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## A new genus for the eastern dwarf galagos (Primates: Galagidae)

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*Original Citation:*

*Availability:*

This version is available <http://hdl.handle.net/2318/1618044> since 2018-01-22T10:34:59Z

*Published version:*

DOI:10.1093/zoolinnean/zw028

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(Article begins on next page)

This is the author's final version of the contribution published as:

Masters, Judith C.; Génin, Fabien; Couette, Sébastien; Groves, Colin P.; Nash, Stephen D.; Delpero, Massimiliano; Pozzi, Luca. A new genus for the eastern dwarf galagos (Primates: Galagidae). ZOOLOGICAL JOURNAL OF THE LINNEAN SOCIETY. None pp: 0-0.

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**A new genus for the eastern dwarf galagos (Primates: Galagidae)**

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|------------------|--|
| Journal:         | <i>Zoological Journal of the Linnean Society</i>   |
| Manuscript ID    | ZOJ-06-2016-2657.R1  |
| Manuscript Type: | Original Article   |
| Keywords:        | bushbaby, biogeography < Geography, craniodental morphometrics, <i>Galagooides</i>, <i>Paragalago</i>, molecular phylogeny < Genetics, vocalisations |
|                  |  |

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## ABSTRACT

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2 The family Galagidae (African galagos or bushbabies) comprises five genera: *Euoticus* Gray  
3 1872; *Galago* Geoffroy Saint-Hilaire, 1796; *Galagoidea* Smith, 1833; *Otolemur* Coquerel,  
4 1859; and *Sciurocheirus* Gray, 1872, none of which is regarded as monotypic, but some  
5 (*Euoticus*, *Otolemur*) certainly qualify as oligotypic. We argue for the recognition of a sixth  
6 genus, if the taxonomy is to reflect galagid evolution accurately. Genetic evidence has  
7 consistently demonstrated that the taxa currently referred to the genus *Galagoidea* are not  
8 monophyletic, but form two clades (a western and an eastern clade) that do not share an  
9 exclusive common ancestor; we review 20 years of genetic studies that corroborate this  
10 conclusion. Further, we compare vocalisations emitted by small-bodied galagids with  
11 proposed phylogenetic relationships, and demonstrate congruence between these data sets.  
12 Morphological evidence, however, is not entirely congruent with genetic reconstructions;  
13 parallel dwarfing in the two clades has led to convergences in skull size and shape that have  
14 complicated the classification of the smaller species. We present a craniodental morphometric  
15 analysis of small-bodied galagid genera that identifies distinguishing characters for the  
16 genera, and supports our proposal that five taxa currently subsumed under *Galagoidea* (*Gs*  
17 *cocos*, *Gs granti*, *Gs orinus*, *Gs rondoensis* and *Gs zanzibaricus*) be placed in their own  
18 genus, for which we propose the name *Paragalago*.

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19 ADDITIONAL KEYWORDS: Bushbaby – Biogeography – Craniodental morphometrics –  
20 *Galagoidea* – *Paragalago* – Molecular phylogeny – Vocalisations

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## INTRODUCTION

In *A Field Guide to the Larger Mammals of Africa* (Dorst & Dandelot, 1970) Pierre Dandelot illustrated five species of galagos (or bushbabies) and two species of pottos. Four of the galagid taxa were subsumed under the genus *Galago*: i.e. *G. alleni*, *G. crassicaudatus*, *G. demidovi* (*sic*, now referred to as *G. demidoff* in accordance with its initial description: Jenkins, 1987; Groves, 2001) and *G. senegalensis*. The needle-clawed galagos were classified in their own genus, *Euoticus*, in accordance with the taxonomies of Schwarz (1931), Simpson (1945) and Hill (1953). Forty-five years later, all five taxa are regarded as distinct genera, none of which is generally viewed as monotypic, although much of the detailed research has yet to be conducted. In this contribution we discuss evidence that *Galagoidea*, as construed by Olson (1979) on morphological grounds, does not constitute a clade in molecular phylogenetic reconstructions (DelPero *et al.*, 2000; Masters *et al.*, 2007; Fabre, Rodrigues & Douzery, 2009; Springer *et al.*, 2012; Pozzi, Disotell & Masters, 2014; Pozzi *et al.*, 2015; Pozzi, 2016) and its members are unlikely to have shared an exclusive common ancestor. More specifically, the dwarf galagos confined to the forests of East and southern Africa require the designation of a new genus. In the subsequent text we abbreviate *Galagoidea* as *Gs* to distinguish it from the abbreviation of *Galago* (*G.*).

## HISTORY OF GALAGID GENERA

The first galagid genus to enter the scientific literature was *Galago*, described by Etienne Geoffroy Saint-Hilaire (1796), and was based on a lesser galago specimen collected in Senegal, West Africa. The name was taken from the Senegalese vernacular name for these animals. The genus *Galagoidea* was proposed by Sir Andrew Smith (1833) to distinguish the dwarf (*G. demidoff*) and lesser (*G. senegalensis*) galagos from what Smith considered to be

1  
2  
3 46 the “true Galagos” among which he included species now referred to the genera *Microcebus*  
4  
5 47 and *Otolemur*. *Galagoides* is now restricted to the dwarf galago taxa. *Otolemur* was  
6  
7 48 introduced as the generic epithet to denote the greater galagos by Charles Coquerel (1859)  
8  
9 49 with *Otolemur agisymbanus* (= *garnettii*) from Zanzibar as the type species. The genus  
10  
11 50 *Euoticus*, which distinguishes the needle-clawed species, was introduced initially by John  
12  
13 51 Gray (1863) as a subgenus under the genus *Otogale* which also included the greater galagos.  
14  
15 52 A few years later he elevated *Euoticus* to the status of a full genus (Gray, 1872). In the same  
16  
17 53 publication, Gray (1872) proposed *Sciurocheirus* as the generic designation of a squirrel  
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19 54 galago specimen (*S. alleni*, *sensu lato*) deriving from Fernando Po [Bioko Island].  
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24 55 The genus *Galagoides* was redefined on morphological grounds by Olson (1979) and  
25  
26 56 employed subsequently by many authors (Honest & Bearder, 1996; Kingdon, 1997;  
27  
28 57 Wickings, Ambrose & Bearder, 1998; DelPero *et al.*, 2000; Masters & Bragg, 2000; Masters  
29  
30 58 & Brothers, 2002; Butynski *et al.*, 2006). It comprised the true dwarf galagos (*Gs demidoff*,  
31  
32 59 *Gs thomasi*), the ‘Zanzibar’ galagos (*Gs cocos*, *Gs granti*, *Gs zanzibaricus*), and the squirrel  
33  
34 60 galagos (*Gs alleni*, *s.l.*). Honest & Bearder (1996) and Kingdon (1997) recognised three new  
35  
36 61 dwarf galago species just before the turn of the twenty-first century: *Gs orinus*, originally  
37  
38 62 described by Lawrence and Washburn (1936) as a subspecies of *Gs demidoff* from the  
39  
40 63 Uluguru Mountains, *Gs rondoensis* from the Rondo plateau, and *Gs udzungwensis* from the  
41  
42 64 Udzungwa Mountains. All three localities are in Tanzania. *Gs udzungwensis* has since been  
43  
44 65 downgraded to a subspecies of *Gs zanzibaricus* confined to the Tanzanian mainland, while  
45  
46 66 *Gs z. zanzibaricusis* reserved for the form on Zanzibar Island. *Gs orinus* and *Gs rondoensis*  
47  
48 67 are now recognised as valid species.  
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53 68 The morphological characters uniting Olson’s (1979) genus *Galagoides* were not  
54  
55 69 made explicit, but from our own observations (Groves, 2001; Masters & Couette, 2015) they  
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57 70 include moderate basicranial flexion (i.e. stronger than in most lemuriforms and lorids, but  
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3 71 not as strong as in the genera *Galago* or *Euoticus*), anterior upper premolar ( $P^2$ ) not  
4  
5 72 caniniform (sometimes with a hypocone), third upper molar ( $M^3$ )  $\geq$  posterior upper premolar  
6  
7 73 ( $P^4$ ), and premaxillaries extended into a tube that projects way beyond the lower jaw. The  
8  
9  
10 74 premaxillary tube is longest in dwarf galagos, moderate in ‘Zanzibar’ galagos, and least  
11  
12 75 pronounced in squirrel galagos. *Euoticus*, *Galago* and *Otolemur* have no premaxillary tube,  
13  
14 76 and the anterior margin of the snout is square; in the absence of a tube, the square-snouted  
15  
16 77 galagos have a relictual nub on the midline beneath the nasal aperture, suggesting that  
17  
18 78 extended premaxillaries may have been the ancestral condition. Among the lorises, the two  
19  
20 79 small-bodied genera, *Arctocebus* and *Loris*, both have premaxillary tubes. *Galagoidea* is  
21  
22 80 further characterized by small body size (smaller in the western clade than in the squirrel  
23  
24 81 galagos or most taxa of the eastern clade), a concave nasal profile, and dark circumocular  
25  
26 82 rings that range in colour from dark brown to black, separated by a grey to white nose stripe.  
27  
28 83 While the deep russet colouration of squirrel galagos makes them instantly recognisable, a  
29  
30 84 survey of other museum specimens designated as *Galagoidea* revealed variable pelage  
31  
32 85 colouration, both within and between populations. In most cases, the animals were covered in  
33  
34 86 dense, soft hairs with dark-grey roots, but brown to bright russet tips on the head, dorsum and  
35  
36 87 outer surfaces of the limbs. The tips of the hairs on the under surfaces are yellow-buff to  
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38 88 white, and the animals have brown to blackish tails.  
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90 OVERVIEW OF MOLECULAR GENETIC EVIDENCE FOR RELATIONSHIPS AMONG  
91 GALAGID LINEAGES

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93 Genetic studies – from their earliest days – have consistently indicated that *Galagoidea* is  
94 polyphyletic, implying that the grouping based on morphological similarity is probably based

