heard, and recorded, the calls of the species is approximately 4 km north of Kumbira Forest (11° 04’S, 14° 15’E).

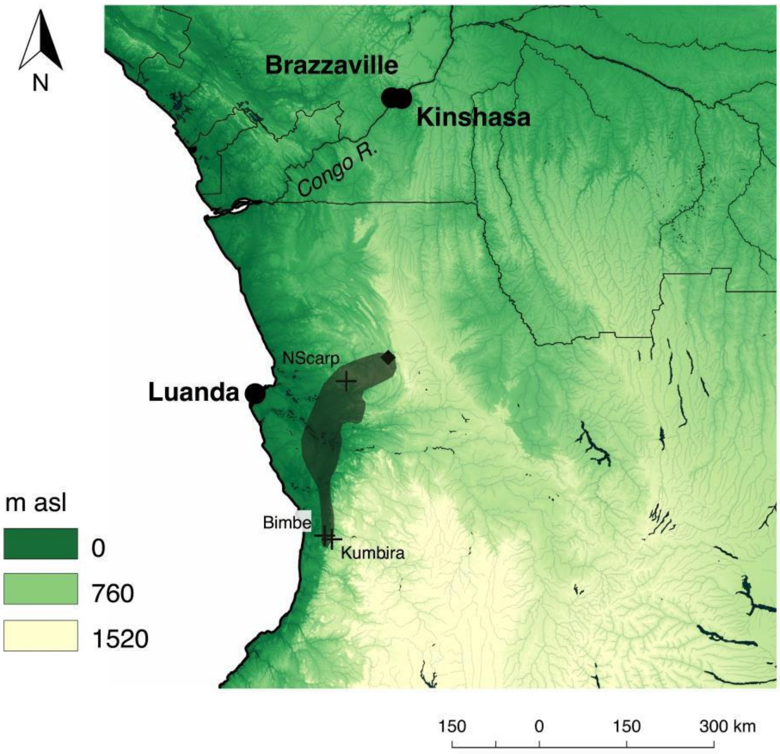

Fig. 1. Extent of occurrence (EOO) of *Gd. kumbiraensis* sp. nov. Key: + study sites where the species was observed in 2013; ♦ location where museum specimen were collected in 1954.

The facial morphology and vocal behavior identified the new species as a western dwarf galago, *Galagoides* sp., but in terms of general appearance, size and mass it was more similar to a lesser galago, *Galago* spp. The new species was observed to use mid to high strata, with a median height of 12 m (n = 36) and ranging between 2 and 32 m (see more details in Bersacola et al., 2015). It was observed leaping and climbing on branches of all sizes, but it was never observed on the ground. During the surveys we also observed and recorded calls of *Gd. demidovii*, *O. crassicaudatus* and *G. moholi*. We here describe the new species: the Angolan dwarf galago (*Galagoides kumbirensis* sp. nov.).

Galagoides kumbirensis Svensson, Bersacola, Mills, Munds, Nijman, Perkin, Masters, Couette, Nekaris, Bearder **sp. nov.** ZooBank LSID urn:lsid:zoobank.org:pub:5A044D3B-06D9-4B6F-9366-27EAF470F374 (Article published 2017).

Syntypes

FMNH 81755 adult female, skin and skull; FMNH 81756, adult male, skin and skull (Fig. 2A-B) and FMNH 81758 adult female, skin and skull. Collected by G. H. Heinrich in 1954 in Cuanza Norte, Camebatela, 30 km W, Canzele, Quai Sai River (this appears to be a typographic error and most likely refers to the Cuale do Sul River), Angola (08°19'S, 15°11'E) 800 m above sea level (asl). Housed at FMNH.

Fig. 2. A-B) Skin and skull of one of the syntypes of *Gd. kumbirensis* sp. nov. (FMHN 81756); C) paratype (*in situ* Kumbira Forest)

Paratype

Adult in photograph (Fig. 2C). Photograph taken in type locality in Kumbira Forest, Angola (11°08’S, 14°17’E) 900 m asl. The Kumbira population is designated as the source population for physical specimens in support of the FMNH syntypes.

