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

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**ABSTRACT**

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**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.

64 Previously unrecognized species of terrestrial mammals are being discovered at an ever-  
65 increasing rate as researchers expand their activities into new areas of forests and woodlands,  
66 and conduct extensive surveys (Ceballos and Ehrlich, 2009; Wilson and Mittermeier, 2011;  
67 Mittermeier et al., 2013). Some of these discoveries are made because of a change in views of  
68 what a species is, i.e. dependent on which species concept is adopted (Isaac et al., 2004;  
69 Groves and Grubb, 2011; Cotterill et al., 2014) and owing to the use of different  
70 technologies, including molecular analysis, to recognize species diversity within cryptic taxa  
71 (i.e. species that are very similar morphologically even though they are reproductively  
72 isolated: Bickford et al., 2007). In the field crucial information on the presence of cryptic taxa  
73 is often gathered with the aid of new methodologies such as camera trapping and remote  
74 recording (Hart et al., 2012; Li et al., 2015). In an era when many new species descriptions  
75 rely heavily on genetic evidence, it has become atypical to distinguish new taxa based on  
76 morphology and vocalizations alone. However, in groups such as molluscs (Alvim and  
77 Pimenta, 2013), crustaceans (Vonk and Jaume, 2014), insects (Gibbs, 2010; Hertach et al.,  
78 2015), birds (Ng et al., 2016), and nocturnal mammals (Helgen et al., 2010; Munds et al.,  
79 2013; Reeder et al., 2013), new taxa continue to be described in the absence of molecular  
80 data. The delimitation of these taxa using molecular data have repeatedly confirmed  
81 separations based on morphology and vocalizations (Wollscheid-Lengeling et al., 2001;  
82 Nekaris and Bearder, 2011; Mittermeier et al., 2013; Pozzi et al., 2014; Pozzi et al., 2015).

83         The well-studied Order Primates is a case in point: most new primate species  
84 recognized in the 21st century are the result of the taxonomic elevation of previously known  
85 subspecies to species (Groves, 2001; *Macaca* spp.: Kitchener and Groves, 2002; *Aotus* spp.:  
86 Defler and Bueno, 2007; *Nomascus* spp.: Thinh et al., 2010; *Microcebus* spp.: Hotaling et al.,  
87 2016). Taxa wholly new to science, however, are also being described (e.g. *Rungwecebus*

88 *kipunji*: Jones et al., 2005; Davenport et al., 2006; *Tarsius tumpara*: Shekelle et al., 2008;  
89 *Rhinopithecus strykeri*: Geissmann et al., 2010; *Nycticebus kayan*: Munds et al., 2013).

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

102 Galagos are a monophyletic taxon originating in the Late Eocene that comprises six  
103 distinct radiations, (Pozzi et al., 2014, 2015; Pozzi, 2016). Dwarf galagos occur over much of  
104 Africa, with *Galagoides thomasi* and *Gd. demidovii* (also referred to as *Gd. demidoff*, Olson,  
105 1979; Jenkins, 1987; Groves, 2001; Masters and Couette, 2015) occurring as far west as  
106 Senegal and Guinea Bissau, and *Paragalago granti* occurring as far east as the shores of  
107 Mozambique, with some species and subspecies being endemic to montane complexes (*P.*  
108 *orinus*) and offshore islands (*P. zanzibaricus zanzibaricus* and *Gd. demidovii poensis*)  
109 (Nekaris, 2013).

110 The nocturnal galagos fit the cryptic pattern in that they recognize each other and  
111 communicate via vocal, chemical and subtle morphological differences that may be cryptic to  
112 humans, rather than adopting the colorful pelages and sexually dimorphic features of diurnal

113 primates (Masters, 1993; Pozzi et al., 2015). In the field, researchers have relied particularly  
114 on vocalizations and behavior to distinguish otherwise morphologically similar and difficult  
115 to distinguish species (Zimmermann, 1990; Bearder and Svoboda, 2013; Nash et al., 2013).  
116 In multiple classical studies it has been shown that it is possible to differentiate between  
117 species by observing their locomotion, behavior and habitats (Charles-Dominique and  
118 Bearder, 1979; Harcourt and Nash, 1986; Crompton et al., 1987; Weisenseel et al., 1993;  
119 Ambrose, 1999). All galagos produce advertising calls that are used to maintain contact  
120 between dispersed individuals, indicating spatial position and movement (Bearder et al.,  
121 1995). Galago species can be categorized into eight different vocal groups: click callers  
122 (*Euoticus* spp.), croak callers (*Sciurocheirus* spp.), repetitive callers (*G. senegalensis*, *G.*  
123 *moholi* and *G. matschiei*), trailing callers (*Otolemur* spp.), rolling callers (*P. rondoensis* and  
124 *P. zanzibaricus*), scaling callers (*P. orinus*), incremental callers (*P. cocos* and *P. granti*) and  
125 crescendo callers (*Gd. thomasi* and *Gd. demidovii*) (Grubb et al., 2003). Advertising calls  
126 exhibit marked specific variations, which make them particularly suitable for species  
127 discrimination (Masters, 1993; Bearder et al., 1995). In addition, complex vocal repertoires  
128 are often species-unique. For example, after being considered the same species for over 50  
129 years, lesser galagos *G. moholi* and *G. senegalensis* were eventually classified as separate  
130 species due to substantially different vocal repertoires (Zimmermann et al., 1988;  
131 Zimmermann, 1990). This separation of the *G. senegalensis* and *G. moholi* was also  
132 suggested based on differences in adult body mass and reproductive parameters (Izard and  
133 Nash, 1988).