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2  
3 95 on plesiomorphic or homoplastic characters. The first such evidence came from allozymes  
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5 96 (Masters *et al.*, 1994), highly repeated DNA sequences (Crovella *et al.*, 1994) and 12S  
6  
7 97 ribosomal mitochondrial DNA sequences (rDNA; Bayes, 1998). All of these studies  
8  
9  
10 98 reconstructed the taxon called *Galagoides alleni* (*s.l.*) as the sister taxon to *Otolemur* spp.,  
11  
12 99 although morphological synapomorphies for this group remain elusive. The only shared  
13  
14 100 character Masters and Brothers (2002) identified from their dataset was large, square,  
15  
16 101 bunodont molars, indicative of a predominantly frugivorous diet and potentially homoplastic.  
17  
18 102 The first Zanzibar galago sequences were published by Del Pero *et al.* (2000). The specimen  
19  
20 103 sampled was probably *Gs granti*, as it had been collected in northern Mozambique, but was  
21  
22 104 classified as *Gs zanzibaricus* on the basis of craniodental morphometrics (Masters & Bragg,  
23  
24 105 2000). Using partial sequences of three mitochondrial genes (12S and 16S rDNA and  
25  
26 106 cytochrome *b*), DelPero and colleagues reconstructed *Gs demidoff* and so-called *Gs*  
27  
28 107 *zanzibaricus* as independent lineages that showed higher levels of genetic divergence from  
29  
30 108 one another than either lineage showed from any other galagid taxon in their sample of eight  
31  
32 109 taxa. This result, coupled with the alliance of *Gs alleni* with *Otolemur*, led DelPero *et al.*  
33  
34 110 (2000) to describe the genus *Galagoides* as a “wastebasket taxon of plesiomorphic species”.  
35  
36 111 This contention has been supported by more recent and more comprehensive studies. The  
37  
38 112 squirrel galagos continue to be recovered as the sister to the *Otolemur* clade, and Gray’s  
39  
40 113 (1872) genus, *Sciurocheirus*, has been resuscitated (Grubb *et al.*, 2003; Masters *et al.*, 2007).  
41  
42 114 Despite the paucity of morphological synapomorphies for this grouping, it derives support  
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44 115 from the sparse fossil record. Wesselman (1984) described a fossil hypodigm from  
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46 116 approximately 3 Myr sediments in Ethiopia that comprises a fragmentary maxilla, an isolated  
47  
48 117 M<sub>2</sub>, and an edentulous mandible. On the basis of its bunodont teeth and its intermediate size  
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50 118 between *Otolemur* and *Sciurocheirus*, he interpreted the taxon (now termed *O. howelli*;  
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3 119 Harrison, 2010) as a member of the *Sciurocheirus/Otolemur* clade, with its closest affinities  
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5 120 to *Otolemur*.  
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7

8 121 Following the removal of the squirrel galagos from *Galagoides*, the western and  
9  
10 122 eastern dwarf galagos have continued to be reconstructed as paraphyletic or even  
11  
12 123 polyphyletic in molecular analyses, indicating that the genus still includes two independent  
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14 124 clades that did not share an exclusive common ancestor. The western clade comprises the  
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16 125 “true” dwarf galagos, *Gs demidoff* and *Gs thomasi*, and the eastern clade includes *Gs*  
17  
18 126 *zanzibaricus* and its allies. Using complete sequences of the cytochrome *b* gene, Roos *et al.*  
19  
20 127 (2004) recovered *Gs demidoff* as the first galagid lineage to diverge, and *Gs zanzibaricus* as  
21  
22 128 the sister taxon of *Galago*, a topology supported by Chatterjee *et al.* (2009) and Fabre *et al.*  
23  
24 129 (2009). The tree of Masters *et al.* (2007) also depicted *Galagoides* as polyphyletic, but did  
25  
26 130 not group *Gs zanzibaricus* with the genus *Galago*. More recently, a more comprehensive  
27  
28 131 phylogenetic study of primates supported a sister taxon relationship between the Zanzibar  
29  
30 132 galagos and the *Otolemur/Sciurocheirus* clade, with *Gs demidoff* and *Gs thomasi* again  
31  
32 133 forming an independent clade (Springer *et al.*, 2012).  
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38 134 The disagreement among these studies regarding the phylogenetic placement of the  
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40 135 eastern and western lineages may be related to incomplete lineage sorting (or the failure of  
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42 136 two or more lineages in a population to coalesce, leading one of the lineages to coalesce first  
43  
44 137 with a lineage from a less closely related population), or possibly past introgression events, as  
45  
46 138 they were all based solely on mitochondrial sequences. To address this problem, Pozzi *et al.*  
47  
48 139 (2014) assembled a molecular dataset including 27 independent nuclear loci and inferred  
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50 140 phylogenetic relationships also using coalescent-based species tree methods to account for  
51  
52 141 incomplete lineage sorting. Their results strongly confirmed the polyphyletic status of  
53  
54 142 *Galagoides*, as well as a sister-taxon relationship between the eastern clade and the lesser  
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56 143 galagos (*Galago* spp.). The largest molecular dataset compiled for galagids to date, combining  
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3 144 53 nuclear loci and three mitochondrial genes, confirmed these results (Pozzi, 2016). Figure 1  
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5 145 represents our current understanding of relationships among the loroid primates based on  
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7 146 both nuclear and mitochondrial sequence data, derived from the studies of Pozzi *et al.*, (2014,  
8  
9 147 2015) and Pozzi (2016).

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13 148 [FIGURE 1 ABOUT HERE]

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16 149 Despite these large nuclear datasets, the sister-group relationships of two eastern  
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18 150 dwarf galagos, *Galagoides rondoensis* and *Gs orinus*, remain unresolved because of limited  
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20 151 representative specimens and genetic data; a handful of specimens is distributed across  
21  
22 152 museum collections in North America and Europe. A molecular study based on complete  
23  
24 153 mitochondrial cytochrome *b* sequences strongly supported an affinity between these species  
25  
26 154 and the Zanzibar galagos to the exclusion of the western *Galagoides* clade (Pozzi *et al.*,  
27  
28 155 2015), leading us to include them in the proposed new genus, which hence comprises five  
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30 156 species distributed in forests east of the African rift and distinct from the true dwarf galagos,  
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32 157 *Gs demidoff* and *Gs thomasi*, in the west (Figure 2).

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36 158 [FIGURE 2 ABOUT HERE]

#### 37 38 39 159 OVERVIEW OF EVIDENCE FROM VOCAL REPERTOIRES

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42 160 Vocalisations are particularly important indicators of galagid diversity because, as nocturnal  
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44 161 animals, galagos do not rely on morphologically-encoded visual signals for the location and  
45  
46 162 attraction of conspecific mates. Many galagid species and species groups have been identified  
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48 163 on the basis of differences in loud calls (or advertisement calls), which has led to their being  
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50 164 grouped according to call structures: crescendo callers, scaling callers, rolling callers,  
51  
52 165 incremental callers and repetitive callers (Bearder *et al.*, 1996; Kingdon, 1997; Butynski *et*  
53  
54 166 *al.*, 2013). Like all characters that are crucial to specific-mate recognition, specific loud calls  
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3 167 are qualitatively different between closely related species, and the rapidity of their evolution  
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5 168 may obscure their phylogenetic signal at older levels of divergence (Masters, 2007). For  
6  
7 169 instance, rolling and crescendo calls are polyphyletic when compared with species  
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9  
10 170 relationships determined by molecular sequence data, indicating a degree of homoplasy:  
11  
12 171 *Galagoides granti* and *Gs cocos* are both described as crescendo callers (Bearder *et al.*, 1996;  
13  
14 172 Kingdon, 1997; Butynski *et al.*, 2013), whereas *Gs zanzibaricus*, which is reconstructed as  
15  
16 173 the sister taxon to *Gs cocos* (see Figure 1), is a rolling caller, just like *Gs rondoensis*. In  
17  
18 174 contrast to advertisement calls, anti-predatory calls tend to be highly conserved  
19  
20  
21 175 phylogenetically, making them more useful as grouping criteria at deeper phylogenetic levels.  
22  
23 176 Vocal homologies among the small-bodied galagos (i.e. excluding *Sciurocheirus* and  
24  
25 177 *Otolemur* spp.) can be identified in at least three call types: two anti-predatory calls (mobbing  
26  
27 178 yaps and buzzy alarms; Génin *et al.*, 2016) and the loud socio-territorial calls. These vocal  
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29 179 homologies are congruent with phylogenetic relationships among these lineages indicated by  
30  
31 180 molecular analyses, and further justify the creation of a new genus for the eastern dwarf  
32  
33 181 galagos.

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36  
37 182 *Mobbing yaps*. The mobbing yap is emitted by all small-bodied galagos under similar  
38  
39 183 contexts, and is often recorded while an animal is circling around to face the observer (FG,  
40  
41 184 personal observations). It appears to be homologous to the loud call of *Euoticus* spp. (Figure  
42  
43 185 3). It is a high frequency atonal call repeated at frequent intervals, often after the emission of  
44  
45 186 a few buzzy alarms. The wide frequency range covered by the call that makes it sound atonal  
46  
47 187 to human ears is due to very rapid modulation that is likely to be perceived by the animals.

