

RADAR

Research Archive and Digital Asset Repository

OXFORD
BROOKES
UNIVERSITY

Svensson, M. S., Bersacola, E., Mills, M.S.L., Munds, R.A., Nijman, V., Perkin, A., Masters, J.C., Couette, S., Nekaris, K. A-I., Bearder, S.K. (2017) 'A giant among dwarfs: a new species of galago (Primates: Galagidae) from Angola', *American Journal of Physical Anthropology*

DOI: 10.1002/ajpa.23175

This document is the authors' Accepted Manuscript.

License: <https://creativecommons.org/licenses/by-nc-nd/4.0/>

Available from RADAR: <https://radar.brookes.ac.uk/radar/items/d1c05dec-15cf-48fb-806f-bba8d0e95388/1/>

Copyright © and Moral Rights are retained by the author(s) and/ or other copyright owners unless otherwise waved in a license stated or linked to above. A copy can be downloaded for personal non-commercial research or study, without prior permission or charge. This item cannot be reproduced or quoted extensively from without first obtaining permission in writing from the copyright holder(s). The content must not be changed in any way or sold commercially in any format or medium without the formal permission of the copyright holders.

[WWW.BROOKES.AC.UK/GO/RADAR](https://www.brookes.ac.uk/go/radar)

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

3

4 Magdalena S Svensson¹, Elena Bersacola¹, Michael SL Mills², Rachel A Munds³, Vincent
5 Nijman¹, Andrew Perkin^{1,4}, Judith C Masters⁵, Sébastien Couette⁶, K Anne-Isola Nekaris¹,
6 Simon K Bearder¹

7

8 ¹ Nocturnal Primate Research Group, Oxford Brookes University, Oxford, OX3 0BP, UK

9 ² A. P. Leventis Ornithological Research Institute, University of Jos, 930001, Nigeria

10 ³Department of Anthropology, University of Missouri Columbia, Columbia, Missouri, 65211, USA

11 ⁴Tanzania Forest Conservation Group, Dar es Salaam, Tanzania

12 ⁵African Primate Initiative for Ecology and Speciation, Africa Earth Observatory Network – Earth
13 Stewardship Science Research Institute, Nelson Mandela Metropolitan University, Port Elizabeth
14 6031, South Africa

15 ⁶EPHE, PSL Research University, Paris, France & UMR CNRS 6282 "Biogéosciences", Univ.
16 Bourgogne Franche-Comté, Dijon, 21000, France

17

18 **Corresponding author:**

19 Magdalena Svensson, Nocturnal Primate Research Group, Oxford Brookes University, Oxford, UK.

20 E-mail: svensson_magdalena@hotmail.com

21 Tel. No: +44 7586 313301

22

23 **Number of text pages (incl. bibliography):** 39

24 **Number of figures:** 6

25 **Number of tables:** 2

26

27 **Running headline:** New species of *Galagoides* in Angola

28

29 **Keywords:** Bushbaby; Cryptic species; *Galagoides*; Morphology; Strepsirrhine

30

31

32

33

34

35

36

ABSTRACT

37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63

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.

178

179

MATERIALS AND METHODS

180

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).

201

202

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.

209

210

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.

225

226

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.

259

260

261

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>	
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	Uprturned muzzle	Uprturned 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
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 <i>Gd. kumbirensis</i> 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

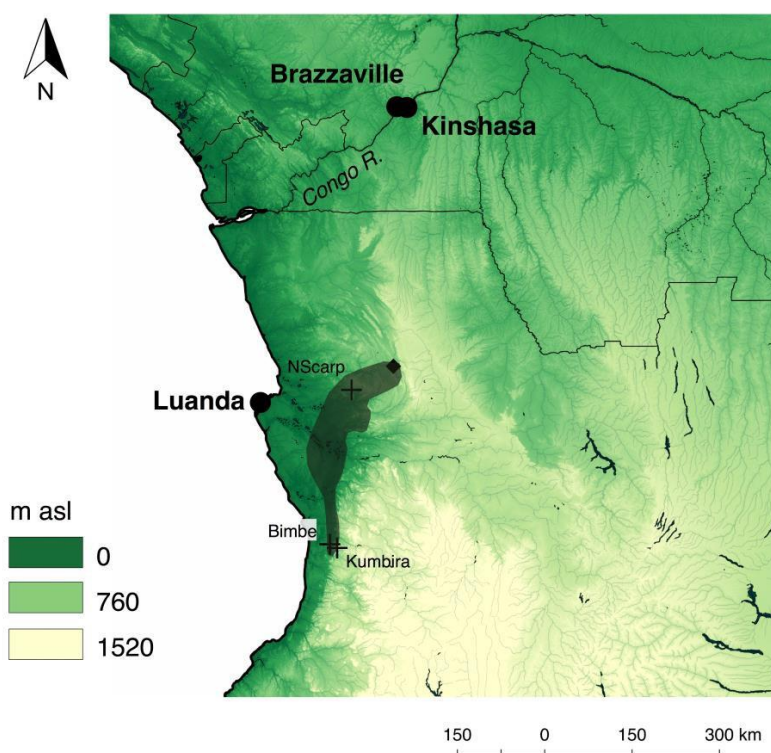
262 *All measurements taken from Butynski, Kingdon & Kalina (2013) except the ones for *Galagoides kumbirensis* sp. nov.

