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

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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; *Galagoides* 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 *Galagoides* 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 *Galagoides* (*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 *Galagoides* – *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

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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
18
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
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26 56 employed subsequently by many authors (Honest & Bearder, 1996; Kingdon, 1997;
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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*,
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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 lorises, but
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3 71 not as strong as in the genera *Galago* or *Euoticus*), anterior upper premolar (P^2) not
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5 72 caniniform (sometimes with a hypocone), third upper molar (M^3) \geq posterior upper premolar
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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
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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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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
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7 97 ribosomal mitochondrial DNA sequences (rDNA; Bayes, 1998). All of these studies
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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
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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.
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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
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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
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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
43
44 115 from the sparse fossil record. Wesselman (1984) described a fossil hypodigm from
45
46 116 approximately 3 Myr sediments in Ethiopia that comprises a fragmentary maxilla, an isolated
47
48 117 M₂, 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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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
13
14 124 clades that did not share an exclusive common ancestor. The western clade comprises the
15
16 125 “true” dwarf galagos, *Gs demidoff* and *Gs thomasi*, and the eastern clade includes *Gs*
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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
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30 132 galagos and the *Otolemur/Sciurocheirus* clade, with *Gs demidoff* and *Gs thomasi* again
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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
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44 137 with a lineage from a less closely related population), or possibly past introgression events, as
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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
49
50 140 phylogenetic relationships also using coalescent-based species tree methods to account for
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52 141 incomplete lineage sorting. Their results strongly confirmed the polyphyletic status of
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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
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46 162 attraction of conspecific mates. Many galagid species and species groups have been identified
47
48 163 on the basis of differences in loud calls (or advertisement calls), which has led to their being
49
50 164 grouped according to call structures: crescendo callers, scaling callers, rolling callers,
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52 165 incremental callers and repetitive callers (Bearder *et al.*, 1996; Kingdon, 1997; Butynski *et*
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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:
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12 171 *Galagoides granti* and *Gs cocos* are both described as crescendo callers (Bearder *et al.*, 1996;
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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
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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
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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
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33 181 galagos.

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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
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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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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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3 192 often the first indicator of the presence of an animal that has not yet been detected visually
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5 193 (FG, personal observations). Animals emit several buzzy alarms that may precede or alternate
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7 194 with yaps. The call is bi-syllabic, consisting of an initial high frequency unit followed by a
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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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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*
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9 220 habitats (Génin *et al.*, 2016). The specific diversity of this group still requires investigation,
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11 221 as only three call structures (scaling, rolling and incremental) have been described for at least
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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
22
23 226 by the scarcity of exemplars of some species, but also by their strong convergence with
24
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 M³ with a very small hypocone (a
38
39 234 very rare occurrence in other eastern dwarf galagos); collection locality (east of the Rift); and
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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
52
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,
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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
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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
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16 248 western dwarf galagos (*Galagoides demidoff* and *Gs thomasi*, n = 322; see Masters &
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18 249 Couette, 2015 for specimen list), lesser galagos (*Galago moholi*, n = 150) and squirrel
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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)
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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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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
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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
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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*
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17 273 *al.*, 2012).

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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
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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
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51 289 Temporal Constriction, Supraoccipital Length and Mastoid Width, with negative values. The
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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
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5 292 *Galagoides* on PC2. Although the three groups were clearly distinguished on PC1, they
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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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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
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28 302 individualised on the first two axes, with high percentages of correct classification: 100% for
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30 303 *Galago*, 98.14% for *Galagoides*, 91.3% for the eastern dwarf galagos and 86% for
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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*
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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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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
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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
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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
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5 341 three smaller-sized genera, our multivariate analyses indicated marked differences in cranial
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7 342 shape among them. From a univariate perspective, the eastern dwarf group differed mainly in
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9 343 Supraoccipital Length (intermediate between *Galago* and *Galagoides*), Interorbital
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11 344 Constriction, Cheek Teeth Width and Total Skull Length (higher values in the eastern dwarf
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13 345 group). These morphometric differences reinforce our proposal to distinguish the eastern
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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,
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34 352 1912; *Galago demidovii orinus* Lawrence & Washburn, 1936; *Galagoides udzungwensis*
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36 353 Honess, 1996; *Galagoides rondoensis* Honess, 1996.
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39 354 **DIAGNOSIS:** Medium to small sized galagos (60 – 250 g), overlapping in size with *Galago*
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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 (P²)
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 (P⁴s) 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
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7 365 hypocone is absent or minute, but commonly observed in *Galago* spp. Coronoid
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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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18 369 DESCRIPTION: The snout is longer than in *Galago*, chiefly because premaxillaries extend
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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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49 384 The colour of the dorsal pelage is drab-brown to cinnamon with varying degrees of
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51 385 rufous wash; outer surfaces of limbs similar to dorsum in colouration. Individual hairs are
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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
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5 388 may be yellowish (Groves, 2001). The ears are dark brown to black, depending on the
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7 389 species, and the tail varies from rufous brown to chocolate or even black. *Paragalago granti*
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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 *Galago* and *Galago* taxa. Eastern dwarf galagos tend to leap more often than
17
18 394 *Galago*, 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.