134 Other features used to distinguish galago species include pelage characteristics, facial  
135 markings, reproductive anatomy and other morphological attributes. Anderson (1999; 2001)  
136 and Anderson et al. (2000) used the cuticle scales of hairs and the arrangement of friction  
137 pads on the hands and feet to help distinguish between *G. senegalensis* and *G. moholi*, and

138 between greater galagos *Otolemur crassicaudatus* and *O. garnetti*. Ambrose (2003; 2013)  
139 described a new species of squirrel galago (*Sciurocheirus makandensis*) based on facial  
140 markings, vocalization and pelage coloration. The eastern dwarf galagos (*P. orinus*, *P.*  
141 *rondoensis*, *P. granti*, *P. cocos* and *P. zanzibaricus*) can all be classified as distinct species on  
142 the basis of correlated differences in vocalizations and penile morphology (Anderson, 1999;  
143 Perkin, 2007; Masters et al., 2017). Although differences in skull morphology are more subtle  
144 in cryptic species, Masters and Bragg (2000) found that *O. crassicaudatus* and *O. garnettii*  
145 could be discriminated using ear and palate length, and *Gd. demidovii* and *Gd. thomasi* using  
146 ear and skull length.

147         Here we report on a new species of dwarf galago from Angola that has a unique  
148 combination of traits, and several features that are diagnostically different from other  
149 galagos. In terms of pelage coloration, skull shape and vocal behavior this species resembles  
150 other western dwarf galagos (*Galagoides* spp.), but their body size is like that of lesser  
151 galagos (*Galago* spp.). Three galagid species have been reported to occur in Angola, i.e. *O.*  
152 *crassicaudatus monteiri*, *G. moholi*, and *Gd. demidovii phasma*, whereas the occurrence of a  
153 fourth species, *Gd. thomasi* in the country is based solely on museum specimens (Nekaris,  
154 2013; Bersacola et al., 2015). Machado (1969) reported *Gd. demidovii* to occur only in parts  
155 of the Lunda Norte Province, situated in the far north-east of the country, and in the north-  
156 western Angolan provinces of Zaire and Uige.

157         A Perkin and JC Masters examined the collections of the Field Museum of Natural  
158 History in Chicago (FMNH) in 2007 and considered three specimens labelled as ‘*Galago*’  
159 collected in the escarpment area of Angola to be distinct due to their large body size, and  
160 noted that they possessed a *Galagoides* type skull rather than a *Galago* one. Masters and  
161 Couette (2015) identified these skulls using multivariate morphometrics as *Gd. thomasi*.  
162 Based on museum specimens, Nash et al. (1989) tentatively listed *Gd. thomasi* as present in

163 northern Angola, including the Angolan Escarpment (termed ‘Luanda highlands’ by Nash et  
164 al., 1989). Reviewing geographic variation of *Gd. thomasi*, Kingdon (2015) was of the  
165 opinion that distinct populations, possibly even a new subspecies or species, occurred on the  
166 Angolan Escarpment and in the Katanga Province of the Democratic Republic of Congo  
167 (DRC). In contrast, neither Groves (2001), based on studies of museum specimens, nor  
168 Bersacola et al. (2015), based on field surveys, found evidence of *Gd. thomasi* in Angola.

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

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## 179 MATERIALS AND METHODS

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### Study area

181 Four biomes represent the land ecosystems in Angola, namely the Zambebian biome  
182 (covering 85% of the country), Guinea-Congolese biome (10.7%), the Karoo-Namib biome  
183 (2.6%) and the Afro-Upstream biome (0.5%) (Kuedikuenda and Xavier, 2009). Within  
184 Angola these biomes include 15 different ecoregions, including desert, savannah woodlands,  
185 grasslands, dry forests, montane forest-grassland mosaics, forest-savannah mosaic, miombo  
186 woodlands and mangroves (Olson et al., 2001). The Angolan Escarpment is located in the  
187 western part of the country, and stretches for 1000 km from north to south, forming part of



188 the Great Escarpment of southern Africa (hereafter “Great Escarpment”) (Clark et al., 2011).  
189 Several ecological regions meet at the Angolan Escarpment, making it a complex area where  
190 topographical features have led to significant levels of endemism and floristic diversity (Hall,  
191 1960; Figueiredo, 2010; Clark et al., 2011; Romeiras et al., 2014). Angola is believed to  
192 support more vertebrate species endemic to the Great Escarpment than any other country,  
193 except South Africa (Clark et al., 2011). Between the early 1970s and 2002, surveys in  
194 Angola were limited due to the protracted civil war, and subsequently the expense and  
195 logistical difficulties of operating in the country prevented much biological exploration. Now  
196 that systematic biological surveys are resumed, researchers expect that further endemic  
197 species will be discovered in this region (Vetter, 2003; Clark et al., 2011). We visited four  
198 study sites in north-western Angola: Kumbira forest (sub-montane/dry Congo basin forest);  
199 Bimbe (dry thicket islands in tall grass savannah with stream beds); Northern Scarp Forest  
200 (moist forest) and Calandula (miombo woodland/gallery forest).