Type locality

Kumbira Forest (around 11°08’S, 14°17’E), within the Angolan Escarpment of north-western Angola.

Diagnosis

Galagoides kumbirensis sp. nov. is allied to the other West African *Galagoides* by its distinctive crescendo call, unlike the East African species of *Paragalago* that do not give a crescendo. *Galagoides kumbirensis* sp. nov. is easily distinguished from other western *Galagoides* by the unique pattern of units within the call, the ‘crescendo-twitter’: a relatively short sequence (1-2 sec) of longer notes (2-3 sec^{-1}) becoming louder and changing to a variable series (0.3-1.3 sec) of staccato notes (10 sec^{-1}) that descend in pitch (twitter). The crescendo-twitter is only ever given once per bout (Fig. 3). The new species is similar in size and markings to *G. moholi* (Fig. 4; Table 1) but its skull shape is characterized by a slender, longer muzzle, making it more similar to that of *Galagoides* (Fig. 5). In a Principal Components Analysis based on the craniodental morphology of the four small-bodied galagid genera (*Galago, Galagoides, Paragalago* and *Sciurocheirus*), the major variable contributing to generic separation was Premaxillary Length, i.e. the length of the premaxillary tube that gives *Galagoides* its long, tapering upper jaw (Masters et al., 2017). The snout of *Galago* species is short, with a small relictual nub on the median line between the two premaxillae, which suggests that the extended dwarf galago condition is ancestral (Génin et al., 2016). The premaxillae of *Paragalago* spp. are intermediate in length between those seen in *Galago* and *Galagoides*. The face of the new species is relatively gray with a short and broad white nose stripe.

Description

We describe *G. kumbirensis* sp. nov. based on both the syntypes and the paratype. A small gray-brown galago with a darker, long-haired tail. Degree of sexual dimorphism is unknown but likely to be low, as in most small-bodied galago taxa. Muzzle slightly up-turned, pink below and dark above, merging into dark eye-rings with a conspicuous white nose stripe between the eyes. The remainder of the face gray, suffused with brown and set off from white cheeks, chin and neck. Inner ears white towards the base and yellowish towards margins. Ears gray above with two light spots where the ears join the crown. Crown, dorsum, forelimbs, thighs and flanks gray with a brown wash. Ventrum, surface of forelimbs and hindlimbs creamy yellow. Yellow strongest where the light ventrum merges into the darker dorsum. Tail darker towards the tip and slightly longer than the body. Tail held curled when at rest. Head-body measures range 170-200 mm (n = 3), tail 170-240 mm (n = 3), hind foot 50-53 mm (n = 3), ear 29-33 mm (n = 3) (sexes combined for all measurements, Table 1).