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26 397 NOTES: The new genus embraces several taxa originally allied with lesser or dwarf galagos,
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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
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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.*
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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
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48 408 necessary to confirm this.

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53 409 *Paragalago cocos*, which is morphologically indistinguishable from *P. zanzibaricus*, was
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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
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5 413 possibly parts of Malawi, where it has been referred to under the rubric *Galagoides nyasae*
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7 414 Elliot, 1907; Grubb *et al.*, 2003) into southern Tanzania. The type and only known skin of
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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).

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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.
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19 419 *Paragalago orinus* is a montane endemic and occurs within a restricted habitat at high
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21 420 altitude in the Udzungwa and Uluguru mountains of Tanzania. *Paragalago rondoensis* has a
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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).
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27 423 The apparent heterochronic disjunction between the eruption of adult dentition and the
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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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14
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16
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18
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22
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55
56
57
58
59
60

REFERENCES

- 457
458 Adams DC, Otarola-Castillo E 2013. Geomorph: an R package for the collection and analysis
459 of geometric morphometric shape data. *Methods in Ecology and Evolution* 4: 393-399.
- 460 Bayes M. 1998. A molecular phylogenetic study of the galagos, strepsirrhine primates and
461 archontan mammals. Unpublished D. Phil. Thesis, Oxford Brookes University.
- 462 Bearder SK, Honess PE, Bayes M, Ambrose L, Anderson, M. 1996. Assessing galago
463 diversity – a call for help. *African Primates* 2: 11-15.
- 464 Burnaby TP. 1966. Growth-invariant discriminant functions and generalized distances.
465 *Biometrics* 22: 96–110.
- 466 Butynski TM, de Jong Y, Perkin AW, Bearder SK, Honess PE. 2006. Taxonomy,
467 distribution, and conservation status of three species of dwarf galagos (*Galagoides*) in eastern
468 Africa. *Primate Conservation* 21: 63-79.
- 469 Butynski TM, Kingdon J, Kalina J. 2013. *Mammals of Africa. Volume II. Primates*. London:
470 Bloomsbury
- 471 Chatterjee HJ, Ho SYW, Barnes I, Groves C. 2009. Estimating the phylogeny and divergence
472 times of primates using a supermatrix approach. *BMC Evolutionary Biology* 9: 259.
- 473 Coquerel C. 1859. Notes de mammalogie. 1. Genre nouveau de Lémurien. *Revue et Magasin*
474 *Zoologique* 2: 457-464.
- 475 Crovella S, Masters JC, Rumpler Y. 1994. Highly repeated DNA sequences as phylogenetic
476 markers among the Galaginae. *American Journal of Primatology* 32: 177-185.