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50 [FIGURE 3 ABOUT HERE]  
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53 189  
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55 190 *Buzzy alarms*. Buzzy alarms are homologous in *Galagoides*, *Galago* and the eastern dwarf  
56  
57 191 galagos, but have very different structures in the three groups (Figure 3). Buzzy alarms are  
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2  
3 192 often the first indicator of the presence of an animal that has not yet been detected visually  
4  
5 193 (FG, personal observations). Animals emit several buzzy alarms that may precede or alternate  
6  
7 194 with yaps. The call is bi-syllabic, consisting of an initial high frequency unit followed by a  
8  
9  
10 195 highly modulated, lower frequency screech. In western *Galago* spp. the buzz is extremely  
11  
12 196 brief. In *Galago* spp. it is a brief, noisy, low frequency cough-like call (cho-ha). In the eastern  
13  
14 197 dwarf galago species, the buzz is a long screech peculiar to the group.  
15

198

199 *Loud calls.* Loud calls are far more variable between taxa than anti-predatory calls. Each of  
200 the three small-bodied genera emits a different kind of loud call associated with different  
201 contexts, indicating that the various calls evolved different functions associated with different  
202 habitats and socio-territorial systems. On the basis of our own observations as well as those  
203 of other authors (Bearder *et al.*, 1996; Kingdon, 1997; Butynski *et al.*, 2013), western  
204 *Galago* spp. are crescendo callers; the crescendo either consists of a single trill (*Gs*  
205 *demidoff*) or a short sequence of trills (*Gs thomasi*), starting with an increase in pitch and  
206 amplitude (overtone crescendo) followed by repeated, insect-like, high frequency clicks  
207 (Figure 3). The call is typically used as a gathering call emitted when animals leave or return  
208 to their nests. Lesser galagos (*Galago* spp.) are repetitive callers. They have low frequency  
209 metronomic and tonal calls which are emitted throughout the night, indicating a territorial  
210 function. Homology between the loud calls of eastern dwarf galago species and *Galago*  
211 crescendo calls is difficult to establish, but such homology with *Galago* repetitive calls is  
212 clear, as they share a basic temporal structure of repeated units forming syllables.

213 The loud calls emitted by eastern dwarf galagos are so variable that they are difficult  
214 to characterise. The group could be called the “varied callers” or “modulated callers”, as their  
215 loud calls consist of repeated, highly modulated units emitted at higher frequency than  
216 *Galago* repetitive calls. Their function is also less clear, as they are given when animals leave

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2  
3 217 or return to their sleeping sites, as well as throughout the night when animals interact. The  
4  
5 218 calls could hence be categorised as long distance contact calls adapted to habitats that are  
6  
7 219 generally drier than those of western *Galago*ides, but wetter and more closed than *Galago*  
8  
9 220 habitats (Génin *et al.*, 2016). The specific diversity of this group still requires investigation,  
10  
11 221 as only three call structures (scaling, rolling and incremental) have been described for at least  
12  
13 222 five species.  
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### 19 224 MORPHOLOGICAL DIFFERENTIATION: NEW ANALYSES

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21 225 Morphological characterization of the eastern dwarf galagos has been complicated not only  
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23 226 by the scarcity of exemplars of some species, but also by their strong convergence with  
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25 227 members of the western clade. In a canonical variate morphometric analysis, the skulls of the  
26  
27 228 type specimens of *Gs orinus* and *Gs rondoensis* clustered with the western clade,  
28  
29 229 contradicting their genetic affinity to *Gs granti* and *Gs zanzibaricus* (Masters & Couette,  
30  
31 230 2015). In an attempt to resolve this contradiction, we searched through museum collections in  
32  
33 231 the USA and Europe, and identified seven probable *Gs rondoensis* specimens in addition to  
34  
35 232 the type specimen held in the Natural History Museum, London. Their identification was  
36  
37 233 based on three factors: the consistent presence of a square M<sup>3</sup> with a very small hypocone (a  
38  
39 234 very rare occurrence in other eastern dwarf galagos); collection locality (east of the Rift); and  
40  
41 235 a disjunction between the completion of the eruption of the permanent dentition and skull  
42  
43 236 maturation. In most galagid genera the attainment of adult body size occurs shortly after the  
44  
45 237 complete eruption of the adult dentition. In the putative *Gs rondoensis* specimens we  
46  
47 238 identified, animals with adult (and often worn) dentition had unfused cranial sutures, and are  
48  
49 239 likely to have continued to grow had their lives not been prematurely ended. Groves (2001)  
50  
51 240 based his assessment of *Gs rondoensis* as the smallest living galagid on the type specimen  
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53 241 which had a body weight of 60 g, but animals trapped in the field may be 20 – 25 g heavier  
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3 242 (Andrew Perkin, personal communication). The type specimen has its permanent dentition,  
4  
5 243 but its morphology is juvenile, and fully grown members of this species are likely to be larger  
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7 244 than *G. orinus* adults.  
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10 245 *Materials and methods used in the new morphometric analyses.* In order to investigate the  
11  
12 246 morphological distinctiveness of the eastern dwarf galagos from other small-bodied galagids,  
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14 247 a set of 12 linear craniodental measurements was taken from 610 galago specimens including  
15  
16 248 western dwarf galagos (*Galagoides demidoff* and *Gs thomasi*, n = 322; see Masters &  
17  
18 249 Couette, 2015 for specimen list), lesser galagos (*Galago moholi*, n = 150) and squirrel  
19  
20 250 galagos (*Sciurocheirus alleni*, *s.l.*, n = 58), plus specimens formerly identified as *Galagoides*  
21  
22 251 *cocos*, *Gs granti*, *Gs orinus*, *Gs rondoensis*, *Gs udzungwensis* and *Gs zanzibaricus* (n = 80).  
23  
24 252 Accession details of these specimens are listed in Table 1 of the supplementary data, and the  
25  
26 253 institutions in which mensural data were collected are listed in the Acknowledgements. We  
27  
28 254 followed the methodology of Masters & Couette (2015): measurements (Figure 4, Table 1)  
29  
30 255 were recorded using digital callipers, and the sample was composed only of specimens with  
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32 256 fully erupted dentition.  
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38 257 [FIGURE 4 ABOUT HERE]

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40  
41 258 [TABLE 1 ABOUT HERE]

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44 259 Raw data were size-adjusted using the Burnaby (1966) procedure which consists of  
45  
46 260 extracting an isometric vector from the multivariate dataset and back-projecting the values in  
47  
48 261 a multivariate subspace orthogonal to this vector (Klingenberg, 1996). The geometric mean  
49  
50 262 (GM) was computed using the isometric vector and served as a proxy for size. Thus size  
51  
52 263 (GM) and shape (size corrected variables = shape variables) are considered independently  
53  
54 264 through ANOVA (size) or MANOVA, PCA and CVA (log transformed values of shape). We  
55  
56 265 performed a Between Group Principle Component Analysis (BGPCA, Mitteroecker &  
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3 266 Bookstein, 2011), which is a classic PCA based on the mean values for each group with no  
4  
5 267 regard for intragroup variation. Specimens are then back-plotted in the morphospace by  
6  
7 268 multiplying the morphological data matrix (log transformed values of shape) by the  
8  
9 269 coefficient of the BGPCA; the PCs are computed only on the intergroup variation rather than  
10  
11 270 on a mix of intra- and intergroup variation. All statistics were performed with R 3.0.2.  
12  
13 271 software (R Core Team, 2013) and the packages “candisc” (Friendly & Fox, 2015), “car” (Fox  
14  
15 272 & Weisberg, 2011), “geomorph” (Adams & Otarola-Castillo, 2013) and “smatr” (Warton *et*  
16  
17 273 *al.*, 2012).

20  
21 274 *Results of the morphometric analyses.* MANOVA results attested to significant differences in  
22  
23 275 cranial morphology among genera (Pillai Trace = 1.84,  $F = 86.09$ ,  $df = 33$ ,  $p < 0.001$ ). In the  
24  
25 276 BGPCA, three PCs summed up the entire variation in our sample: PC1, PC2 and PC3  
26  
27 277 accounted for 88.9%, 9.91% and 1.19%, respectively. The genera *Galago*, *Galagoides* and  
28  
29 278 *Sciurocheirus* were well separated in the PC1 x PC2 morphospace, with no overlap except for  
30  
31 279 some outlier specimens (Figure 5). The presence of outliers and the degree of dispersion  
32  
33 280 evident in Figure 5 may mean that some subadult skulls were included, along with their  
34  
35 281 correlated allometric shape differences. The cranial morphology of *Galagoides* individuals  
36  
37 282 was clearly different from that of the *Galago* specimens, and the differences constituted the  
38  
39 283 major variation along PC1. On this axis all of the variables had similar loadings (values  
40  
41 284 between -0.24 and 0.07) except for premaxillary length, for which the loading was very high  
42  
43 285 (0.91); hence the greater part of variation along PC1 was due to differences in the length of  
44  
45 286 the tip of the muzzle. PC2 separated the genus *Sciurocheirus* (positive values) and the genera  
46  
47 287 *Galago* and *Galagoides* (negative values). The variation along PC2 was mainly structured by  
48  
49 288 Cheek Tooth Width, Snout Length and Toothcomb Length, with positive values, and  
50  
51 289 Temporal Constriction, Supraoccipital Length and Mastoid Width, with negative values. The  
52  
53 290 eastern dwarf galagos showed intermediate cranial morphologies, and fell between *Galago*  
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3 291 and *Galagoides* on PC1 and between *Sciurocheirus* and the group composed of *Galago* and  
4  
5 292 *Galagoides* on PC2. Although the three groups were clearly distinguished on PC1, they  
6  
7 293 overlapped on PC2. The putative *Gs rondoensis* specimens were scattered in the space  
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9  
10 294 between the eastern dwarf species and *Galagoides*, and their variation in body size was  
11  
12 295 evident (Figure 5); despite our best efforts, it is possible our sample included representatives  
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14 296 of more than one species. The *Gs orinus* specimens formed part of the main eastern dwarf  
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16 297 cluster, although they overlapped with some *Gs rondoensis* specimens.  
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18