263

264

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)

301

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⁻¹) becoming louder and changing to a
319 variable series (0.3-1.3 sec) of staccato notes (10 sec⁻¹) 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**

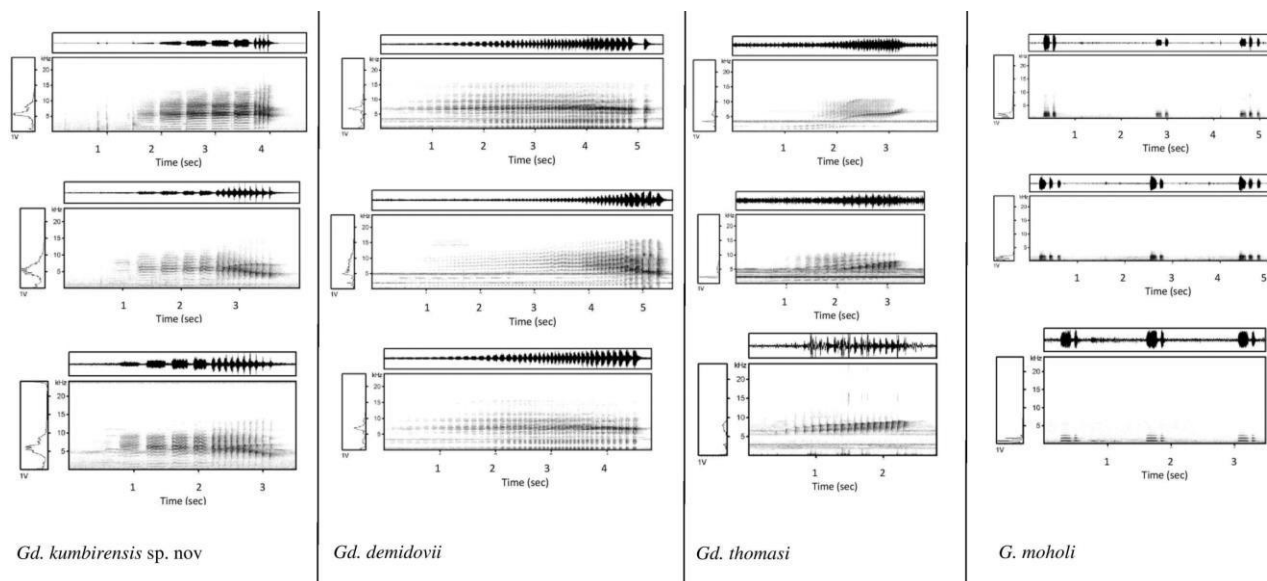
333 We describe *G. kumbirensis* sp. nov. based on both the syntypes and the paratype. A small
334 gray-brown galago with a darker, long-haired tail. Degree of sexual dimorphism is unknown
335 but likely to be low, as in most small-bodied galago taxa. Muzzle slightly up-turned, pink
336 below and dark 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).

345

346

347

348



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.

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 ± 311 kHz ($n = 14$) and the mean formant 3721 ± 1713 kHz ($n =$
 360 14); mean crescendo unit length 0.269 ± 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

368

369

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 km² (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 km² or 405,000 km²,
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 km², 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