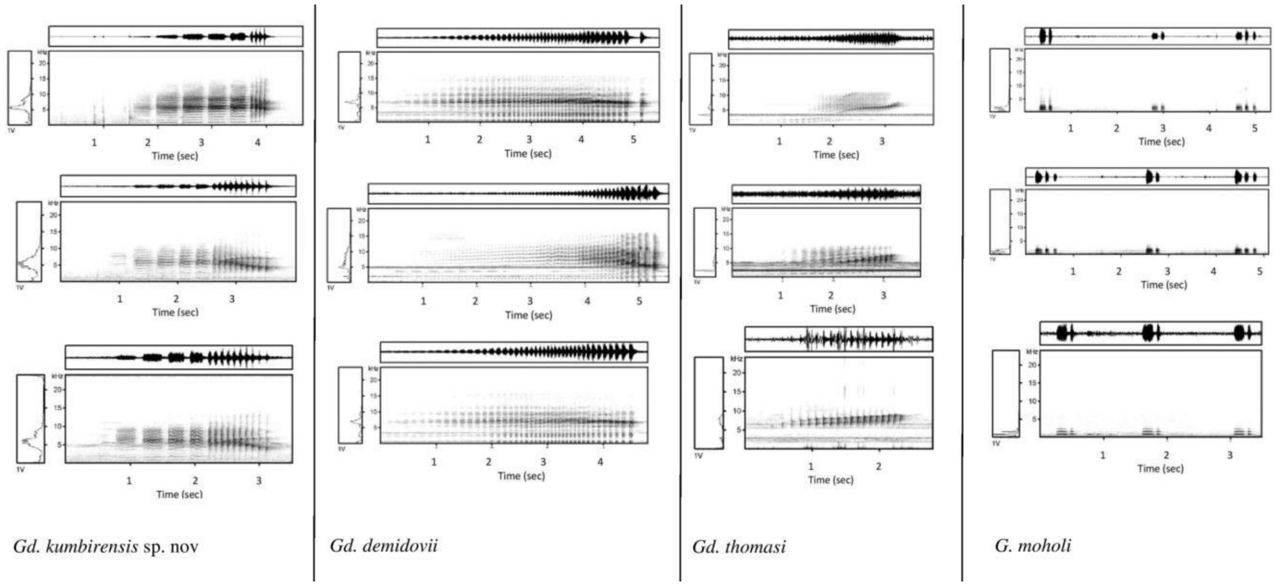

Fig. 3. Vocalisation spectrograms of advertisement calls. *Gd. kumbirensis* sp. nov –crescendo-twitter; *Gd. demidovii* – crescendo; *Gd. thomasi* – multiple crescendo; *G. moholi* – bark. Vocalization recordings of Gd. kumbirensis sp. nov are available at www.wildsolutions.nl.

Vocalization

The distinguishing vocal feature of *Gd. kumbirensis* sp. nov. is the twitter sequence following the crescendo call (Table 1). In the recorded calls of *Gd. kumbirensis* sp. nov. that were of suitable quality for spectrographic analysis ($n = 14$), the number of crescendo units in a call ranged between 2-17 and twitter units between 4-10. The mean fundamental frequency of the crescendo-twitter was 1039 ± 311 kHz ($n = 14$) and the mean formant 3721 ± 1713 kHz ($n = 14$); mean crescendo unit length 0.269 ± 0.044 s ($n = 14$) and mean twitter unit length 0.068 ± 0.015 s ($n = 14$) (Fig. 3). The four species showed clear differences in the values obtained for these four call parameters (ANOVA, all $F_{3,57} > 8.204$, all $p < 0.001$) (Table 1). Post-hoc tests show that *Gd. kumbirensis* sp. nov. differs in its fundamental frequency from *Gd. thomasi* (Tukey HSD, mean difference -1148, $p = 0.003$), and in its formant from *Gd. demidovii* (mean difference -2092, $p < 0.001$) and from *G. moholi* (mean difference -2711, $p < 0.006$), but not from *Gd. thomasi* (mean difference -1420, $p < 0.115$).

Table 2. Loadings of the cranial variables on the first two axes of the Between Group Principle Component Analysis

Variables	PC1	PC2
Supraoccipital length	0.210	0.039
Cranial height	0.090	-0.050
Frontal length	0.122	0.533
Interorbital constriction	0.012	-0.392
Cheek teeth width	-0.010	-0.346
Palate width	0.124	-0.346
Total skull length	0.011	-0.296
Snout length	-0.102	-0.211
Mastoid width	0.096	-0.023
Temporal constriction	0.181	-0.102
Premaxilla	-0.913	0.101
Toothcomb length	0.179	0.428

Habitat

Observed in moist, tall forest, primary and secondary (Kumbira and Northern Scarp Forest) and semi-arid baobab savannah-woodland in areas where tree-lined water courses allowed access (Bimbe; Table 1). Encounter rate was higher in moist forest (2.60 - 2.67 individuals/km) compared to savannah-woodland (0.17 individuals/km, see Bersacola et al., 2015 for more information and statistical analyses).

The species has been observed at altitudes of between 285 – 910 m asl, i.e. 860 to 910 m asl in Kumbira, 285 m asl in Bimbe and 465 to 745 m asl in Northern Scarp Forest. The 2005 vocalization recordings were made at 900 m asl, and the syntypes was collected at 800 m asl. Forest in the northern Angolan Escarpment descends down to approximately 250 m and up to 1,200 m asl and *Gd. kumbirensis* sp. nov. was observed over most of this range.