19 [FIGURE 5 ABOUT HERE]  
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22 299 Canonical Discriminant Analysis defined three significant canonical axes, accounting  
23  
24 300 for 70.98%, 27.06% and 1.96% of interclass variation (Figure 6). The variable Premaxilla  
25  
26 301 contributed the main discrimination along the first axis. The four genera were well  
27  
28 302 individualised on the first two axes, with high percentages of correct classification: 100% for  
29  
30 303 *Galago*, 98.14% for *Galagoides*, 91.3% for the eastern dwarf galagos and 86% for  
31  
32 304 *Sciurocheirus*. As is evident in visual comparisons of skulls, the elongation of the premaxilla  
33  
34 305 is greatest in *Galagoides*, smaller in the eastern dwarf galagos and smallest in *Galago*  
35  
36 306 (TukeyHSD post hoc test  $p$  values  $< 0.01$  among these genera), but the difference in  
37  
38 307 premaxillary length between the eastern dwarf galagos and *Sciurocheirus* was not significant.  
39  
40 308 The variables with highest loading on the second axis were Total Skull Length, Snout Length  
41  
42 309 and Cheek Tooth Width. The eastern dwarf galagos differed significantly in Snout Length  
43  
44 310 from *Galago* and *Sciurocheirus*, but not from *Galagoides*. All of the genera differed  
45  
46 311 significantly in Cheek Tooth Width, with values increasing from *Galago* through *Galagoides*  
47  
48 312 to the eastern dwarfs and finally *Sciurocheirus*, the large bunodont molars of which evince its  
49  
50 313 affinity to *Otolemur* spp. A similar trend is noticeable for Total Skull Length measurements,  
51  
52 314 with the smallest values in *Galagoides*, increasing in *Galago* and the eastern dwarfs, and with  
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54 315 *Sciurocheirus* having the longest skulls. As in the BGPCA analysis, the *Gs rondoensis*  
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3 316 specimens occupied the morphospace between the eastern dwarf galagos and *Galagoides*,  
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5 317 while *Gs orinus* was more closely grouped with the eastern dwarf species. Specimens of *Gs*  
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7 318 *rondoensis* and *Gs orinus* show intermediate morphology and overlap with eastern dwarf  
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9  
10 319 galagos and specimens of the genus *Galagoides*.

11  
12 [FIGURE 6 ABOUT HERE]  
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14  
15 321 An ANOVA of skull size repeats the pattern shown by Total Skull Length (p value <  
16  
17 322 0.001 and all Tukey HSD multiple comparison of means p values below 0.001). In order to  
18  
19 323 test the relationship of size (GM) and shape (logged size corrected variable), we performed a  
20  
21 324 multivariate regression considering the effect of size on shape, genus and the interaction  
22  
23 325 between size and genus. We used a Type II ANOVA to test each term of the linear model.  
24  
25 326 Size, genus and the interaction had a significant effect on shape with p values below 0.001,  
26  
27 327 attesting that shape variation is explained by size variation (allometry). The common  
28  
29 328 allometry, that is the proportion of shape explained by size across the entire sample, was  
30  
31 329 77.7%, but considering the allometric vectors for each genus yielded much lower values: size  
32  
33 330 accounted for 15.1% of shape variation in *Galago*, 20% in *Galagoides*, 13.8% in the eastern  
34  
35 331 dwarfs and 8.7% in *Sciurocheirus*. Pairwise comparison of multivariate allometric patterns  
36  
37 332 demonstrated significant differences between the eastern dwarfs and *Galago* (p value of angle  
38  
39 333 between allometric vectors = 0.0428), *Galagoides* (p = 0.019) and *Sciurocheirus* (p = 0.014)  
40  
41 334 (Figure 7). With respect to univariate differences in allometries among genera, *Sciurocheirus*  
42  
43 335 presented a very different pattern from all other genera: the allometric slopes of the variables  
44  
45 336 SL, CH, FL, CTW, PW, MW, TC, and P were all significantly different. The eastern dwarf  
46  
47 337 galagos differed in slope from *Galago* for variables SL and CTW, and from *Galagoides* for  
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49 338 variables IC, CTW, TSL and P.  
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56 339 [FIGURE 7 ABOUT HERE]  
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3 340 *Sciurocheirus* is hence clearly differentiated in both size and shape. Comparing the  
4  
5 341 three smaller-sized genera, our multivariate analyses indicated marked differences in cranial  
6  
7 342 shape among them. From a univariate perspective, the eastern dwarf group differed mainly in  
8  
9 343 Supraoccipital Length (intermediate between *Galago* and *Galagoides*), Interorbital  
10  
11 344 Constriction, Cheek Teeth Width and Total Skull Length (higher values in the eastern dwarf  
12  
13 345 group). These morphometric differences reinforce our proposal to distinguish the eastern  
14  
15 346 dwarf galagos from *Galago* and *Galagoides* at the generic level.  
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22 348 SYSTEMATICS

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25 349 *Paragalago gen. nov.*  
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29 350 TYPE SPECIES: *Galago zanzibaricus* Matschie, 1893.  
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32 351 INCLUDED SPECIES: *Galago granti* Thomas & Wroughton, 1907; *Galago cocos* Heller,  
33  
34 352 1912; *Galago demidovii orinus* Lawrence & Washburn, 1936; *Galagoides udzungwensis*  
35  
36 353 Honess, 1996; *Galagoides rondoensis* Honess, 1996.  
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38

39 354 **DIAGNOSIS:** Medium to small sized galagos (60 – 250 g), overlapping in size with *Galago*  
40  
41 355 spp. and notably smaller than *Sciurocheirus*, *Euoticus* and *Otolemur* spp. Two species  
42  
43 356 (*Paragalago orinus* and *P. rondoensis*) show convergence in shape and size with *Galagoides*  
44  
45 357 spp. Cranium ovoid in shape, narrowing posteriorly so that the pneumatized mastoids  
46  
47 358 protrude. Premaxillaries protracted into a short tube that extends beyond lower jaw, as in  
48  
49 359 *Galagoides* and *Sciurocheirus*; the tubular extension in *Paragalago* is intermediate in length  
50  
51 360 between the premaxillary tubes of the smaller and larger taxa. Anterior upper premolar (P<sup>2</sup>)  
52  
53 361 double-rooted, slender but distally trenchant, as in *Galagoides*, not caniniform as in *Euoticus*  
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55 362 and some *Galago* spp. Upper posterior premolars (P<sup>4</sup>s) are slightly larger than upper posterior  
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3 363 molars ( $M^3$ s) in most *Paragalago* specimens examined. In *Galago*  $M^3$  is either larger or  
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5 364 equivalent in size to  $P^4$ , while in *Galago*  $M^3$  is much reduced. In *Paragalago* spp. the  $M^3$   
6  
7 365 hypocone is absent or minute, but commonly observed in *Galago* spp. Coronoid  
8  
9 366 processes delicate and curved, extending almost as far back as glenoid process, as in  
10  
11 367 *Sciurocheirus* and *Galago*; not flattened and foreshortened, as in *Galago* and *Euoticus*.

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15 368 **Distribution east of the Great African Rift.**

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17  
18 369 DESCRIPTION: The snout is longer than in *Galago*, chiefly because premaxillaries extend  
19  
20 370 well beyond the lower jaw, although not to the degree seen in *Galago*. The facial profile  
21  
22 371 is distinctly concave (Schwarz, 1931) as in *Galago* and *Sciurocheirus*, not straight or  
23  
24 372 slightly convex as in *Galago*. Canines are slender. Anterior palatal foramina intrude between  
25  
26 373 medial upper incisors, as in most galagid taxa.  $P_4$ s fully molarised as in all crown galagids. In  
27  
28 374 most *Paragalago* specimens examined, the  $M^3$  had no hypocone, although a minute  
29  
30 375 hypocone was present in some specimens from the Rondo Forest (probably *P. rondoensis*).  
31  
32 376 The degree of basicranial flexion is moderate, as seen in *Galago*, *Otolemur* and  
33  
34 377 *Sciurocheirus*, not markedly flexed as in *Euoticus* and in *Galago*. Cranial shape is oblong as  
35  
36 378 in *Galago* and *Sciurocheirus*, not globular as in *Galago* and *Euoticus*. Postorbital bars are  
37  
38 379 generally slender, lacking the flanges sometimes seen in *Euoticus*, *Galago* and even  
39  
40 380 *Galago*, usually in older specimens. Lower anterior premolars ( $P_2$ ) are partially  
41  
42 381 procumbent, but not to the same degree as the tooth-comb, and never erect, as usually seen in  
43  
44 382 male *Galago* (Masters & Couette, 2015). Parietal muscle scars/crests on either side of the  
45  
46 383 medial suture outline a broad parietal plate over the orbits that narrows posteriorly.

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48  
49 384 The colour of the dorsal pelage is drab-brown to cinnamon with varying degrees of  
50  
51 385 rufous wash; outer surfaces of limbs similar to dorsum in colouration. Individual hairs are  
52  
53 386 slate grey near the root, contributing to the overall dark colouration. Hairs on ventrum and  
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3 387 inner surfaces of limbs also with grey roots but cream-buff to yellow-buff tips, and the throat  
4  
5 388 may be yellowish (Groves, 2001). The ears are dark brown to black, depending on the  
6  
7 389 species, and the tail varies from rufous brown to chocolate or even black. *Paragalago granti*  
8  
9  
10 390 and *P. orinus* have a darker tail tip. The cream to white nose stripe is emphasised by dark  
11  
12 391 brown to black eye rings. Mature males of all species have unidentate penile spines (Perkin,  
13  
14 392 2007). Species of *Paragalago* show behavioural differences that distinguish them in the field  
15  
16 393 from both *Galagoidea* and *Galago* taxa. Eastern dwarf galagos tend to leap more often than  
17  
18 394 *Galagoidea*, but not as frequently or extensively as *Galago* spp. Moreover, the three genera  
19  
20 395 can be readily distinguished by vocalisations that differ in structure, in context, and probably  
21  
22 396 in function.