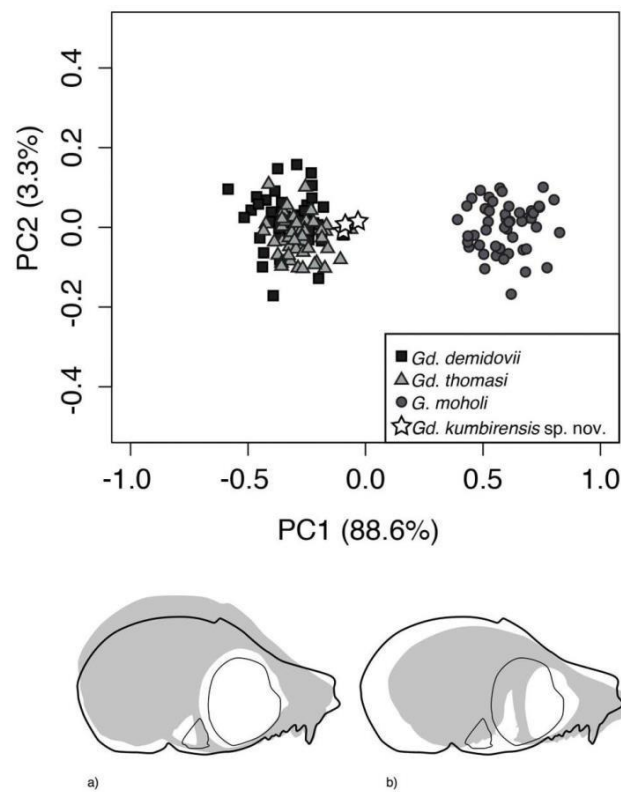
423 **Similar species: habitat use, vocalizations, pelage and facial features** *Galagoides*
 424 *demidovii*. Sympatric with *Gd. kumbirensis* sp. nov. in at least two sites (Bimbe and Northern
 425 Scarp Forest). Prefers undergrowth < 5 m, often in secondary growth and forest edge. Usually
 426 observed running along fine branches (< 1 cm diameter). Crescendo with a long series (> 4
 427 sec) of rapid notes (10 sec⁻¹) building in pitch and intensity and ending in longer, slower
 428 notes (6 sec⁻¹) 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⁻¹), gradually increasing in speed of repetition (10 sec⁻¹), 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

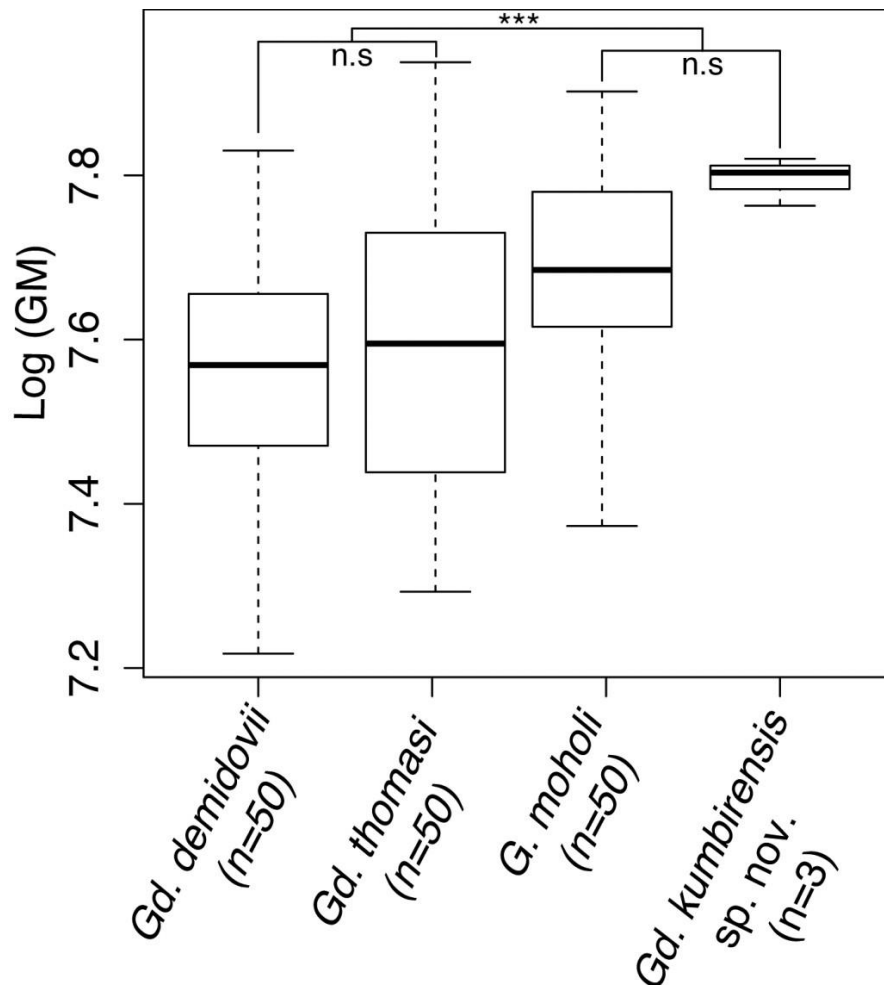
456 **Fig. 5.** Top: Between Group Principal Component Analysis (BGPCA) on the twelve size corrected
 457 variables of four species of galago. Principal Component Analysis was conducted on the mean of each
 458 species and specimens were projected in this space. Distances between specimens relate to 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). *Galagoideus 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 *Galagoideus* 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 *Galagoideus* 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 *Galagoideus*.