Distribution and conservation status

Currently known only from four sites (Fig. 1). Based on the habitat types in which we observed *Gd. kumbirensis* sp. nov., and its altitudinal distribution, and taking into account geographical barriers, including the steep escarpment, three scenarios can be envisaged. The first is a conservative one, assuming the species is confined to the central and northern portion of the Angolan Escarpment, thus including the four known locations, in which its extent of occurrence (EOO, IUCN, 2014) is just under 20,000 km^2 (Fig. 1). Using a more liberal estimate, its range may extend in the north up to the Congo River (including small parts of the DRC), with its north-west range restricted by the relatively steep ridge west of Kinshasa or by the Kasai River, increasing its area to 112,000 km^2 or 405,000 km^2, respectively.

While the exact distribution range of *Gd. kumbirensis* sp. nov. is not known, some inferences as to its conservation status can be made. While still largely forested, its area of occurrence is subject to severe pressure from commercial timber logging and deforestation for farming and charcoal production (Hansen et al., 2013; Bersacola et al., 2015; Cáceres et al., 2016). None of the locations where we observed this species falls within a protected area. In the absence of data from the more northern and north-eastern areas, and applying a cautionary principle, we recommend that *Gd. kumbirensis* sp. nov. should be listed as Vulnerable on the IUCN Red List on the basis of criteria B1ab(iii); i.e. an estimated EOO of less than 20,000 km^2, known from fewer than 10 locations, and a continued decline in the area, extent and/or habitat quality (IUCN, 2014) When more information on the species' distribution and its threats becomes available this assessment should be re-evaluated.

All primates are listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), apart from those listed in Appendix I. Angola joined the Convention in October 2013, which came into force in December 2013. In the absence of any data on international trade in the species (Svensson et al., 2015) we suggest adopting the default position and including the species in Appendix II, thus regulating but not banning any future international trade.

Etymology

The species was first observed *in situ* in Kumbira Forest, an area under great pressure from commercial logging (Bersacola et al., 2015; Cáceres et al., 2016). Kumbira is considered a hotspot for many endemic species in Angola (Cáceres et al., 2015) and by using this name we aim to draw attention to the area.

Suggested common name

Angolan dwarf galago (English), galago angolano (Portuguese).

Fig. 4. Comparison of skins and skulls: *Gd. kumbirensis* sp. nov., *Gd. demidovii*, *Gd. thomasi* and *G. moholi*

Similar species: habitat use, vocalizations, pelage and facial features *Galagoides demidovii.* Sympatric with *Gd. kumbirensis* sp. nov. in at least two sites (Bimbe and Northern Scarp Forest). Prefers undergrowth < 5 m, often in secondary growth and forest edge. Usually observed running along fine branches (< 1 cm diameter). Crescendo with a long series (> 4 sec) of rapid notes (10 sec^{-1}) building in pitch and intensity and ending in longer, slower notes (6 sec^{-1}) that descend in pitch (Fig. 3). Usually given only once or twice per bout. Other calls in the repertoire include ‘chips’ (alarm call) and ‘explosive buzz’ (contact avoidance) (Ambrose, 1999). Facial markings are similar to *Gd. kumbirensis* sp. nov. (Table 1), although *Gd. demidovii* is considerably smaller in size. Dorsum and tail browner, tail relatively thin and short (Fig. 4B). Nose narrow and upturned, ears relatively shorter and eye sockets less broad (Bearder et al., 1995; Ambrose and Butynski, 2013; Nekaris, 2013).

Galagoides thomasi. Not known to be sympatric with *Gd. kumbirensis* sp. nov. Occupies similar height in the canopy as *Gd. kumbirensis* sp. nov. (Table 1), usually > 5 m on branches of any size. Crescendo consists of a relatively short series (2-3 sec) of brief notes (6 sec^{-1}), gradually increasing in speed of repetition (10 sec^{-1}), pitch and volume until the end of the call which is high pitched (almost inaudible, Fig. 3). Each individual usually repeats these calls in a sequence, with the first call being the loudest and subsequent calls becoming quieter (multiple crescendo). Other calls in the repertoire include ‘trills’ (assembly call) and ‘chips’ (alarm call) which are often interspersed with ‘grunts’ and ‘buzzes’ (Ambrose, 1999). Somewhat smaller in size, dorsal pelage darker and browner with less contrast between the dorsum and ventrum (Fig. 4C). Tail browner, shorter and less bushy. Circumocular markings indistinct and long light nose stripe broadens on forehead (Bearder et al., 1995; Ambrose and Butynski, 2013; Nekaris, 2013).