23  
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26 397 NOTES: The new genus embraces several taxa originally allied with lesser or dwarf galagos,  
27  
28 398 depending on body size. *Paragalago zanzibaricus* was described by Paul Matschie (1893) as  
29  
30 399 a pale cinnamon-coloured lesser galago from western Zanzibar, although the species also  
31  
32 400 occurs on the Tanzanian mainland (see Figure 2). A recent conservation risk assessment  
33  
34 401 conducted by the Primate Specialist Group of the International Union for the Conservation of  
35  
36 402 Nature (IUCN) considered populations on small islands to be particularly vulnerable, and  
37  
38 403 deserving of subspecific recognition for the purpose of conservation monitoring. The  
39  
40 404 Zanzibar population of dwarf galagos was hence designated as the subspecies *P. z.*  
41  
42 405 *zanzibaricus*, while the mainland representatives of this species were classified as *P. z.*  
43  
44 406 *udzungwensis*. Preliminary genetic studies of mainland and island populations (Pozzi,  
45  
46 407 unpublished data) support their conspecific identity, but a more extensive comparison is  
47  
48 408 necessary to confirm this.

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53 409 *Paragalago cocos*, which is morphologically indistinguishable from *P. zanzibaricus*, was  
54  
55 410 described by Heller (1912) from the Kenyan mainland. *Paragalago granti*, with a type  
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57 411 locality in southern Mozambique, has the largest geographical range among representatives  
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3 412 of the genus, extending from the north-east of South Africa throughout Mozambique (and  
4  
5 413 possibly parts of Malawi, where it has been referred to under the rubric *Galagoides nyasae*  
6  
7 414 Elliot, 1907; Grubb *et al.*, 2003) into southern Tanzania. The type and only known skin of  
8  
9 415 *Galago mertensi* Frade, 1924 was collected at a locality not far west of the type locality of *P.*  
10  
11 416 *granti*, and has, rightly or wrongly, been subsumed under this species (Schwarz, 1931).

12  
13  
14  
15 417 The two smallest members of the genus, *P. orinus* and *P.rondoensis*, are the most  
16  
17 418 recent members of the eastern dwarf clade to have been accorded full species status.  
18  
19 419 *Paragalago orinus* is a montane endemic and occurs within a restricted habitat at high  
20  
21 420 altitude in the Udzungwa and Uluguru mountains of Tanzania. *Paragalago rondoensis* has a  
22  
23 421 highly fragmented range in scattered lowland forest patches throughout Tanzania, but is no  
24  
25 422 longer considered to be of critical conservation concern (A. Perkin, personal communication).  
26  
27 423 The apparent heterochronic disjunction between the eruption of adult dentition and the  
28  
29 424 cessation of growth in this species may explain why both it and the genus to which it belongs  
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31 425 have defied characterisation for so long.

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36 426 Our demonstration that the eastern dwarf galagos constitute a genus entirely distinct  
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38 427 from the western dwarf galagos reinforces the conclusions of Groves (in press) that the  
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40 428 Eastern Arc Mountains and the Swahilian (Tanzanian/northern Mozambique) coastal forests  
41  
42 429 constitute a separate subregion of the African fauna, the Zanj subregion. The Zanj  
43  
44 430 mammalian fauna is unique and restricted, and deserves the highest conservation priority.

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#### 49 50 51 432 ACKNOWLEDGEMENTS

52  
53 433 Our project was funded primarily by National Research Foundation grants 93924 awarded to  
54  
55 434 FG, and 92541 and 90772 awarded to JCM; grant number GB-TAF 4120 awarded by the  
56  
57 435 Synthesys Program to SC; and an ABIC grant awarded to JCM by the Royal Museum for  
58  
59  
60

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2  
3 436 Central Africa through a Framework Agreement with the Belgian Development Co-  
4  
5 437 operation. Our research was further made possible by the support of the hard-working  
6  
7 438 curators and collection managers of fifteen museums who kindly gave us access to their  
8  
9 439 specimens: American Museum of Natural History (AMNH, New York, USA); Carnegie  
10  
11 440 Museum of Natural History (CMNH, Pittsburgh, USA); Ditsong Natural History Museum  
12  
13 441 (Transvaal Museum; TM, Pretoria, South Africa); Field Museum of Natural History (FMNH,  
14  
15 442 Chicago, USA); Museum für Naturkunde (MFN, Berlin, Germany); Muséum national  
16  
17 443 d'Histoire naturelle (MNHN, Paris, France); Museum of Comparative Zoology (MCZ;  
18  
19 444 Harvard Museum of Natural History, Cambridge, USA); Natural History Museum (NHM,  
20  
21 445 London, UK); Royal Museum of Central Africa (RMCA, Tervuren, Belgium); National  
22  
23 446 Museum of Kenya (NMK, Nairobi, Kenya); Powell-Cotton Museum (PCM, Birchington,  
24  
25 447 UK); National Museum of Natural History (USNM, Smithsonian Institution, Washington  
26  
27 448 DC, USA); National Museum of Scotland (NMS, Edinburgh, UK); Naturmuseum  
28  
29 449 Senckenberg (SFR, Frankfurt-am-Main, Germany); Zoologisches Forschungsmuseum  
30  
31 450 Alexander Koenig (ZFMK, Bonn, Germany). We express our gratitude to two reviewers  
32  
33 451 whose suggestions improved the final text significantly, and to the colleagues who have  
34  
35 452 advised, assisted and encouraged us, particularly Simon Bearder, Iris Dröscher, Paula  
36  
37 453 Jenkins, Nokuthula Kom, John Oates, Andrew Perkin, Hajarimanitra Rambeloarivony,  
38  
39 454 Magdalena Svensson and Ayabulela Yokwana. This is publication no. 5 of the African  
40  
41 455 Primate Initiative for Ecology and Speciation (APIES).  
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3 588 **Figure legends**

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6 589 Figure 1: Phylogenetic relationships among galagos. The tree represents a summary of our  
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8 590 current understanding of relationships among the lorisooid primates based on both nuclear and  
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10 591 mitochondrial sequence data, derived from the studies of Pozzi *et al.* (2014, 2015) and Pozzi  
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12 592 (2016). The western dwarf galago clade is identified by a red rectangle, while the eastern  
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14 593 clade is enclosed within a blue square.

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18 594 Figure 2: Map showing approximate geographic ranges of the two independent dwarf galago  
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20 595 clades, *Galagoideus* (red) and the eastern dwarf galagos (blue). The type localities of the  
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22 596 species comprising the genera are indicated by symbols. In the case of *Galagoideus demidoffi*,  
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24 597 the type locality is estimated from Fischer's (1806) description.

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28 598 Figure 3: Sonograms of vocalisations emitted by small-bodied galagid species. Calls of  
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30 599 *Euoticus* (Cameroon) and *Galagoideus granti* (Tshanini, South Africa) were recorded by FG.  
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32 600 All other sonograms were downloaded from the East African Primate Diversity and  
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34 601 Conservation website (<http://www.wildsolutions.nl/vocal-profiles>).

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37 602 Figure 4: Schematic depiction of an eastern dwarf galago skull showing the 12 craniodental  
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39 603 measurements included in the multivariate morphometric analyses. Descriptions of the  
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41 604 variables are presented in Table 1.

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44 605 Figure 5: Between Group Principle Component Analysis (BGPCA) calculated on the twelve  
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46 606 shape variables. Crosses indicate the mean values of each group that defined the principle  
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48 607 component axes to analyse inter-group variation. Specimen data were back-projected in this  
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50 608 space. Specimens of the two smallest eastern taxa, *orinus* and *rondoensis*, are indicated.