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### **Data acquisition**

203 MS Svensson, E Bersacola, MSL Mills and SK Bearder conducted nocturnal surveys in  
204 Angola between 5 and 19 September 2013. The surveys lasted for 39 hours, walking on small  
205 roads and established paths and recording the habitat use and height in the canopy for each  
206 animal observed (for a more detailed description of the survey method see Bersacola et al.,  
207 2015). Nocturnal animals were photographed with a Canon EOS 600D camera, with Canon  
208 70-200mm EF Zoom lens and Canon Speedlight 430EX II flash.

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### **Vocalizations**

211 At each survey site we recorded calls of galagos before sunrise (04:30 - 05:30) and after  
212 sunset (18:00-22:00). We remained stationary at recording sites throughout recording

213 sessions. We made recordings using a Fostex Field Recorder equipped with a Sennheiser K6-  
214 ME67 directional microphone. We digitized calls using Avisoft SASLab Pro software (R.  
215 Specht, Berlin; version 5.2). We compared our results with vocalizations of the *Galagoidea*  
216 taxa (*Gd. demidovii* and *Gd. thomasi*), as these are the only other crescendo callers, and with  
217 *G. moholi* as the only other small galago found in Angola (a repetitive caller, Bearder et al.,  
218 1995). Recordings were converted into spectrograms with a frequency resolution of 48 kHz  
219 (FFT length 512; 50% overlap; Hamming window). We focused on fundamental frequency  
220 (first harmonic, measured in kHz), crescendo unit length (the basic element of the crescendo  
221 phrase, measured in s), twitter unit length (the basic element of the twitter phrase, measured  
222 in s) and formant (dominant frequency, measured in kHz). We used a one-way ANOVA to  
223 test for differences among the four species followed by Tukey's HSD post-hoc test for  
224 pairwise differences between species.

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### **Morphology**

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

232 In order to assess the taxonomic status of the three specimens from Angola we ran a  
233 multivariate analysis based on a set of twelve linear measurements of skulls and teeth. JC  
234 Masters measured the frontal, supraoccipital, snout, premaxilla, toothcomb and skull  
235 lengths, the cranial height, the first lower molar, mastoid and palate widths, and the widths of  
236 the interorbital and temporal constrictions (for description and schematic illustration see  
237 Masters and Couette, 2015 Table 1 and Fig. 1). The dataset was composed of 50 specimens

238 of *Gd. demidovii*, 50 specimens of *Gd. thomasi* and 50 specimens of *G. moholi*, plus the three  
239 specimens from Angola. JC Masters collected measurements in several institutions around  
240 the world [American Museum of Natural History, New York, USA (AMNH); Museum of  
241 Comparative Zoology, Cambridge, USA (MCZ); Field Museum of Natural History, Chicago,  
242 USA (FMNH); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Natural  
243 History Museum, London, UK (NHM); National Museum of Kenya, Nairobi, Kenya (NMK);  
244 Royal Museum of Central Africa, Tervuren, Belgium (RMCA) and National Museum of  
245 Zimbabwe, Bulawayo, Zimbabwe (NMZ)] and measured specimens using digital calipers  
246 according to the procedure described in Masters and Couette (2015). JC Masters measured 40  
247 specimens twice and estimated the percentage of intra-observer measurement error using the  
248 method proposed by Bailey and Byrnes (1990). Error represented 2.4% of total variation in  
249 our sample and can be considered as insignificant.

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

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

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

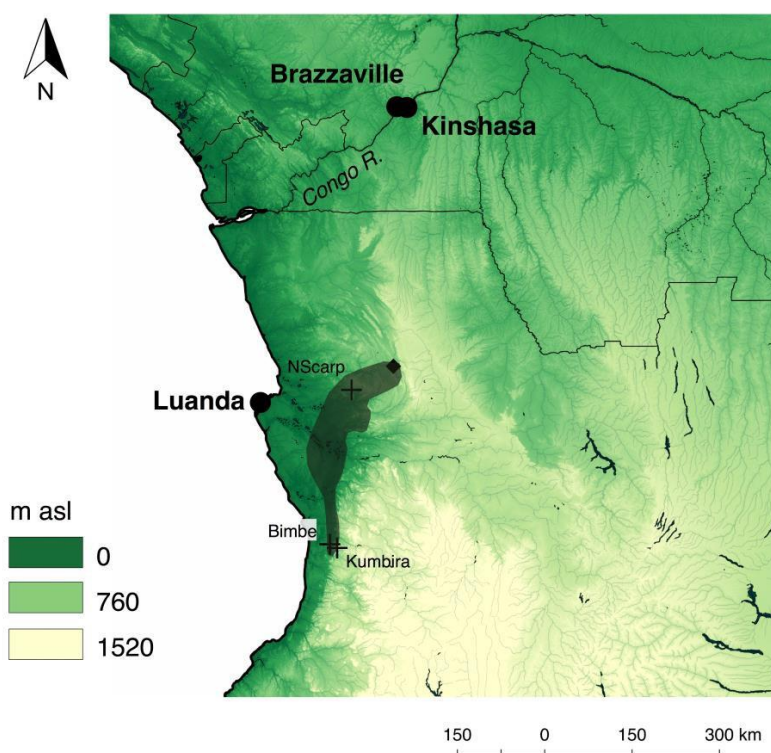
262 \*All measurements taken from Butynski, Kingdon & Kalina (2013) except the ones for *Galagoides kumbirensis* sp. nov.