Galago moholi. Not known to be sympatric with *Gd. kumbirensis* sp. nov. but also present in Angola. Prefers drier woodland-savannah and edge vegetation. Observed using all strata on branches of all sizes. Like other members of the genus *Galago*, the advertising call is a repetitive call: a series of single, double or triple barks repeated many times (Fig. 3). Never heard to give a crescendo. Similar in body size (Fig. 4D) but longer hind limbs suited to long leaps and hops along the ground. Dorsum without a brown wash and tail similar in size and color but less bushy, particularly towards the base. Circumocular markings black and diamond-shaped, inner ears darker and muzzle shorter, broader and lighter in color (Bearder et al., 1995; Nekaris, 2013; Pullen and Bearder, 2013; Génin et al., 2016).

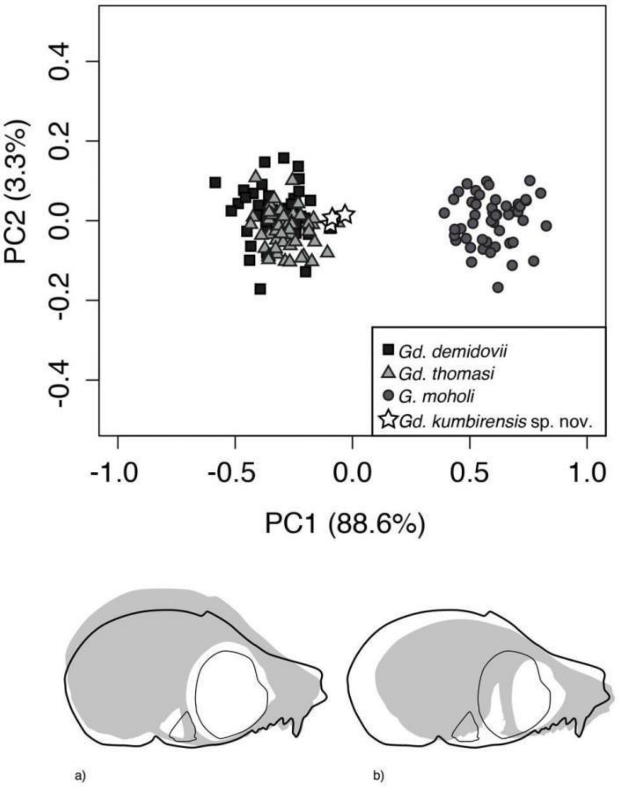

Fig. 5. Top: Between Group Principal Component Analysis (BGPCA) on the twelve size corrected variables of four species of galago. Principal Component Analysis was conducted on the mean of each species and specimens were projected in this space. Distances between specimens relate to cranial shape differences. Bottom: Comparison of galago skulls based on average greatest length of skull, A) *Gd. kumbirensis* sp. nov. (black line) vs. *G. moholi* (gray), B) *Gd. kumbirensis* sp. no. (black line) vs. *Gd. demidovii* (gray).

Comparison among *Gd. kumbirensis* sp. nov., *Gd. demidovii*, *Gd. thomasi* and *G. moholi*

Size of skull : Figure 6 presents the boxplot of the log (GM) by species. The three specimens from Angola show a mean size of 7.79 with a standard deviation of 0.02. Their mean value of log (GM) plotted in the higher part of the size range of *G. moholi* (mean = 7.68, SD = 0.13), greater than the size of *Gd. demidovii* (mean = 7.55, SD = 0.14) and *Gd. thomasi* (mean = 7.59, SD = 0.17). We compared skull size across the four species using an ANOVA, and the difference was significant (F = 8.6, n = 153, p < 0.001). Tukey HSD post-hoc statistics allowed the distinction of two size groups: a first group composed of *Gd. demidovii* and *Gd. thomasi*, and a second group composed of *G. moholi* and the *Gd. kumbirensis* sp. nov. Therefore, size analysis indicated a similarity in size between the *Gd. kumbirensis* sp. nov. and *G. moholi*.