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54 609 Figure 6: Canonical Variate Analysis of the twelve shape variables. Crosses indicate the  
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56 610 centroid of each group. The first two roots illustrate significant differences in skull shape  
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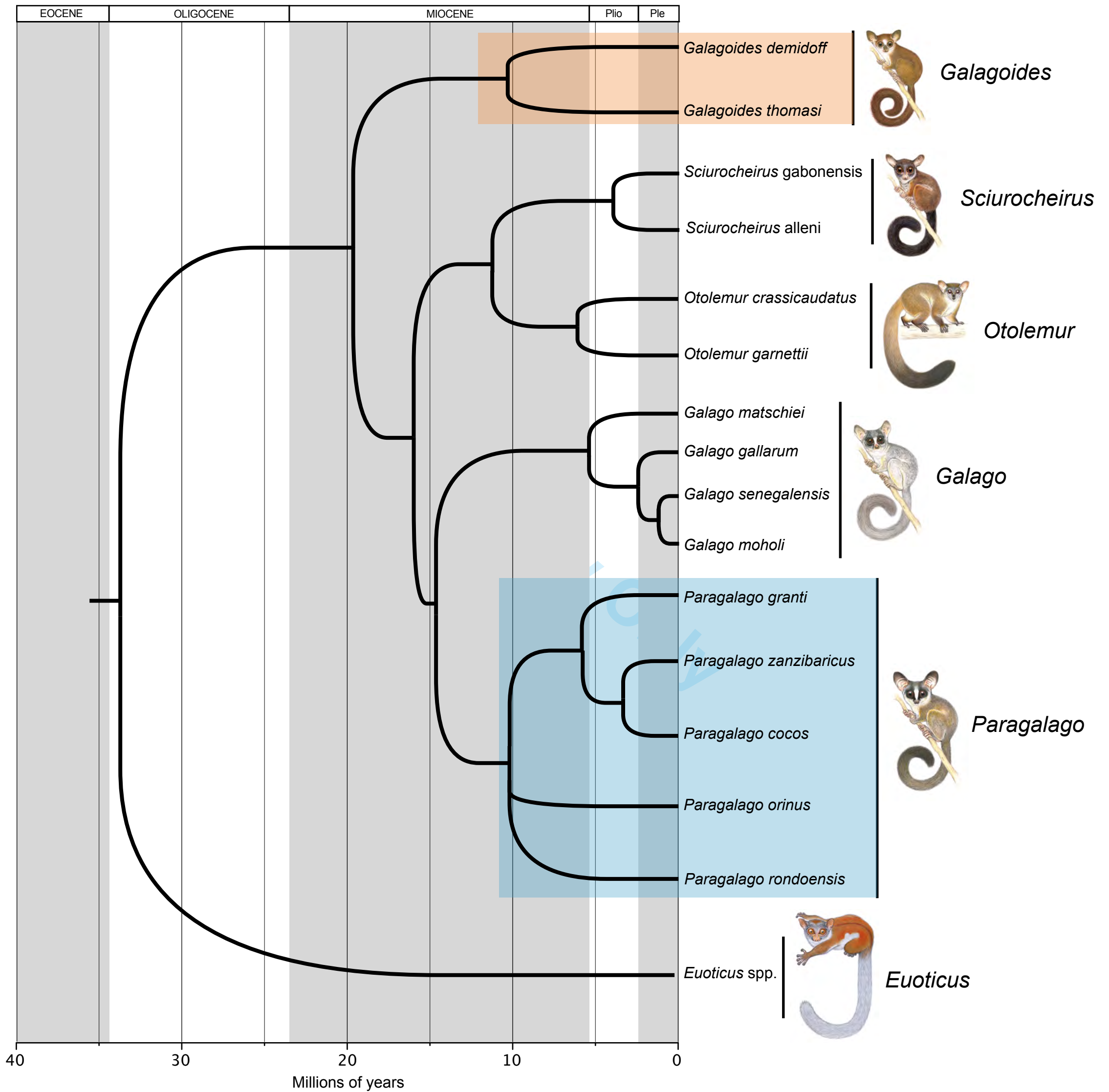
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10 614 PC1 against the log-transformed centroid size. The allometric patterns are different among  
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12 615 genera. Unlike the other genera, the eastern dwarf galago taxa do not show significant  
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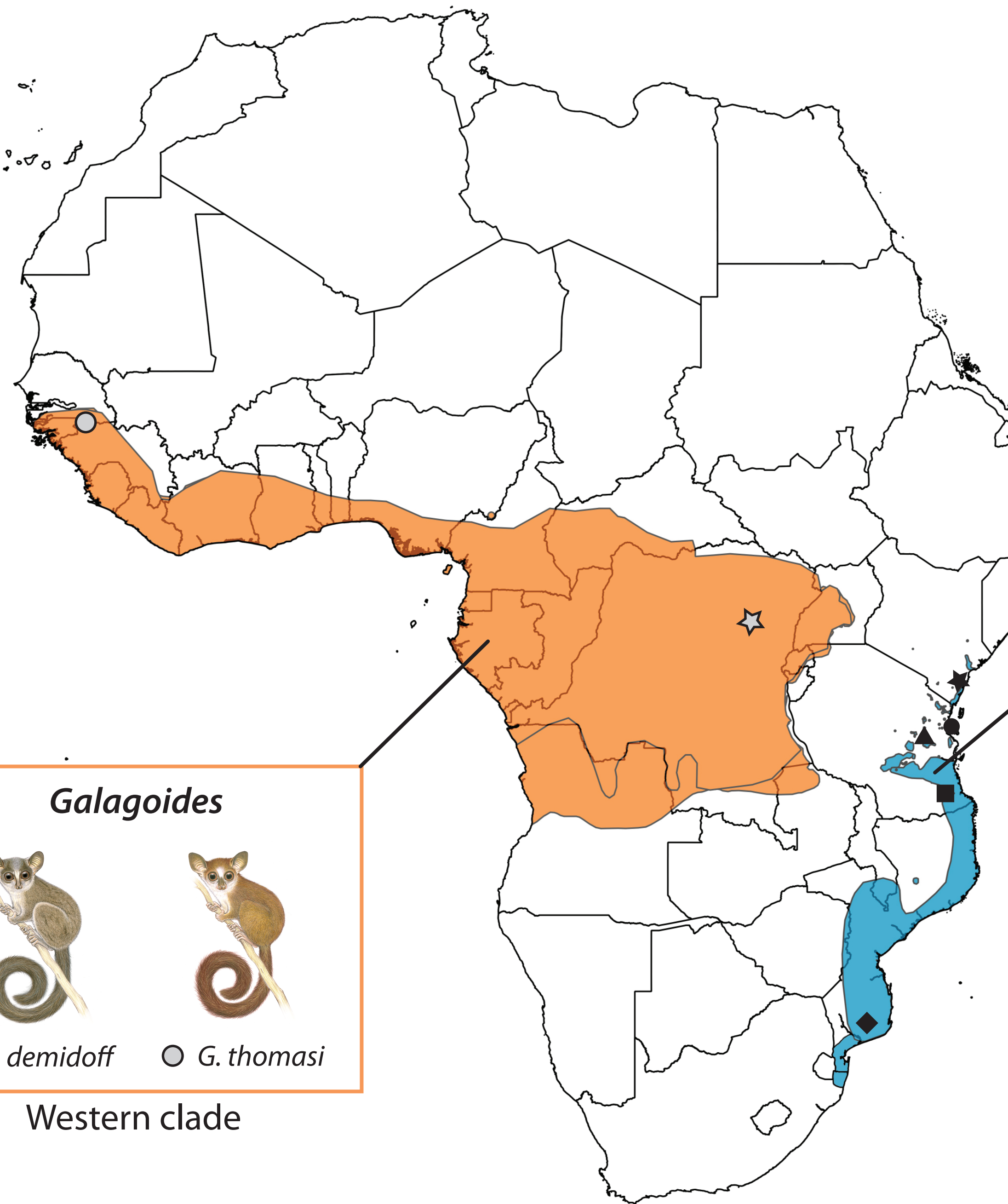
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21 618 Table 1: Cranial measurements used in the study (illustrated in figure 1)  
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**Paragalago**

★ *P. cocos*   ● *P. zanzibaricus*   ◆ *P. granti*

▲ *P. orinus*   ■ *P. rondoensis*

**Galagoides**

★ *G. demidoff*   ○ *G. thomasi*

Eastern clade

Western clade

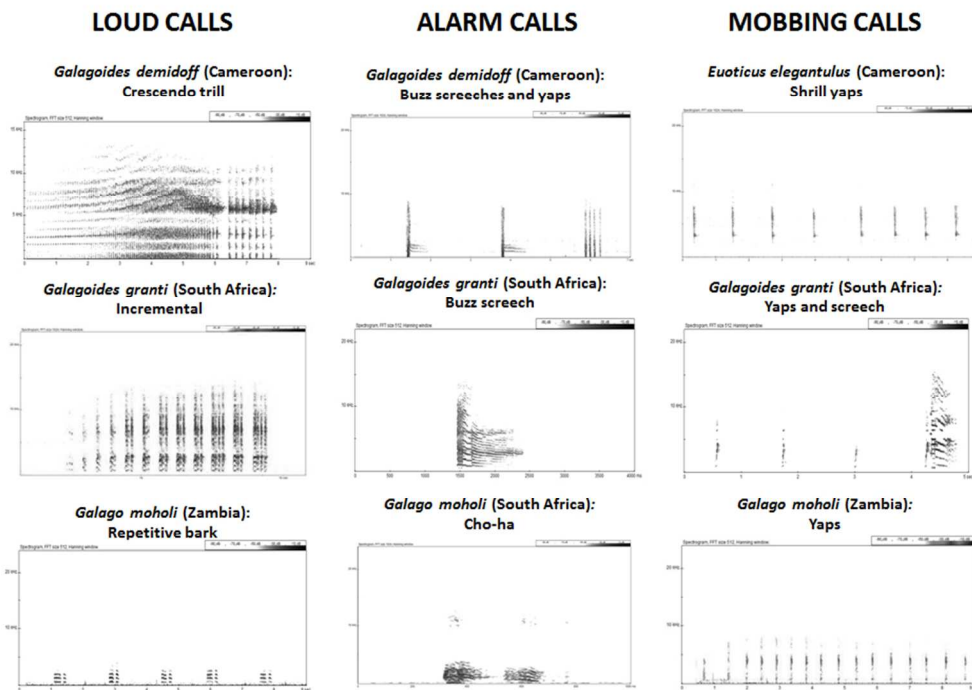


Figure 3: Sonograms of vocalisations emitted by small-bodied galagid species. Calls of *Eutoticus* (Cameroon) and *Galagoides granti* (Tshanini, South Africa) were recorded by FG. All other sonograms were downloaded from the East African Primate Diversity and Conservation website (<http://www.wildsolutions.nl/vocal-profiles>).