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 *Galagoideus* 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

ACKNOWLEDGEMENTS

592 Special thanks go to CP Groves and JF Oates who provided advice throughout this project.
593 We also thank American Museum of Natural History, New York, USA; Museum of
594 Comparative Zoology, Cambridge, USA; Field Museum of Natural History, Chicago, USA;
595 Muséum National d'Histoire Naturelle, Paris, France; Natural History Museum, London, UK;
596 National Museum of Kenya, Nairobi, Kenya; Royal Museum of Central Africa, Tervuren,
597 Belgium and National History Museum of Zimbabwe, Bulawayo, Zimbabwe, for allowing us
598 to study their collections and to FMNH for allowing us to publish the pictures of the type
599 specimens. Our thanks also go to MH Ahsan for helping us gather information from FMNH
600 and to C McMahon for her hospitality whilst in Angola. We thank T Baron for his assistance
601 with Angolan visas. We are grateful for support from the Fredrika Bremer Förbundet and the
602 Iris Jonzén-Sandbloms & Greta Jonzéns Stiftelse. We thank two anonymous reviewers for
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

610

REFERENCES

- 611 Alvim, J., & Pimenta, A. D. (2013). Taxonomic review of the family Discodorididae
 612 (Mollusca: Gastropoda: Nudibranchia) from Brazil, with descriptions of two new
 613 species. *Zootaxa*, 3745(2), 152 - 198.
- 614 Ambrose, L. (1999). *Species diversity in West and Central African galagos (primates,*
 615 *Galagonidae): the use of acoustic analysis* (Unpublished PhD dissertation). Oxford
 616 Brookes University, Oxford.
- 617 Ambrose, L. (2003). Three acoustic forms of Allen's galagos (Primates; Galagonidae) in the
 618 Central African region. *Primates*, 44(1), 25 - 39.
- 619 Ambrose, L. (2013). *Scirocheirus makandensis* - Makandé squirrel galago. In: T. M.
 620 Butynski, J. Kingdon & J. Kalina (Eds.), *Mammals of Africa - volume II Primates*.
 621 (pp. 421 - 422). London: Bloomsbury Publishing.
- 622 Ambrose, L., & Butynski, T. M. (2013). *Galagoides thomasi*-Thomas's dwarf galago. In: T.
 623 M. Butynski, J. Kingdon & J. Kalina (Eds.), *Mammals of Africa - volume II*
 624 *Primates* (pp. 462 - 466). London: Bloomsbury Publishing.
- 625 Anderson, M. J. (1999). Penile morphology and classification of bush babies (Subfamily
 626 Galagoninae). *Int J Primatol*, 21 (5), 815 - 836.
- 627 Anderson, M. J. (2001). The use of hair morphology in the classification of galagos
 628 (Primates, subfamily Galagoninae). *Primates*, 42 (2), 113 - 122.

- 629 Anderson, M. J., Ambrose, L., Bearder, S. K., Dixson, A. F., & Pullen, S. (2000).
630 Intraspecific variation in the vocalisations and hand pad morphology of southern
631 lesser bush babies (*Galago moholi*): a comparison with *G. senegalensis*. *Int J*
632 *Primatol*, 21, 537 - 556.
- 633 Anonymous (2007). *National biodiversity strategy and action plan (NBSAP)*. Luanda,
634 Angola: Ministry of Urban Affairs and Environment.
- 635 Bailey, R. C., & Byrnes, J. (1990). A new, old method for assessing measurement error in
636 both univariate and multivariate morphometric studies. *Syst Zool*, 39, 124.
- 637 Bearder, S. K., & Svoboda, N. S. (2013). *Otolemur crassicaudatus* - large-eared greater
638 galago. In: T. M. Butynski, J. Kingdon & J. Kalina (Eds.), *Mammals of Africa -*
639 *volume II Primates* (pp. 409 - 413). London: Bloomsbury Publishing, London.
- 640 Bearder, S. K., Honess, P. E., & Ambrose, L. (1995). Species diversity among galagos with
641 special reference to mate recognition. In: L. Alterman, G. A. Doyle. & M.K. Izard
642 (Eds.), *Creatures of the dark: the nocturnal prosimians* (pp. 331 - 352). New York:
643 Plenum Press, New York.
- 644 Bearder, S. K., Honess, P. E., Bayes, M., Anderson, M., & Ambrose, L. (1996). Assessing
645 galago diversity: a call for help. *Afr. Primates*, 2 (1), 11 - 15.
- 646 Bersacola, E., Svensson, M. S., & Bearder, S. K. (2015). Niche partitioning and
647 environmental factors affecting abundance of strepsirrhines in Angola. *Am J*
648 *Primatol*, 77(11), 1179 - 1192.
- 649 Bersacola, E., Svensson, M. S., Bearder, S. K., Mills, M., & Nijman, V. (2014). Hunted in
650 Angola: surveying the bushmeat trade. *Swara*, Jan-March, 31 - 36.
- 651 Bickford, D., Lohman, D. J., Sodhi, N. S., Ng, P. K. L., Meier, R., Winker, K., ... Das, I.
652 (2007). Cryptic species as a window on diversity and conservation. *Trends Ecol*
653 *Evol*, 22(3), 148 - 155.