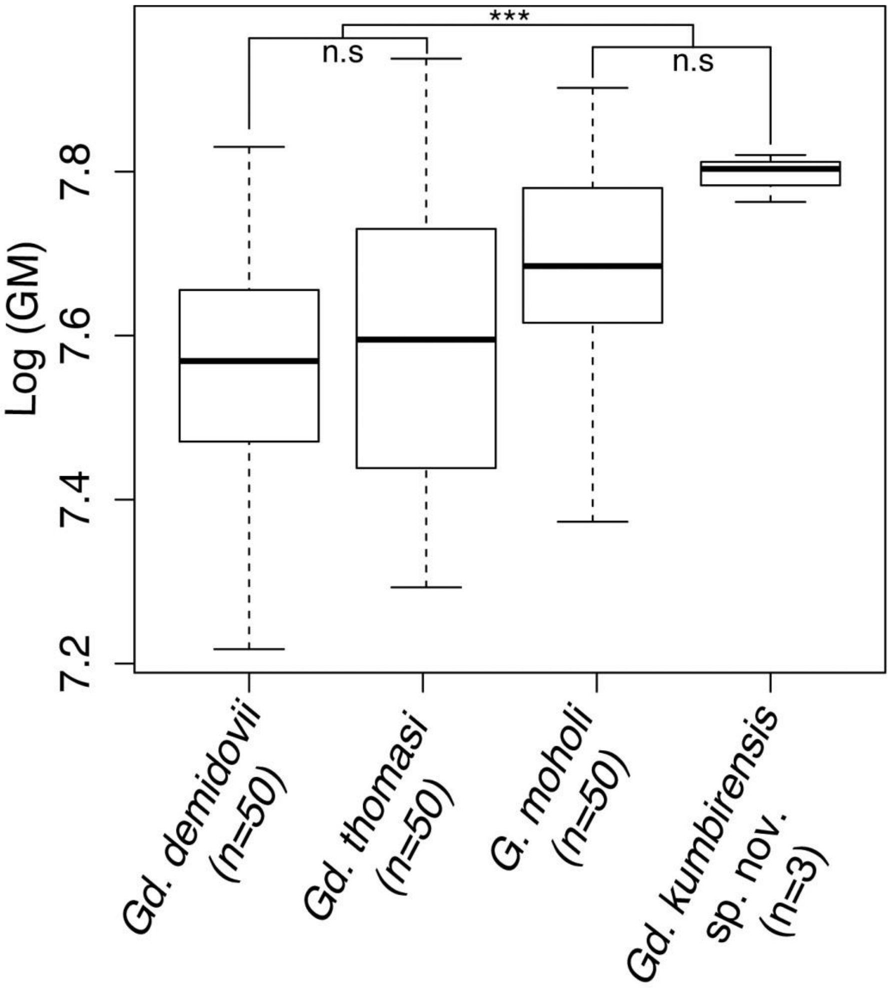

Fig. 6. Boxplot of the logged Geometric Mean by species illustrating the differences in cranial size. ANOVA test and post hoc Tukey HSD were conducted highlighting significant size differences (***, P < 0.001) for non-significant size variation (n.s., P > 0.05) between species.

Shape of skull: We applied a Between Group Principle Component Analysis (BGPCA) on the logged size-corrected measurements of all 153 specimens. This method consists of computing a PCA on the mean values for each group, defining the BGPCA space and projecting the individuals in this space by applying the BGPCA parameters (i.e. the variable loadings) to the shape variables of each specimen (Mitteroecker and Bookstein, 2011). BGPCA extracted two components that express 91% of the total variation, with PC1 accounting for 88.6% and PC2 accounting for 3.3% of the variance (Fig. 5). Group variation along PC1 describes essentially the variation in shape of the premaxilla, with longer premaxillae having negative scores and shorter ones having positives scores along the PC (Table 2). *Galagoides demidovii* and *Gd. thomasi* grouped together on the negative end of PC1, whereas *G. moholi* specimens were separated positively from the other on PC1. All three Angolan specimens were grouped together and very close to the group composed of *Gd. demidovii* and *Gd. thomasi*. The *Galagoides* spp. largely overlapped so that it was not possible to attribute *Gd. kumbirensis* sp. nov. to one or the other species based on shape analysis. It is clear that, in terms of shape, the Angolan specimens group with the genus *Galagoides* rather than *Galago*. In the BGPCA performed by Masters et al. (2017), the new genus *Paragalago* fell in an intermediate position between *Galago* and *Galagoides*.