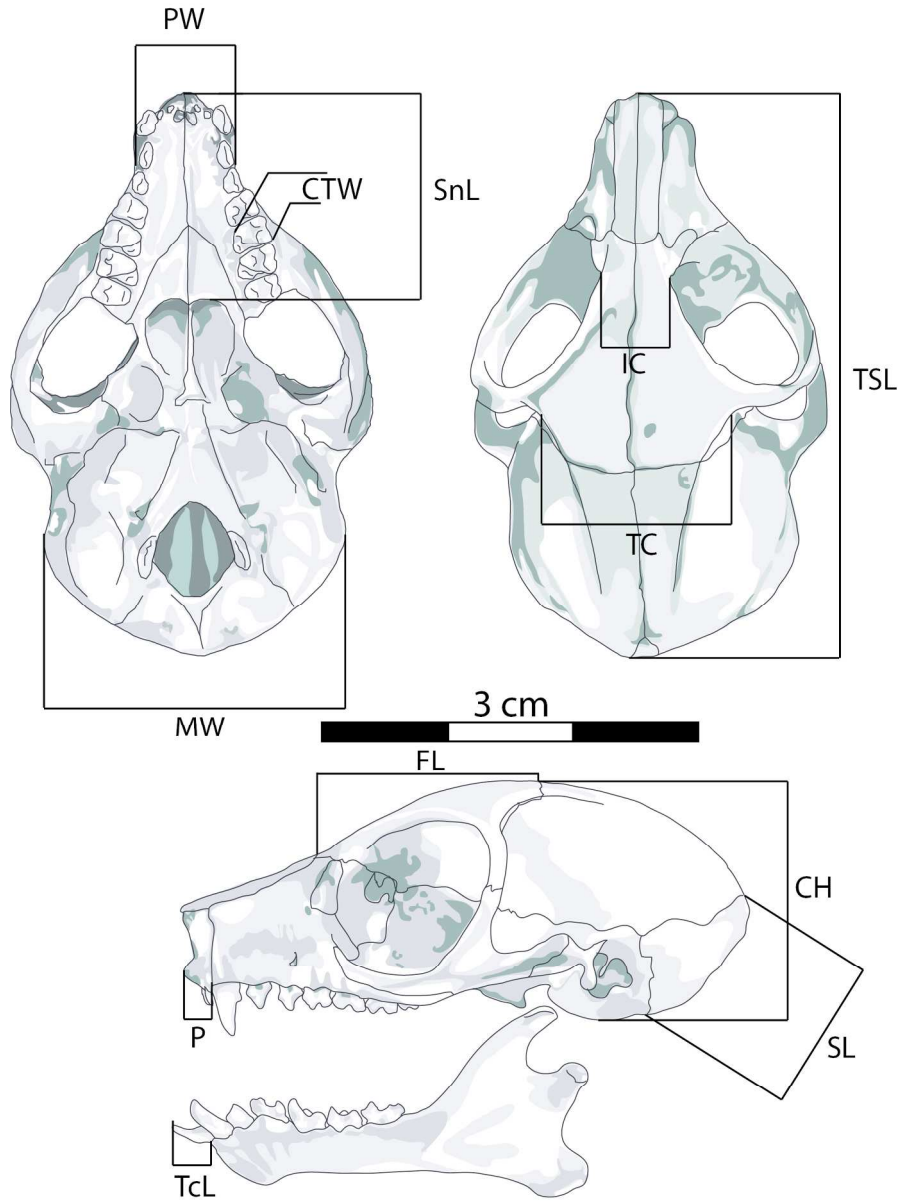


Figure 4: Schematic depiction of an eastern dwarf galago skull showing the 12 craniodental measurements included in the multivariate morphometric analyses. Descriptions of the variables are presented in Table 1.

163x220mm (300 x 300 DPI)

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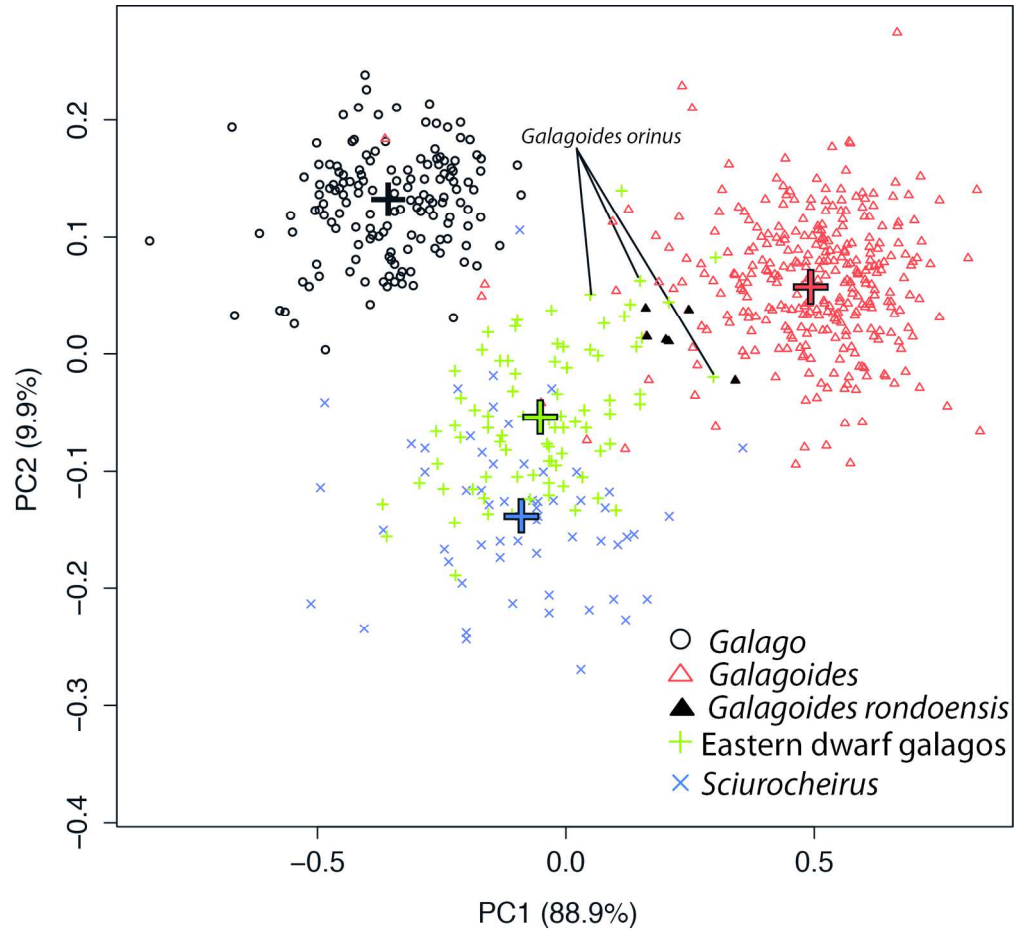


Figure 5: Between Group Principle Component Analysis (BGPCA) calculated on the twelve shape variables. Crosses indicate the mean values of each group that defined the principle component axes to analyse inter-group variation. Specimen data were back-projected in this space. Specimens of the two smallest eastern taxa, *orinus* and *rondoensis*, are indicated.

174x161mm (300 x 300 DPI)

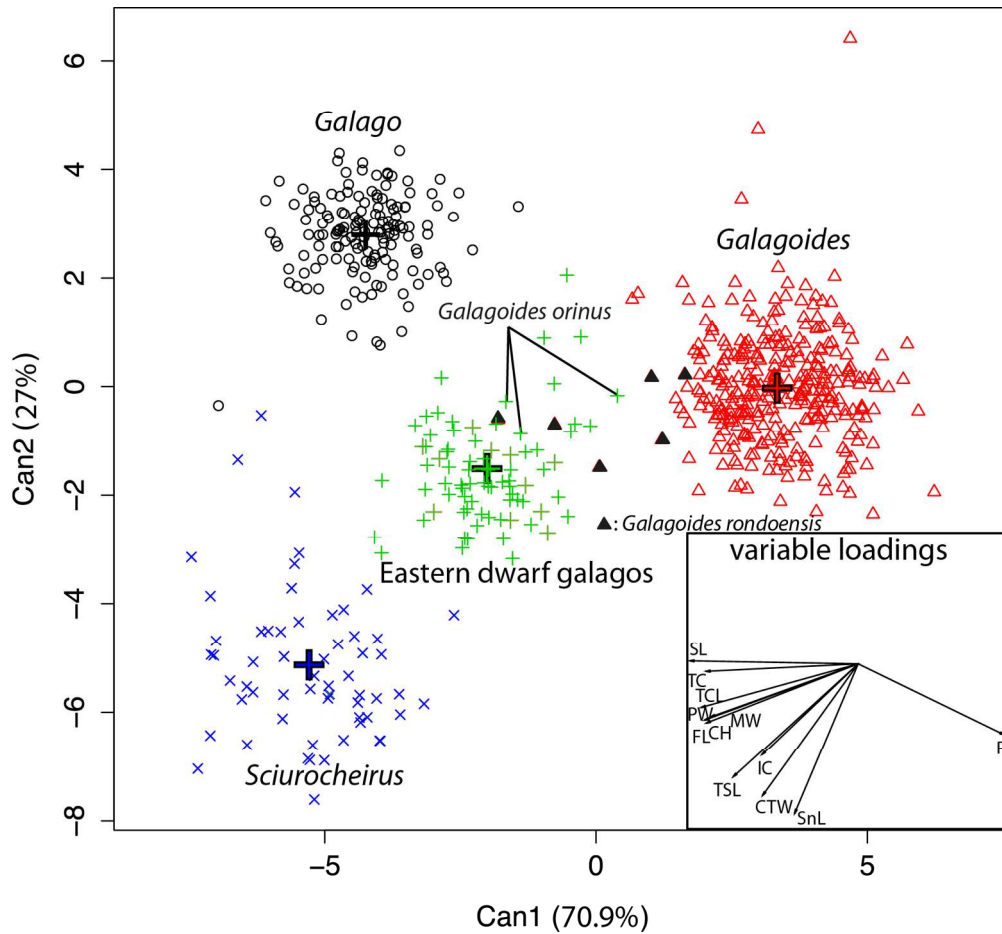


Figure 6: Canonical Variate Analysis of the twelve shape variables. Crosses indicate the centroid of each group. The first two roots illustrate significant differences in skull shape among genera. Specimens of the two smallest eastern taxa, *orinus* and *rondoensis*, are indicated.