- 654 Burnaby, T. P. (1966). Growth-invariant discriminant functions and generalized distances.
655 *Biometrics*, 22, 96 - 110.
- 656 Butynski, T. M., Kingdon, J., & Kalina, J. (2013). *Mammals of Africa - volume II Primates*.
657 London: Bloomsbury Publishing.
- 658 Cáceres, A., Melo, M., Barlow, J., & Mills, M. S. L. (2016). Radiotelemetry reveals key data
659 for the conservation of *Sheppardia gabela* (Rand, 1957) in the Angolan Escarpment
660 forest. *Afr J Ecol*, 54(3), 317 - 327.
- 661 Cáceres, A., Melo, M., Barlow, J., Cardoso, P., Maiato, F., & Mills, M. S. L. (2015).
662 Threatened birds of the Angolan Central Escarpment: distribution and response to
663 habitat change at Kumbira Forest. *Oryx*, 49(4), 727 - 734.
- 664 Ceballos, G., & Ehrlich, P. R. (2009). Discoveries of new mammal species and their
665 implications for conservation and ecosystem services. *Proc Natl Acad Sci U S A*,
666 106(10), 3841 - 3846.
- 667 Charles-Dominique, P., & Bearder, S. K. (1979). Field studies of lorid behavior:
668 Methodological aspects. In: G. A. Doyle & R. D. Martin (Eds.), *The Study of*
669 *prosimian behaviour* (pp. 567 - 629). London: Academic Press.
- 670 Clark, V. R., Barker, N. P., & Mucina, L. (2011). The Great Escarpment of South Africa: a
671 new frontier for biodiversity exploration. *Biodivers Conserv*, 20, 2543 - 2561.
- 672 Cotterill, F. P., Taylor, P. J., Gippoliti, S., Bishop, J. M., & Groves, C. P. (2014). Why one
673 century of phenetics is enough: response to “are there really twice as many bovid
674 species as we thought?”. *Syst Biol*, 63(5), 819 - 832.
- 675 Cracraft, J. (1989). Speciation and its ontology: the empirical consequences of alternative
676 species concepts for understanding patterns and processes of differentiation. In D.
677 Otte & J. A. Endler (Eds.), *Speciation and its consequences* (pp. 28–59).
678 Sunderland: Sinauer.

- 679 Crompton, R. H., Lieberman, S. S., & Oxnard, C. E. (1987). Morphometrics and niche
680 metrics in prosimian locomotion: an approach to measuring locomotion, habitat and
681 diet. *Am J Phys Anthropol*, 73, 149 - 177.
- 682 Davenport, T. R., Stanley, W. T., Sargis, E. J., De Luca, D. W., Mpunga, N. E., Machaga, S.
683 J., & Olson, L. E. (2006). A new genus of African monkey, *Rungwecebus*:
684 morphology, ecology, and molecular phylogenetics. *Science*, 312(5778), 1378 -
685 1381.
- 686 Defler, T. R., & Bueno, M. L. (2007). *Aotus* diversity and species problem. *Primate*
687 *Conservation*, 22, 55 - 70.
- 688 Figueiredo, E. (2010). Diversity and endemism of Rubiaceae in Angola. In: X, Van der
689 Burgt, J. Van der Maesen & J-M, Onana, J-M (Eds.), *Systematics and conservation*
690 *of African plants* (pp. 15 - 22). Kew: Royal Botanic Gardens, Kew.
- 691 Fjeldså, J., & Lovett, J. C. (1997). Geographical patterns of old and young species in African
692 forest biota: the significance of specific montane areas as evolutionary centres.
693 *Biodivers Conserv*, 6, 325 - 346.
- 694 Génin, F., Yokwana, A., Kom, N. Couette, S., Dieuleveut, T. Nash, S.D. & Masters, J.C.
695 (2016). A new galago species for South Africa (Primates: Strepsirhini: Galagidae).
696 *Afr Zool*, 51, 135-143.
- 697 Geissmann, T., Lwin, N., Aung, S. S., Aung, T. N., Aung, Z. M., Hla, T. H., ... Momberg, F.
698 (2010). A new species of snub-nosed monkey, genus *Rhinopithecus* Milne-Edwards,
699 1872 (Primates, Colobinae), from Northern Kachin State, Northeastern Myanmar.
700 *Am J Primatol*, 72, 1 - 12.
- 701 Gibbs, G. W. (2010). Micropterigidae (Lepidoptera) of the Southwestern Pacific: a revision
702 with the establishment of five new genera from Australia, New Caledonia and New
703 Zealand. *Zootaxa*, 2520, 1 - 48.