We tested the difference in shape variables between groups using a MANOVA, and the results indicated a significant difference in shape between genera (F = 51.1, Pillai's trace = 1.03, p < 0.001). The difference was in accordance with the PCA results. In order to allocate the Angolan specimens to one or another genus based on the shape analysis, we computed a Linear Discriminant Analysis, grouping by genus. We used all the specimens for this analysis except the Angolan ones. Two discriminant axes were significant, perfectly separating the genus *Galago* from the two *Galagoides* spp. After cross validation, all specimens of *G. moholi* were correctly classified by the analysis, whereas a third of the *Gd. demidovii* specimens were classified as *Gd. thomasi* and vice versa. After integrating *Gd. kumbirensis* sp. nov. into the analysis, all three specimens were allocated to *Gd. thomasi* with posterior classification of 93.7, 76.0 and 78.7%. The cranial shape of the Angolan specimens is highly similar to that of *Gd. thomasi*.

DISCUSSION

In this paper we have demonstrated significant differences in morphology and size as well as advertising call structures between *Gd. kumbirensis* sp. nov. and closely related taxa (Table 1). We ascribe *Gd. kumbirensis* sp. nov. to the genus *Galagoides* on the basis of its crescendo call and similar skull shape characterized by a slender, upturned, muzzle. *Galagoides* skulls can be differentiated from those of *Paragalago* by fact that the premaxillae are noticeably more extended, and the skulls are more globular in shape; the skulls of *Paragalago* spp. tend to be more ovoid (Masters et al., 2017). The recognition of *Gd. kumbirensis* sp. nov. as a species distinct from other galagos is valid when following a Phylogenetic Species Concept, i.e. it represents a phylogeny cluster, diagnosably distinct from other such clusters, within which there is a parental pattern of ancestry and descent (Cracraft, 1989; Groves, 2001), but also under the Recognition Concept (Paterson, 1985) on the basis of its unique specific mate recognition call

The use of habitat by *Gd. kumbirensis* sp. nov. appears to be most similar to *Gd. thomasi* (running, climbing and leaping on supports of all sizes mostly above 5 m) but *Gd. kumbirensis* sp. nov. can be distinguished from this species by its larger size, different coloration and distinctive pattern of calling. *Galagoides demidovii* was found sympatrically with the new species in two out of three sites, using lower vegetation strata where it was mainly limited to small branches (Bersacola et al., 2015, in which *Gd. kumbirensis* sp. nov. was referred to as *Galagoides* sp. nov. 4). Again, there are distinctive differences in body size, pelage color and vocalizations. The new species was most similar in size to *G. moholi,* which appears widespread in Angola but in much drier habitats (Bersacola et al., 2015).

Galago moholi and *Gd. kumbirensis* sp. nov. are not sympatric, and differ markedly in behavior, morphology and ecology. In addition, while the relative abundance of sympatric *Gd. demidovii* appeared to be influenced by structural characteristics of the habitat, Bersacola et al. (2015) could not find any evidence that this was true for *Gd. kumbirensis* sp. nov. However, similar to *Gd. demidovii, Gd. kumbirensis* sp. nov. appeared to occur more often in humid forests, rather than the savannah-woodland environments where most *Galago* spp. are typically found.

Many questions remain to be answered about the distribution, behavior, life history traits and ecology of the new species. Prior to this study, it was provisionally identified as *Gd. thomasi*, which lives sympatrically with *Gd. demidovii* in most parts of its range, including the adjacent Congo basin (Ambrose and Butynski, 2013). At present we have no evidence of *Gd. thomasi* in Angola, where it appears to be replaced by the ecologically similar *Gd. kumbirensis* sp. nov., that also lives sympatrically with *Gd. demidovii*.