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## RESULTS

265 During nocturnal surveys in September 2013 36 live individuals of the new species of dwarf  
 266 galago were observed in north-western Angola, i.e. on 17 occasions in Kumbira, one in  
 267 Bimbe and on 18 occasions in the Northern Scarp Forest (Fig. 1). Where possible we took  
 268 photographs. All observations were made within 3-10 m of the animals using red light, so  
 269 that we were able to observe and identify the species clearly without the animals being  
 270 blinded or disturbed by our lights (Svensson and Bearder, 2013). We recorded 37  
 271 vocalizations of the new species at all three sites: Kumbira (n = 15), Bimbe (n = 3) and  
 272 Northern Scarp Forest (n = 19), 14 of which were crescendo-twitter calls of high enough  
 273 quality to be analyzed (see below). The location where, in 2005, MSL Mills had previously  
 274 heard, and recorded, the calls of the species is approximately 4 km north of Kumbira Forest  
 275 ( $11^{\circ} 04'S$ ,  $14^{\circ} 15'E$ ).



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

278

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

287

288 ***Galagoides kumbirensis*** Svensson, Bersacola, Mills, Munds, Nijman, Perkin, Masters,  
289 Couette, Nekaris, Bearder **sp. nov.** ZooBank LSID urn:lsid:zoobank.org:pub:5A044D3B-  
290 06D9-4B6F-9366-27EAF470F374 (Article published 2017).

291

292

#### Syntypes

293 FMNH 81755 adult female, skin and skull; FMNH 81756, adult male, skin and skull (Fig.  
294 2A-B) and FMNH 81758 adult female, skin and skull. Collected by G. H. Heinrich in 1954 in  
295 Cuanza Norte, Camebatela, 30 km W, Canzele, Quai Sai River (this appears to be a  
296 typographic error and most likely refers to the Cuale do Sul River), Angola (08°19'S,  
297 15°11'E) 800 m above sea level (asl). Housed at FMNH.



298

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

300

paratype (*in situ* Kumbira Forest)

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302

303

304

**Paratype**

305 Adult in photograph (Fig. 2C). Photograph taken in type locality in Kumbira Forest, Angola  
306 (11°08'S, 14°17'E) 900 m asl. The Kumbira population is designated as the source  
307 population for physical specimens in support of the FMNH syntypes.

308

309

**Type locality**

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

312

313

**Diagnosis**

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



329 premaxillae of *Paragalago* spp. are intermediate in length between those seen in *Galago* and  
330 *Galagoides*. The face of the new species is relatively gray with a short and broad white nose  
331 stripe.

### 332 **Description**

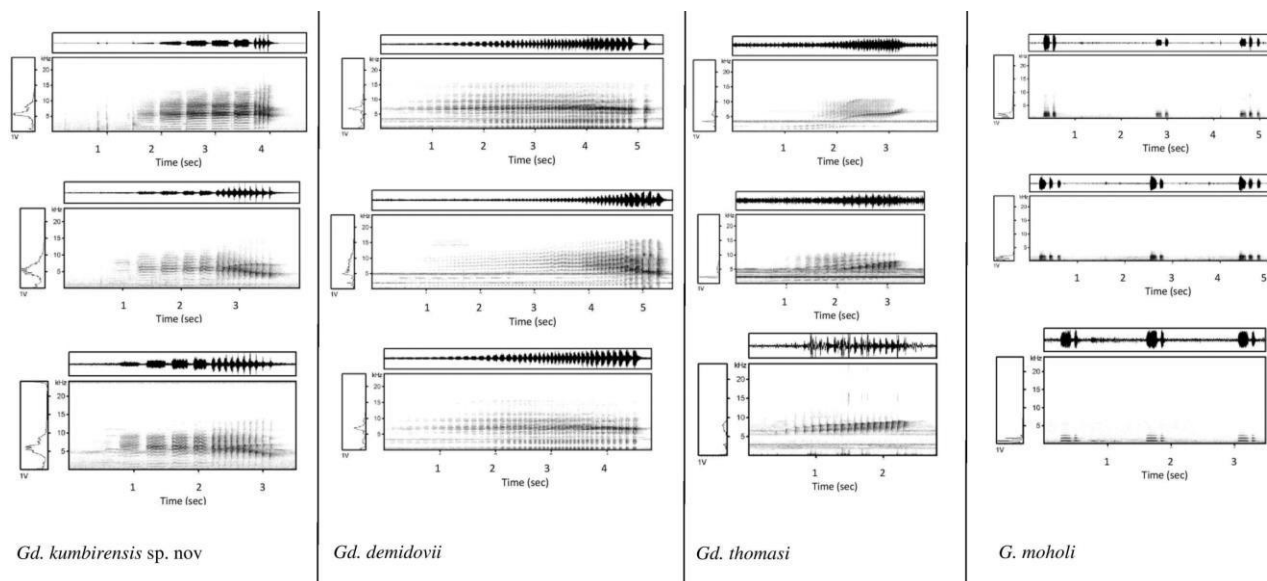
333 We describe *G. kumbirensis* sp. nov. based on both the syntypes and the paratype. A small  
334 gray-brown galago with a darker, long-haired tail. Degree of sexual dimorphism is unknown  
335 but likely to be low, as in most small-bodied galago taxa. Muzzle slightly up-turned, pink  
336 below and dark above, merging into dark eye-rings with a conspicuous white nose stripe  
337 between the eyes. The remainder of the face gray, suffused with brown and set off from white  
338 cheeks, chin and neck. Inner ears white towards the base and yellowish towards margins.  
339 Ears gray above with two light spots where the ears join the crown. Crown, dorsum,  
340 forelimbs, thighs and flanks gray with a brown wash. Ventrums, surface of forelimbs and  
341 hindlimbs creamy yellow. Yellow strongest where the light ventrum merges into the darker  
342 dorsum. Tail darker towards the tip and slightly longer than the body. Tail held curled when  
343 at rest. Head-body measures range 170-200 mm (n = 3), tail 170-240 mm (n = 3), hind foot  
344 50-53 mm (n = 3), ear 29-33 mm (n = 3) (sexes combined for all measurements, Table 1).