- 704 Groves, C. P. (2001). *Primate taxonomy*. Washington, D.C: Smithsonian Institution Press.
- 705 Groves, C. P., & Grubb, P. (2011). *Ungulate taxonomy*. Baltimore: The Johns Hopkins
706 University Press.
- 707 Grubb, P., Butynski, T. M., Oates, J. F., Bearder, S. K., Disotell, T. R., Groves, C. P., &
708 Struhsaker, T. T. (2003). Assessment of the diversity of African primates. *Int J*
709 *Primatol*, 24(6), 1301 - 1357.
- 710 Hall, B.P. (1960). The faunistic importance of the scarp of Angola. *Ibis*, 102, 420 - 442.
- 711 Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A.,
712 ... Townshend, J. R. G. (2013). High-resolution global maps of 21st-century forest
713 cover change. *Science*, 342, 850 - 853.
- 714 Harcourt, C. S., & Nash, L. T. (1986). Species differences in substrate use and diet between
715 sympatric galagos in two Kenyan coastal forests. *Primates*, 27(1), 41 - 52.
- 716 Hart, J. A., Detwiler, K. M., Gilbert, C. C., Burrell, A. S., Fuller, J. L., Emetshu, M., ... Tosi,
717 A. J. (2012). Lesula: a new species of *Cercopithecus* monkey endemic to the
718 Democratic Republic of Congo and implications for conservation of Congo's
719 Central Basin. *PLoS One*, 7(9), e44271.
- 720 Helgen, K. M., Leary, T., & Aplin, K. P. (2010). A review of *Microhydromys* (Rodentia:
721 Murinae), with description of a new species from southern New Guinea. *Am. Mus.*
722 *Novit.*, 3676, 1 - 24.
- 723 Hertach, T., Trilar, T., Wade, E. J., Simon, C., & Nagel, P. (2015). Songs, genetics, and
724 morphology: revealing the taxonomic units in the European *Cicadetta cerdaniensis*
725 cicada group, with a description of new taxa (Hemiptera: Cicadidae). *Zool J Linn*
726 *Soc*, 173(2), 320 - 351.
- 727 Hotaling, S., Foley, M., Lawrence, N., Bocanegra, J., Blanco, M., Rasoloarison, R., ... Rock,
728 D. W. (2016). Species discovery and validation in a cryptic radiation of endangered

- 729 primates: coalescent based species delimitation in Madagascar's mouse lemurs. *Mol*
730 *Ecol*, 25(9), 2029 - 2045.
- 731 Isaac, N. J. B., Mallet, J., & Mace, G. M. (2004). Taxonomic inflation: its influence on
732 macroecology and conservation. *Trends Ecol Evol*, 19(9), 464 - 469.
- 733 IUCN. (2014) *Guidelines for using the IUCN Red List categories and criteria. Version 11.*
734 Gland, Switzerland: IUCN Standards and Petitions Subcommittee.
- 735 Izard, M. K., & Nash, L. T. (1988). Contrasting reproductive parameters in *Galago*
736 *senegalensis braccatus* and *G. s. moholi*. *Int J Primatol*, 9 (6), 519 – 527.
- 737 Jenkins P. D. (1987). *Catalogue of primates in the British Museum (Natural History) and*
738 *elsewhere in the British Isles. Part IV: Suborders Strepsirrhini, including the*
739 *subfossil Madagascan lemurs and Family Tarsiidae*. London: Trustees of British
740 Museum (Natural History).
- 741 Jones, T., Ehardt, C. L., Butynski, T. M., Davenport, T. R. B., Mpunga, N. E., Machaga, S. J.,
742 & de Luca, D. W. (2005). The highland mangabey *Lophocebus kipunji*: a new
743 species of African monkey. *Science*, 308, 1161 - 1164.
- 744 Kingdon, J. (2015). *The Kingdon field guide to African Mammals: Second edition*. London:
745 Bloomsbury Publishing.
- 746 Kitchener, A. C., & Groves, C. (2002). New insights into the taxonomy of *Macaca pagensis*
747 of the Mentawai Islands, Sumatra. *Mammalia*, 66(4), 533 - 542.
- 748 Kuedikuenda, S., & Xavier, N. G. (2009). *Framework report on Angola's biodiversity*.
749 Luanda: Republic of Angola Ministry of Environment.
- 750 Li, C., Zhao, C., & Fan, P-F. (2015). White-cheeked macaque (*Macaca leucogenys*): a new
751 macaque species from Modog, Southeastern Tibet. *Am J Primatol*, 77(7), 753 - 766.