- 1
2
3 477 DelPero M, Masters JC, Zuccon D, Cervella P, Crovella S, Ardito G. 2000. Mitochondrial
4
5 478 sequences as indicators of generic classification in bush babies. *International Journal of*
6
7 479 *Primates* 21: 889-904.
8
9
10 480 Dorst J, Dandelot P. 1970. *A field guide to the larger mammals of Africa*. London: Collins.
11
12
13 481 Elliot DG. 1907. Descriptions of apparently new species and subspecies of mammals
14
15 482 belonging to the families Lemuridae, Cebidae, Callitrichidae, and Cercopithecidae in the
16
17 483 collection of the Natural History Museum. *Annals and Magazine of Natural History* (series 7)
18
19 484 20: 185-196.
20
21
22
23 485 Fabre PH, Rodrigues A, Douzery EJP. 2009. Patterns of macroevolution among Primates
24
25 486 inferred from a supermatrix of mitochondrial and nuclear DNA. *Molecular Phylogenetics and*
26
27 487 *Evolution* 53: 808-825.
28
29
30
31 488 Fox J, Weisberg S. 2011. *An {R} companion to applied regression*, 2nd edn. Thousand Oaks,
32
33 489 CA: Sage.
34
35
36 490 Frade F. 1924. Notes de Mammalogie Africaine. 1. Une nouvelle espèce de galago de
37
38 491 Moçambique. *Bulletin de la Société Portugaise des Sciences Naturelles* 9: 127-130.
39
40
41 492 Friendly M, Fox J. 2015. candisc: visualizing generalized canonical discriminant and
42
43 493 canonical correlation analysis. R package version 0.6-7.
44
45
46 494 Génin F, Yokwana A, Kom N, Couette S, Dieuleveut T, Nash SD, Masters, JC. 2016. A new
47
48 495 galago species for South Africa (Primates: Galagidae). *African Zoology* in press.
49
50
51
52 496 Geoffroy Saint-Hilaire E. 1796. Mammifères. Mémoire sur les rapports naturels des makis
53
54 497 *Lemur*, L. et description d'une espèce nouvelle de Mammifère. *Magasin Encyclopédique*
55
56 498 (2)1: 20-50.
57
58
59
60

- 1
2
3 499 Gray JE. 1863. Revision of the species of lemuroid animals, with the description of some new
4
5 500 species. *Proceedings of the Zoological Society of London* 1863(9): 129-152.
6
7
8 501 Gray JE. 1872. Notes on *Propithecus*, *Indris*, and other Lemurs (*Lemurina*) in the British
9
10 502 Museum. *Proceedings of the Zoological Society of London* 1872 (54): 846-860.
11
12
13 503 Groves CP. 2001. *Primate taxonomy*. Smithsonian Institution Press, Washington, DC.
14
15
16 504 Groves CP (in press). Jonathan Kingdon and the East African forests. *Journal of East African*
17
18 505 *Natural History*.
19
20
21 506 Grubb P, Butynski TM, Oates JF, Bearder SK, Disotell TR, Groves CP, Struhsaker TT. 2003.
22
23 507 Assessment of the diversity of African primates. *International Journal of Primatology* 24:
24
25 508 1301-1357.
26
27
28 509 Harrison T. 2010. Later Tertiary Lorisiformes. In: Werdelin L, Sanders WJ, eds. *Cenozoic*
30
31 510 *mammals of Africa*. Berkley, CA: University of California Press, 333-349.
32
33
34 511 Heller E. 1912. New races of insectivores, bats and lemurs from British East Africa.
35
36 512 *Smithsonian Miscellaneous Collections* 60: 1-13.
37
38
39 513 Hill WCO. 1953. *Primates: comparative anatomy and taxonomy. I—Strepsirhini*. Edinburgh:
40
41 514 University of Edinburgh Press.
42
43
44 515 Honess PE. 1996. Speciation among galagos (Primates, Galagidae) in Tanzanian forests.
45
46 516 Unpublished D. Phil. Thesis, Oxford Brookes University.
47
48
49 517 Honess PE, Bearder SK. 1996. Descriptions of the dwarf galago species of Tanzania. *African*
50
51 518 *Primates* 2: 75-79.
52
53
54
55
56
57
58
59
60

- 1
2
3 519 Jenkins PD. 1987. *Catalogue of Primates in the British Museum (Natural History). Part IV:*
4
5 520 *Suborder Strepsirrhini, including the subfossil Madagascan lemurs and Family Tarsiidae.*
6
7 521 London: British Museum (Natural History).
8
9
10 522 Kingdon J. 1997. *The Kingdon field guide to African mammals*. London: Academic Press.
11
12
13 523 Klingenberg CP. 1996. Multivariate allometry. In: Marcus LF, Corti M, Loy A, Naylor GJP,
14
15 524 Slice DE, eds. *Advances in morphometrics*. New York: Plenum, 23–49.
16
17
18 525 Lawrence B, Washburn SL. 1936. A new eastern race of *Galago demidovii*. *Occasional*
19
20 526 *Papers of the Boston Society of Natural History* 8: 255-266.
21
22
23
24 527 Masters JC. 2007. Taking phylogenetics beyond pattern analysis: can models of genome
25
26 528 dynamics guide predictions about homoplasy in morphological and behavioral data sets?
27
28 529 *Journal of Human Evolution* 52: 522-535.
29
30
31 530 Masters JC, Bragg NP. 2000. Morphological correlates of speciation in bush babies.
32
33 531 *International Journal of Primatology* 21: 793-813.
34
35
36 532 Masters JC, Brothers DJ. 2002. Lack of congruence between morphological and molecular
37
38 533 data in reconstructing the phylogeny of the Galagonidae. *American Journal of Physical*
39
40 534 *Anthropology* 177: 79-813.
41
42
43
44 535 Masters JC, Couette S. 2015. Characterizing cryptic species: A morphometric analysis of
45
46 536 craniodental characters in the dwarf galago genus *Galagoides*. *American Journal of Physical*
47
48 537 *Anthropology* 158: 288-299.
49
50
51
52 538 Masters JC, Rayner RJ, Ludewick H, Zimmermann, E, Molez-Verriere N, Vincent F, Nash
53
54 539 LT. 1994. Phylogenetic relationships among the Galaginae as indicated by erythrocytic
55
56 540 allozymes. *Primates* 35: 177-190.
57
58
59
60