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349

350 **Fig. 3.** Vocalisation spectrograms of advertisement calls. *Gd. kumbirensis* sp. nov. –crescendo-twitter;  
 351 *Gd. demidovii* – crescendo; *Gd. thomasi* – multiple crescendo; *G. moholi* – bark. Vocalization  
 352 recordings of *Gd. kumbirensis* sp. nov. are available at [www.wildsolutions.nl](http://www.wildsolutions.nl).

353

354

### Vocalization

355 The distinguishing vocal feature of *Gd. kumbirensis* sp. nov. is the twitter sequence following  
 356 the crescendo call (Table 1). In the recorded calls of *Gd. kumbirensis* sp. nov. that were of  
 357 suitable quality for spectrographic analysis ( $n = 14$ ), the number of crescendo units in a call  
 358 ranged between 2-17 and twitter units between 4-10. The mean fundamental frequency of the  
 359 crescendo-twitter was  $1039 \pm 311$  kHz ( $n = 14$ ) and the mean formant  $3721 \pm 1713$  kHz ( $n =$   
 360  $14$ ); mean crescendo unit length  $0.269 \pm 0.044$  s ( $n = 14$ ) and mean twitter unit length  $0.068 \pm$   
 361  $0.015$  s ( $n = 14$ ) (Fig. 3). The four species showed clear differences in the values obtained for  
 362 these four call parameters (ANOVA, all  $F_{3,57} > 8.204$ , all  $p < 0.001$ ) (Table 1). Post-hoc tests  
 363 show that *Gd. kumbirensis* sp. nov. differs in its fundamental frequency from *Gd. thomasi*  
 364 (Tukey HSD, mean difference -1148,  $p = 0.003$ ), and in its formant from *Gd. demidovii*  
 365 (mean difference -2092,  $p < 0.001$ ) and from *G. moholi* (mean difference -2711,  $p < 0.006$ ),  
 366 but not from *Gd. thomasi* (mean difference -1420,  $p < 0.115$ ).

367

**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

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370

### Habitat

371 Observed in moist, tall forest, primary and secondary (Kumbira and Northern Scarp Forest)  
 372 and semi-arid baobab savannah-woodland in areas where tree-lined water courses allowed  
 373 access (Bimbe; Table 1). Encounter rate was higher in moist forest (2.60 - 2.67  
 374 individuals/km) compared to savannah-woodland (0.17 individuals/km, see Bersacola et al.,  
 375 2015 for more information and statistical analyses).

376 The species has been observed at altitudes of between 285 – 910 m asl, i.e. 860 to 910  
 377 m asl in Kumbira, 285 m asl in Bimbe and 465 to 745 m asl in Northern Scarp Forest. The  
 378 2005 vocalization recordings were made at 900 m asl, and the syntypes was collected at 800  
 379 m asl. Forest in the northern Angolan Escarpment descends down to approximately 250 m  
 380 and up to 1,200 m asl and *Gd. kumbirensis* sp. nov. was observed over most of this range.

381

382

### Distribution and conservation status

383 Currently known only from four sites (Fig. 1). Based on the habitat types in which we  
 384 observed *Gd. kumbirensis* sp. nov., and its altitudinal distribution, and taking into account

385 geographical barriers, including the steep escarpment, three scenarios can be envisaged. The  
386 first is a conservative one, assuming the species is confined to the central and northern  
387 portion of the Angolan Escarpment, thus including the four known locations, in which its  
388 extent of occurrence (EOO, IUCN, 2014) is just under 20,000 km<sup>2</sup> (Fig. 1). Using a more  
389 liberal estimate, its range may extend in the north up to the Congo River (including small  
390 parts of the DRC), with its north-west range restricted by the relatively steep ridge west of  
391 Kinshasa or by the Kasai River, increasing its area to 112,000 km<sup>2</sup> or 405,000 km<sup>2</sup>,  
392 respectively.