- 752 Machado, A de Barros. (1969). Mamíferos de Angola ainda não citados ou pouco
753 conhecida. *Publicações Culturais da Companhia de Diamantes de Angola,*
754 *Lisboa*, 46, 93 - 232.
- 755 Masters, J. C. (1993). Primates and paradigms: problems with the identification of genetic
756 species. In: W. H. Kimbel & L. B. Martin (Eds.), *Species, species concepts and*
757 *primate evolution* (pp. 43 - 64). New York: Plenum Press.
- 758 Masters, J. C., & Bragg, N. P. (2000). Morphological correlates of speciation in bushbabies.
759 *Int J Primatol*, 21 (5), 793 - 813
- 760 Masters, J. C., & Couette, S. (2015). Characterizing cryptic species: a morphometric analysis
761 of craniodental characters in the dwarf galago genus *Galagoides*. *Am J Phys*
762 *Anthropol*, 158, 288 - 299.
- 763 Masters, J. C., Génin , F., Couette, S., Groves, C. P., Nash, S. D., Delperro, M., & Pozzi, L.
764 (2017). A new genus for the eastern dwarf galagos (Primates: Galagidae). *Zool J*
765 *Linn Soc*, Early View, doi: 10.1093/zoolinnean/zlw028
- 766 Mittermeier, R. A., Rylands, A. B., & Wilson, D. E. (2013). *Handbook of the mammals of the*
767 *world -volume III Primates*. Barcelona: Lynx Edicions.
- 768 Mitteroecker, P., & Bookstein, F. L. (2011). Linear discrimination, ordination, and the
769 visualization of selection gradients in modern morphometrics. *Evol Biol*, 38, 100 -
770 114.
- 771 Morley, R. J., & Kingdon, J. (2013). Africa's environmental and climatic past. In: J.
772 Kingdon, D. Happold, M. Hoffmann, T. Butynski, M. Happold & J. Kalina (Eds.),
773 *Mammals of Africa - Volume 1 introductory chapters and Afrotheria* (pp. 43 - 56).
774 London: Bloomsbury Publishing.

- 775 Munds, R. A., Nekaris, K. A. I., & Ford, S. M. (2013). Taxonomy of the Bornean slow loris,
776 with new species *Nycticebus kayan* (Primates, Lorisidae). *Am J Primatol*, 75(1), 46 -
777 56.
- 778 Nash, L. T., Bearder, S. K., & Olson, T. R. (1989). Synopsis of galago species characteristics.
779 *Int J Primatol*, 10, 57 - 80
- 780 Nash, L. T., Zimmermann, E., & Butynski, T. M. (2013). *Galago senegalensis* - Northern
781 lesser galago (Senegal lesser Galago, Senegal lesser bushbaby). In: T. M. Butynski,
782 J. Kingdon & J. Kalina (Eds.), *Mammals of Africa - volume II Primates* (pp. 425 -
783 429). London: Bloomsbury Publishing.
- 784 Nekaris, K. A. I. (2013). Family Galagidae (galagos). In: R. A. Mittermeier, A. B. Rylands &
785 D. E. Wilson (Eds.), *Handbook of the mammals of the world - volume III primates*
786 (pp. 184 - 209). Barcelona: Lynx Edicions.
- 787 Nekaris, K. A. I., & Bearder, S. K. (2011). The Lorisiform primates of Asia and mainland
788 Africa. In: C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder & R. M.
789 Stumpf (Eds.), *Primates in perspective* (pp. 34 - 54). Oxford: Oxford University
790 Press.
- 791 Ng, E. Y. X., Eaton, J. A., Verbelen, P., Hutchinson, R. O., & Rheindt, F. E. (2016). Using
792 bioacoustic data to test species limits in an Indo-Pacific island radiation of
793 *Macropygia* cuckoo doves. *Biol J Linn Soc Lond*, 118(4), 786 - 812.
- 794 Oates, J. F. (2011). *Primates of West Africa: A field guide and natural history*. Arlington:
795 Conservation International.
- 796 Olson, T. R. (1979). *Studies on aspects of the morphology of the genus Otolemur, Coquerel,*
797 *1859* (Unpublished PhD dissertation). University of London, London.