160x152mm (300 x 300 DPI)

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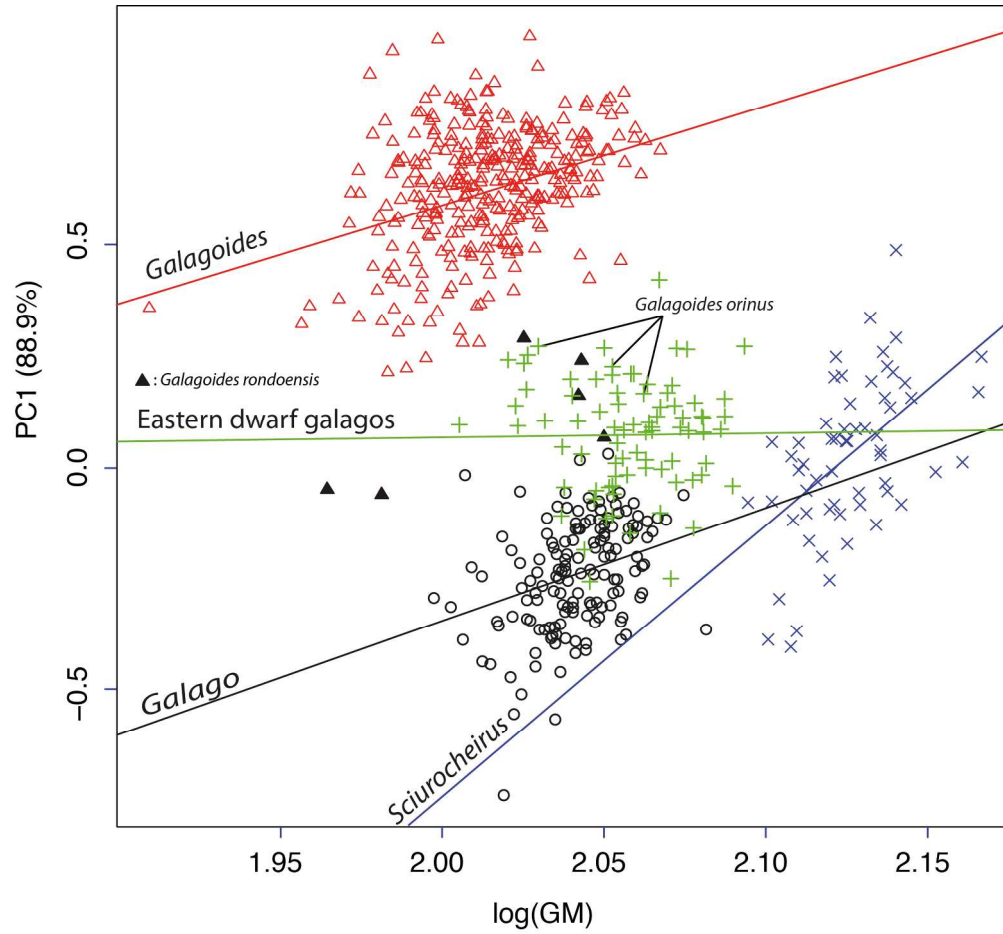


Figure 7: Allometric trajectories for each genus described by the linear regression of PC1 against the log-transformed centroid size. The allometric patterns are different among genera. Unlike the other genera, the eastern dwarf galago taxa do not show significant allometry. Specimens of the two smallest eastern taxa, *orinus* and *rondoensis*, are indicated.

201x187mm (300 x 300 DPI)

TABLE 1. Cranial measurements used in the study (illustrated in Figure 1)

| Abbreviation | Name                      | Definition   |
|--------------|---------------------------|--|
| SL           | Supraoccipital length     | From lambda to opisthion   |
| CH           | Cranial height            | From basioccipital-basisphenoid suture to the highest point of the braincase |
| FL           | Frontal length            | From bregma to nasion  |
| IC           | Interorbital constriction | Minimal distance between the inner margins of the orbits                     |
| CTW          | Cheek teeth width         | Maximum width of right M <sup>1</sup>  |
| PW           | Palate width              | Distance between labial margins of right and left P <sup>2</sup>             |
| TSL          | Total skull length        | From prosthion to opisthocranion   |
| SnL          | Snout length              | From prosthion to nasion   |
| MW           | Mastoid width             | Distance between left and right mastoid processes                            |
| TC           | Temporal constriction     | Minimum distance between left and right fronto-temporals                     |
| P            | Premaxilla                | Length of the premaxillary tube  |
| TCL          | Toothcomb length          | From the base to the tip of the incisors                                     |

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## Supplementary Information

Table 1. Eastern dwarf specimens included in the morphometric analysis of skulls

| Accession number | Genus             | Species           | Subspecies   |          |
|------------------|-------------------|-------------------|--------------|----------|
| FMNH 177220      | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NHM 6.11.8.5     | <i>Galagoides</i> | <i>granti</i>     |              | Paratype |
| NHM 6.11.8.6     | <i>Galagoides</i> | <i>granti</i>     |              | Paratype |
| NHM 6.11.8.7     | <i>Galagoides</i> | <i>granti</i>     |              | Type     |
| NHM 6.11.8.9     | <i>Galagoides</i> | <i>granti</i>     |              | Paratype |
| NHM 6.11.8.10    | <i>Galagoides</i> | <i>granti</i>     |              | Paratype |
| NHM 8.1.1.12     | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NHM 8.1.1.13     | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NHM 8.1.1.15     | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NHM 8.1.1.16     | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NHM 8.1.1.129    | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NHM 94.1.25.22   | <i>Galagoides</i> | <i>granti</i>     |              | Paratype |
| NMZ 28344        | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NMZ 67333        | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NMZ 67340        | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NMZ 67341        | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NMZ 67342        | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NMZ 67344        | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NMZ 67346        | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NMZ 67347        | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NMZ 67349        | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NMZ 67353        | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NMZ 67354        | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NMZ 67355        | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NMZ 67357        | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NMZ 67358        | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NMZ 67359        | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NMZ 67361        | <i>Galagoides</i> | <i>granti</i>     |              |          |
| NMZ 67362        | <i>Galagoides</i> | <i>granti</i>     |              |          |
| USNM 352253      | <i>Galagoides</i> | <i>granti</i>     |              |          |
| USNM 352254      | <i>Galagoides</i> | <i>granti</i>     |              |          |
| USNM 181810      | <i>Galago</i>     | <i>moholi</i>     | <i>cocos</i> | Type     |
| MCZ 22453        | <i>Galagoides</i> | <i>orinus</i>     |              | Type     |
| NHM 54.748       | <i>Galagoides</i> | <i>orinus</i>     |              |          |
| NHM 54.747       | <i>Galagoides</i> | <i>orinus</i>     |              |          |
| SFR 83201        | <i>Galagoides</i> | <i>orinus</i>     |              |          |
| MCZ 38875        | <i>Galagoides</i> | <i>rondoensis</i> |              |          |
| SFR 94901        | <i>Galagoides</i> | <i>rondoensis</i> |              |          |
| ZMB 8903         | <i>Galagoides</i> | <i>rondoensis</i> |              |          |
| ZMB 9130         | <i>Galagoides</i> | <i>rondoensis</i> |              |          |
| ZMB 9131         | <i>Galagoides</i> | <i>rondoensis</i> |              |          |
| NHM 64.1970      | <i>Galagoides</i> | <i>rondoensis</i> |              | Type     |

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| 3  | NHM 1995.251  | <i>Galagoides</i> | <i>udzungwensis</i>  | Type         |
| 4  | MCZ 26446     | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 5  | MCZ 26449     | <i>Galagoides</i> | <i>zanizibaricus</i> |              |
| 6  |               |                   |                      |              |
| 7  | MCZ 26451     | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 8  | ZMB 64201     | <i>Galagoides</i> | <i>zanzibaricus</i>  | Type         |
| 9  | AMNH 187362   | <i>Galagoides</i> | <i>zanzibaricus</i>  | <i>cocos</i> |
| 10 | CMNH 57948    | <i>Galagoides</i> | <i>zanzibaricus</i>  | <i>cocos</i> |
| 11 | CMNH 98107    | <i>Galagoides</i> | <i>zanzibaricus</i>  | <i>cocos</i> |
| 12 |               |                   |                      |              |
| 13 | CMNH 98108    | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 14 | MCZ 22449     | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 15 | MCZ 22450     | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 16 | MCZ 38911     | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 17 | MCZ 38912     | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 18 | MCZ 38915     | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 19 | NMK DM 4533   | <i>Galagoides</i> | <i>zanzibaricus</i>  | <i>cocos</i> |
| 20 | NMK DM 4537   | <i>Galagoides</i> | <i>zanzibaricus</i>  | <i>cocos</i> |
| 21 |               |                   |                      |              |
| 22 | NMK DM 4547   | <i>Galagoides</i> | <i>zanzibaricus</i>  | <i>cocos</i> |
| 23 |               |                   |                      |              |
| 24 | NHM 55.330    | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 25 | NHM 64.972    | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 26 | NHM 64.974    | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 27 | NHM 64.975    | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 28 | NHM 64.976    | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 29 | NHM 64.977    | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 30 | NHM 64.978    | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 31 | NHM 64.979    | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 32 |               |                   |                      |              |
| 33 | NHM 64.980    | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 34 | NHM 20.6.10.2 | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 35 | NHM 20.6.10.3 | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 36 |               |                   |                      |              |
| 37 | NHM 54.738    | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 38 | NHM 54.739    | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 39 | NHM 54.740    | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 40 | TM 45930      | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
| 41 | USNM 184218   | <i>Galagoides</i> | <i>zanzibaricus</i>  | <i>cocos</i> |
| 42 | USNM 184220   | <i>Galagoides</i> | <i>zanzibaricus</i>  | <i>cocos</i> |
| 43 | USNM 184221   | <i>Galagoides</i> | <i>zanzibaricus</i>  | <i>cocos</i> |
| 44 | USNM 184222   | <i>Galagoides</i> | <i>zanzibaricus</i>  | <i>cocos</i> |
| 45 | USNM 184224   | <i>Galagoides</i> | <i>zanzibaricus</i>  | <i>cocos</i> |
| 46 | USNM 241579   | <i>Galagoides</i> | <i>zanzibaricus</i>  |              |
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3 **Key to museums:**  
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5 **AMNH: American Museum of Natural History, New York, USA**  
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7 **CMNH: Carnegie Museum of Natural History, Pittsburgh, USA**  
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9 **FMNH: Field Museum of Natural History, Chicago, USA**  
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11 **MCZ: Museum of Comparative Zoology, Harvard Museum of Natural History, Cambridge**  
12 **MA, USA**  
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15 **NHM: Natural History Museum, London, UK**  
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17 **NMK: National Museum of Kenya, Nairobi, Kenya**  
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19 **NMZ: National Museum of Natural History, Bulawayo, Zimbabwe**  
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21 **SFR: Senckenberg Museum of Natural History, Frankfurt, Germany**  
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23 **TM: Ditsong Museum of Natural History (Transvaal Museum), Pretoria, South Africa**  
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25 **USNM: United States National Museum of Natural History (Smithsonian Institution),**  
26 **Washington DC, USA**  
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29 **ZMB: Museum of Natural History, Berlin, Germany**  
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