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

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

410

### Etymology

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

415

416

### Suggested common name

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

418



419

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

422

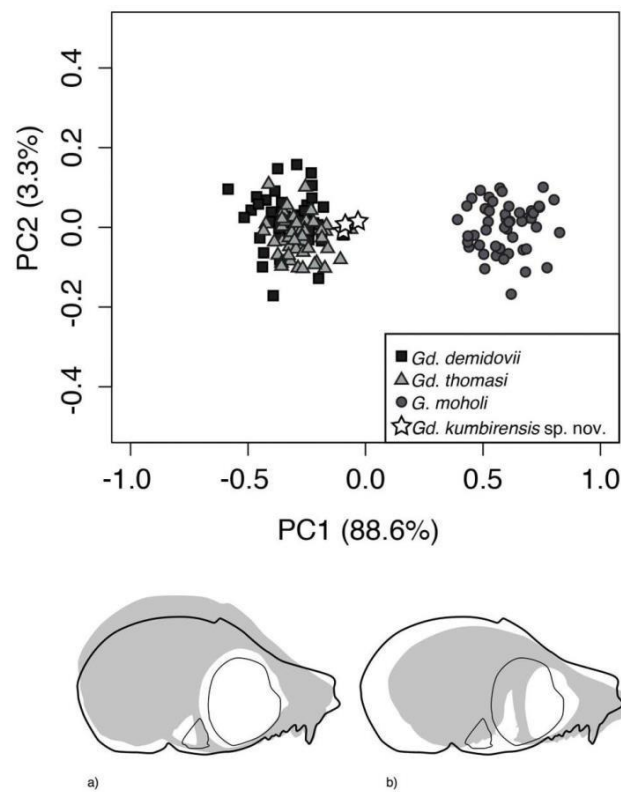
423 **Similar species: habitat use, vocalizations, pelage and facial features** *Galagoides*  
 424 *demidovii*. Sympatric with *Gd. kumbirensis* sp. nov. in at least two sites (Bimbe and Northern  
 425 Scarp Forest). Prefers undergrowth < 5 m, often in secondary growth and forest edge. Usually  
 426 observed running along fine branches (< 1 cm diameter). Crescendo with a long series (> 4  
 427 sec) of rapid notes (10 sec<sup>-1</sup>) building in pitch and intensity and ending in longer, slower  
 428 notes (6 sec<sup>-1</sup>) that descend in pitch (Fig. 3). Usually given only once or twice per bout. Other

429 calls in the repertoire include ‘chips’ (alarm call) and ‘explosive buzz’ (contact avoidance)  
430 (Ambrose, 1999). Facial markings are similar to *Gd. kumbirensis* sp. nov. (Table 1), although  
431 *Gd. demidovii* is considerably smaller in size. Dorsum and tail browner, tail relatively thin  
432 and short (Fig. 4B). Nose narrow and upturned, ears relatively shorter and eye sockets less  
433 broad (Bearder et al., 1995; Ambrose and Butynski, 2013; Nekaris, 2013).

434 *Galagoidees thomasi*. Not known to be sympatric with *Gd. kumbirensis* sp. nov.  
435 Occupies similar height in the canopy as *Gd. kumbirensis* sp. nov. (Table 1), usually > 5 m  
436 on branches of any size. Crescendo consists of a relatively short series (2-3 sec) of brief notes  
437 (6 sec<sup>-1</sup>), gradually increasing in speed of repetition (10 sec<sup>-1</sup>), pitch and volume until the end  
438 of the call which is high pitched (almost inaudible, Fig. 3). Each individual usually repeats  
439 these calls in a sequence, with the first call being the loudest and subsequent calls becoming  
440 quieter (multiple crescendo). Other calls in the repertoire include ‘trills’ (assembly call) and  
441 ‘chips’ (alarm call) which are often interspersed with ‘grunts’ and ‘buzzes’ (Ambrose, 1999).  
442 Somewhat smaller in size, dorsal pelage darker and browner with less contrast between the  
443 dorsum and ventrum (Fig. 4C). Tail browner, shorter and less bushy. Circumocular markings  
444 indistinct and long light nose stripe broadens on forehead (Bearder et al., 1995; Ambrose and  
445 Butynski, 2013; Nekaris, 2013).

446 *Galago moholi*. Not known to be sympatric with *Gd. kumbirensis* sp. nov. but also  
447 present in Angola. Prefers drier woodland-savannah and edge vegetation. Observed using all  
448 strata on branches of all sizes. Like other members of the genus *Galago*, the advertising call  
449 is a repetitive call: a series of single, double or triple barks repeated many times (Fig. 3).  
450 Never heard to give a crescendo. Similar in body size (Fig. 4D) but longer hind limbs suited  
451 to long leaps and hops along the ground. Dorsum without a brown wash and tail similar in  
452 size and color but less bushy, particularly towards the base. Circumocular markings black and

453 diamond-shaped, inner ears darker and muzzle shorter, broader and lighter in color (Bearder  
 454 et al., 1995; Nekaris, 2013; Pullen and Bearder, 2013; Génin et al., 2016).