- 798 Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N.,
799 Underwood, E. C., ...Kassem, K. R. (2001). Terrestrial ecoregions of the world: a
800 new map of life on earth. *Bioscience*, 51(11), 933 - 938.
- 801 Paterson, H. E. H. (1985). The recognition concept of species. In: E. S. Vrba (Ed.), *Species*
802 *and speciation* (pp. 21 – 30). Pretoria: Transvaal museum.
- 803 Perkin, A. (2007). Comparative penile morphology of east African galagos of the genus
804 *Galagoides* (Family Galagidae): implications for taxonomy. *Am J Primatol*, 69, 16 -
805 26.
- 806 Pimley, E. R. (2009). A survey of nocturnal primates (Strepsirrhini: Galaginae, Perodictinae)
807 in southern Nigeria. *Afr J Ecol*, 47 (4), 784 - 787.
- 808 Pozzi, L. (2016). The role of forest expansion and contraction in species diversification
809 among galagos (Primates: Galagidae). *J Biogeogr*, 43 (10), 1930 – 1941.
- 810 Pozzi, L., Disotell, T. R., & Masters, J. C. (2014). A multilocus phylogeny reveals deep
811 lineages within African galagids (Primates: Galagidae). *BMC Evol Biol*, 14, 72.
- 812 Pozzi, L., Nekaris, K. A. I., Perkin, A., Bearder, S. K., Pimley, E. R., Schulze, H., ... Roos,
813 C. (2015). Remarkable ancient divergences amongst neglected loriform primates.
814 *Zool J Linn Soc*, 175(3), 661 - 674.
- 815 Pullen, S., & Bearder, S. K. (2013). *Galago moholi* - Southern lesser galago (South African
816 lesser galago). In: T. M. Butynski, J. Kingdon & J. Kalina (Eds.), *Mammals of*
817 *Africa - volume II Primates* (pp. 430 - 434). London: Bloomsbury Publishing.
- 818 Reeder, D., Helgen, K. M., Vodzak, M., Lunde, D., & Ejotre, I. (2013). A new genus for a
819 rare African vespertilionid bat: insights from South Sudan. *ZooKeys*, 285, 89 - 115.
- 820 Romeiras, M. M., Figueira, R., Duarte, M. C., Beja, P., & Darbyshire, I. (2014).
821 Documenting biogeographical patterns of African timber species using herbarium

- 822 records: a conservation perspective based on native trees from Angola. *PLoS One*,
823 9(7), e103403.
- 824 Ryan, P. G., Sinclair, I., Cohen, C., Mills, M. S. L., Spottiwoode, C. N., & Cassidy, R.
825 (2004). The conservation status and vocalisation of threatened birds from the scarp
826 forest of the Western Angola Endemic Bird Area. *Bird Conserv. Int.*, 14, 247 - 260.
- 827 Shekelle, M., Groves, C., Merker, S., & Supriatna, J. (2008). *Tarsius tumpara*: a new tarsier
828 species from Siau Island, North Sulawesi. *Primate Conservation*, 23, 55 - 64.
- 829 Svensson, M. S., & Bearder, S. K. (2013). Sightings and habitat use of the northern lesser
830 galago (*Galago senegalensis senegalensis*) in Niuni National Park, The Gambia.
831 *Afr. Primates*, 8, 51 – 58.
- 832 Svensson, M. S., Ingram, D. J., Nekaris, K. A. I., & Nijman, V. (2015). Trade and
833 ethnozoological use of African lorisiforms in the last 20 years. *Hystrix*, 26(2), 153 -
834 161.
- 835 Thinh, V. N., Mootnick, A. R., Thanh, V. N., Nadler, T., & Roos, C. (2010). A new species
836 of crested gibbon from the central Annamite mountain range. *Vietnamese Journal of*
837 *Primateology*, 4, 1 - 12.
- 838 Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S. Fourth edition*.
839 New York: Springer.
- 840 Vetter, S. (2003). *Angolan Scarp savanna and woodlands (AT1002)*. Available from:
841 http://www.worldwildlife.org/wildworld/profiles/terrestrial/at/at1002_full.html.
842 (Date of access 16 Aug 2016)
- 843 Vonk, R., & Jaume, D. (2014). *Ingolfiella maldivensis* sp. n. (Crustacea, Amphipoda,
844 Ingolfiellidae) from coral reef sand off Magoodhoo Island, Maldives. *ZooKeys*,
845 (449), 69.

- 846 Weisenseel, K., Chapman, C. A., & Chapman, L. J. (1993). Nocturnal primates of Kibale
847 forest: effects of selective logging on prosimian densities. *Primates*, 34(4), 445 -
848 450.
- 849 Wilson, D. E., & Mittermeier, R. A. (2011). *Handbook of the mammals of the world -volume*
850 *II hoofed mammals*. Barcelona: Lynx Edicions.
- 851 Wollscheid-Lengeling, E., Boore, J., Brown, W., & Wägele, H. (2001). The phylogeny of
852 *Nudibranchia* (Opisthobranchia, Gastropoda, Mollusca) reconstructed by three
853 molecular markers. *Org Divers Evol*, 1, 241 - 256.
- 854 Zimmermann, E. (1990). Differentiation of vocalizations in bushbabies (Galaginae,
855 Prosimiae, Primates) and the significance for assessing phylogenetic relationships. *J*
856 *Zool Syst Evol Res*, 28(3), 217 - 239.
- 857 Zimmermann, E., Bearder, S. K., Doyle, G. A., & Andersson, A. B. (1988). Variations in
858 vocal patterns of Senegal and South African lesser bushbabies and their implications
859 for taxonomic relationships. *Folia Primatol*, 51, 87-105.