The structure of the crescendo call of *Gd. kumbirensis* sp. nov. is more similar to that of *Gd. demidovii* (ending in staccato notes that descend in pitch, Fig. 3) than it is to that of *Gd. thomasi*, possibly indicating a closer evolutionary relationship and a more recent common ancestor between *Gd. kumbirensis* sp. nov. and *Gd. demidovii* than between *Gd. kumbirensis* sp. nov. and *Gd. thomasi*. If this is the case, it is possible that the new species arose when an ancestor of *Gd. demidovii* became isolated along the Angolan Escarpment, and that it later spread north to overlap with *Gd. demidovii* and replace *Gd. thomasi*. Alternatively *Gd. kumbirensis* sp. nov. evolved in isolation and *Gd. demidovii* later expanded southwards onto the Angolan Escarpment.

As noted in the introduction, the escarpment area of Angola is well known as an important biodiversity hotspot, with many endemic and rare species, often strikingly different from species elsewhere (Hall, 1960; Figueiredo, 2010; Clark et al., 2011). These species are thought to have speciated and adapted long before the Quaternary (Morley and Kingdon, 2013). This process was possible as the Angolan Escarpment climate, due to the Benguela Current meeting tropical waters at the Angolan shores, was less affected by climatic changes than other more inland regions. As such the Angolan Escarpment remained constantly humid, allowing birds and mammals to develop in isolation during both wet and dry periods (Hall, 1960; Fjeldså and Lovett, 1997).

Angola ratified the Convention on Biological Diversity (CBD) in 1998 indicating its commitment to biodiversity conservation in the country. Through its National Biodiversity Strategy and Action Plan (Anonymous, 2007) it is committed to incorporating measures for the conservation and sustainable use of biological diversity into development policies and programs. Strategic Areas C (biodiversity management of protected areas), F (institutional strengthening) and G (legislation and implementation), highlighted in the Action Plan, in particular, can bring direct and tangible conservation benefits to *Gd. kumbirensis* sp. nov. if implemented. Both the organization of effective management in existing protected areas and an increase in the protected area network would constitute important strategic interventions. Further, it is recognized that institutional capacity in Angola is often weak in terms of human and financial resources and the implementation of any biodiversity conservation policy or measure crucially depend, on building the capacity of individuals and institutions. Finally, a review and, if needed, urgent correction, of existing legislation is required to ensure environmental agreements, including the CBD and CITES are followed as intended (Anonymous, 2007). The rate of logging in Angola is one of the fastest known in the world (Hansen et al., 2013), with the Angolan Escarpment being a case in point (Cáceres et al., 2016) which underlines the urgent need for further research to set priorities for future conservation, and the need to designate more protected areas.

Although birds are relatively well studied in the Angolan Escarpment (Ryan et al., 2004; Cáceres et al., 2015), there is a dearth of knowledge when it comes to mammal species. Other endemic primates such as *Miopithecus talapoin* and *Cercopithecus mitis mitis* are known to be present (Bersacola et al., 2014), but little is known about their distribution or threats. Recent political and economic developments within Angola have created opportunities to conduct further research into the ecology and status of *Gd. kumbirensis* sp. nov. and other endemic mammals. This research will enable the collection of additional data (genetic, morphological, behavioral, etc.) to be used in a comprehensive phylogenetic analysis to elucidate the evolutionary relationships between *Gd. kumbirensis* sp. nov. and other *Galagoides* species, and, possibly, estimating a date for the separation between *Gd. kumbirensis* sp. nov. and its sister species.

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Svensson, E Bersacola, MSL Mills & SK Bearder collecting the data in the field, A Perkin, RA Munds & JC Masters collected the data in museum collections. V Nijman, S Couette & KAI Nekaris analyzed the data and MS Svensson, E Bersacola, MSL Mills, JC Masters, A Perkin, KAI Nekaris, V Nijman & SK Bearder wrote the article. We have no conflict of interest to report.

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