455

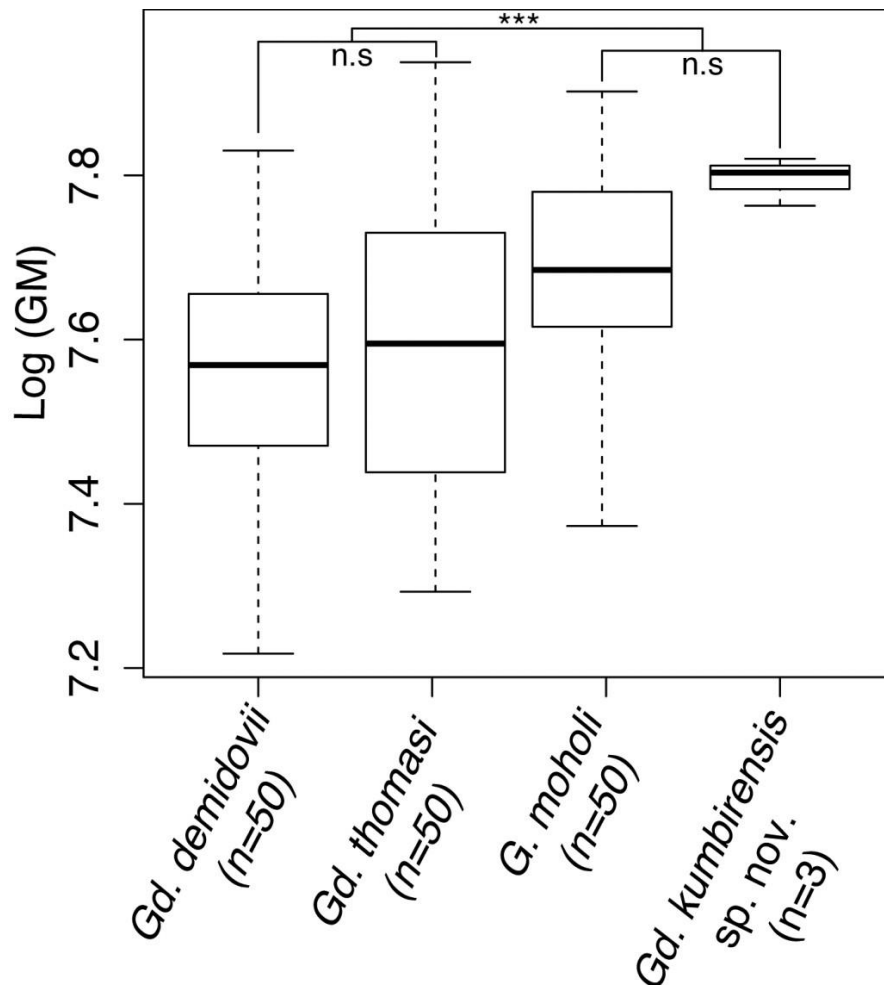
456 **Fig. 5.** Top: Between Group Principal Component Analysis (BGPCA) on the twelve size corrected  
 457 variables of four species of galago. Principal Component Analysis was conducted on the mean of each  
 458 species and specimens were projected in this space. Distances between specimens relate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

462

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

464 **Size of skull :** Figure 6 presents the boxplot of the log (GM) by species. The three specimens  
 465 from Angola show a mean size of 7.79 with a standard deviation of 0.02. Their mean value of  
 466 log (GM) plotted in the higher part of the size range of *G. moholi* (mean = 7.68, SD = 0.13),  
 467 greater than the size of *Gd. demidovii* (mean = 7.55, SD = 0.14) and *Gd. thomasi* (mean =  
 468 7.59, SD = 0.17). We compared skull size across the four species using an ANOVA, and the

469 difference was significant ( $F = 8.6$ ,  $n = 153$ ,  $p < 0.001$ ). Tukey HSD post-hoc statistics  
 470 allowed the distinction of two size groups: a first group composed of *Gd. demidovii* and *Gd.*  
 471 *thomasi*, and a second group composed of *G. moholi* and the *Gd. kumbirensis* sp. nov.  
 472 Therefore, size analysis indicated a similarity in size between the *Gd. kumbirensis* sp. nov.  
 473 and *G. moholi*.



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

477

478 **Shape of skull:** We applied a Between Group Principle Component Analysis (BGPCA) on  
 479 the logged size-corrected measurements of all 153 specimens. This method consists of  
 480 computing a PCA on the mean values for each group, defining the BGPCA space and



481 projecting the individuals in this space by applying the BGPCA parameters (i.e. the variable  
482 loadings) to the shape variables of each specimen (Mitteroecker and Bookstein, 2011).  
483 BGPCA extracted two components that express 91% of the total variation, with PC1  
484 accounting for 88.6% and PC2 accounting for 3.3% of the variance (Fig. 5). Group variation  
485 along PC1 describes essentially the variation in shape of the premaxilla, with longer  
486 premaxillae having negative scores and shorter ones having positive scores along the PC  
487 (Table 2). *Galagoidea demidovii* and *Gd. thomasi* grouped together on the negative end of  
488 PC1, whereas *G. moholi* specimens were separated positively from the other on PC1. All  
489 three Angolan specimens were grouped together and very close to the group composed of *Gd.*  
490 *demidovii* and *Gd. thomasi*. The *Galagoidea* spp. largely overlapped so that it was not  
491 possible to attribute *Gd. kumbirensis* sp. nov. to one or the other species based on shape  
492 analysis. It is clear that, in terms of shape, the Angolan specimens group with the genus  
493 *Galagoidea* rather than *Galago*. In the BGPCA performed by Masters et al. (2017), the new  
494 genus *Paragalago* fell in an intermediate position between *Galago* and *Galagoidea*.

495 We tested the difference in shape variables between groups using a MANOVA, and  
496 the results indicated a significant difference in shape between genera ( $F = 51.1$ , Pillai's trace  
497  $= 1.03$ ,  $p < 0.001$ ). The difference was in accordance with the PCA results. In order to  
498 allocate the Angolan specimens to one or another genus based on the shape analysis, we  
499 computed a Linear Discriminant Analysis, grouping by genus. We used all the specimens for  
500 this analysis except the Angolan ones. Two discriminant axes were significant, perfectly  
501 separating the genus *Galago* from the two *Galagoidea* spp. After cross validation, all  
502 specimens of *G. moholi* were correctly classified by the analysis, whereas a third of the *Gd.*  
503 *demidovii* specimens were classified as *Gd. thomasi* and vice versa. After integrating *Gd.*  
504 *kumbirensis* sp. nov. into the analysis, all three specimens were allocated to *Gd. thomasi* with

505 posterior classification of 93.7, 76.0 and 78.7%. The cranial shape of the Angolan specimens  
506 is highly similar to that of *Gd. thomasi*.

507

508

## DISCUSSION

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

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

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

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

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

552 As noted in the introduction, the escarpment area of Angola is well known as an  
553 important biodiversity hotspot, with many endemic and rare species, often strikingly different  
554 from species elsewhere (Hall, 1960; Figueiredo, 2010; Clark et al., 2011). These species are

555 thought to have speciated and adapted long before the Quaternary (Morley and Kingdon,  
556 2013). This process was possible as the Angolan Escarpment climate, due to the Benguela  
557 Current meeting tropical waters at the Angolan shores, was less affected by climatic changes  
558 than other more inland regions. As such the Angolan Escarpment remained constantly humid,  
559 allowing birds and mammals to develop in isolation during both wet and dry periods (Hall,  
560 1960; Fjeldså and Lovett, 1997).

561         Angola ratified the Convention on Biological Diversity (CBD) in 1998 indicating its  
562 commitment to biodiversity conservation in the country. Through its National Biodiversity  
563 Strategy and Action Plan (Anonymous, 2007) it is committed to incorporating measures for  
564 the conservation and sustainable use of biological diversity into development policies and  
565 programs. Strategic Areas C (biodiversity management of protected areas), F (institutional  
566 strengthening) and G (legislation and implementation), highlighted in the Action Plan, in  
567 particular, can bring direct and tangible conservation benefits to *Gd. kumbirensis* sp. nov. if  
568 implemented. Both the organization of effective management in existing protected areas and  
569 an increase in the protected area network would constitute important strategic interventions.  
570 Further, it is recognized that institutional capacity in Angola is often weak in terms of human  
571 and financial resources and the implementation of any biodiversity conservation policy or  
572 measure crucially depend, on building the capacity of individuals and institutions. Finally, a  
573 review and, if needed, urgent correction, of existing legislation is required to ensure  
574 environmental agreements, including the CBD and CITES are followed as intended  
575 (Anonymous, 2007). The rate of logging in Angola is one of the fastest known in the world  
576 (Hansen et al., 2013), with the Angolan Escarpment being a case in point (Cáceres et al.,  
577 2016) which underlines the urgent need for further research to set priorities for future  
578 conservation, and the need to designate more protected areas.

579           Although birds are relatively well studied in the Angolan Escarpment (Ryan et al.,  
580 2004; Cáceres et al., 2015), there is a dearth of knowledge when it comes to mammal species.  
581 Other endemic primates such as *Miopithecus talapoin* and *Cercopithecus mitis mitis* are  
582 known to be present (Bersacola et al., 2014), but little is known about their distribution or  
583 threats. Recent political and economic developments within Angola have created  
584 opportunities to conduct further research into the ecology and status of *Gd. kumbirensis* sp.  
585 nov. and other endemic mammals. This research will enable the collection of additional data  
586 (genetic, morphological, behavioral, etc.) to be used in a comprehensive phylogenetic  
587 analysis to elucidate the evolutionary relationships between *Gd. kumbirensis* sp. nov. and  
588 other *Galagoidea* species, and, possibly, estimating a date for the separation between *Gd.*  
589 *kumbirensis* sp. nov. and its sister species.

590

591

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603 constructive comments and suggestions for improvement. This project was conceived by MS

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

609

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