- 1
2
3 541 Masters JC, Boniotto M, Crovella S, Roos C, Pozzi L, DelPero M. 2007. Phylogenetic
4
5 542 relationships among the Lorisoidea as indicated by craniodental morphology and
6
7 543 mitochondrial sequence data. *American Journal of Primatology* 69: 6-15.
8
9
10 544 Matschie P. 1893. Über anschienend neue africanische Säugethiere. *Sitzungsberichte der*
11
12 545 *Gesellschaft Naturforschender Freunde zu Berlin* 1893 (4): 107-114.
13
14
15 546 Mitteroecker P, Bookstein FL. 2011. Linear discrimination, ordination, and the visualization
16
17 547 of selection gradients in modern morphometrics. *Evolutionary Biology* 38: 100-114.
18
19
20
21 548 Oates JF. 2011. *Primates of West Africa. A field guide and natural history*. Conservation
22
23 549 International, Washington, DC.
24
25
26
27 550 Olson TR. 1979. Studies on aspects of the morphology of the genus *Otolemur* Coquerel, 1859.
28
29 551 Unpublished D. Phil. Thesis, University of London.
30
31
32 552 Perkin A. 2007. Comparative penile morphology of East African galagos of the genus
33
34 553 *Galagoides* (Family Galagidae): implications for taxonomy. *American Journal of*
35
36 554 *Primatology* 69: 16-26.
37
38
39
40 555 Pozzi L. 2016. The role of forest expansion and contraction in species diversification among
41
42 556 galagos (Primates: Galagidae). *Journal of Biogeography* 43: 1930-1941.
43
44
45
46 557 Pozzi L, Disotell TR, Masters JC. 2014. A multilocus phylogeny reveals deep lineages within
47
48 558 African galagids (Primates: Galagidae). *BMC Evolutionary Biology* 14: 72.
49
50
51 559 Pozzi L, Nekaris KAI, Perkin A, Bearder SK, Pimley ER, Schulze H, Streicher U, Nadler T,
52
53 560 Kitchener A, Zischler H, Zinner D, Roos C. 2015. Remarkable ancient divergences amongst
54
55 561 neglected lorisiform primates. *Zoological Journal of the Linnean Society* 175: 661-674.
56
57
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60

- 1
2
3 562 R Core Team.2015. *R: a language and environment for statistical computing*. Vienna: R
4
5 563 Foundation for Statistical Computing.
6
7
8 564 Roos C, Schmitz J, Zischler H. 2004. Primate jumping genes elucidate strepsirrhine
9
10 565 phylogeny. *Proceedings of the National Academy of Sciences, USA* 101: 10650-10654.
11
12
13 566 Schwarz E. 1931. On the African long-tailed lemurs or galagos. *Annals and Magazine of*
14
15 567 *Natural History* (series 10) 7: 41-66.
16
17
18 568 Simpson GG. 1945. The principles of classification and a classification of the mammals.
19
20 569 *Bulletin of the American Museum of Natural History* 85: 1-350.
21
22
23
24 570 Smith, A.1833. An epitome of African zoology. *South African Quarterly Journal* (series 2) 1:
25
26 571 16-32; 49-51 [Order Quadrumana].
27
28
29 572 Springer MS, Meredith RW, Gatesy J, Emerling CA, Park J, Rabosky DL, Stadler T, Steiner
30
31 573 C, Ryder OA, Janečka JE, Fisher CA, Murphy WJ. 2012. Macroevolutionary dynamics and
32
33 574 historical biogeography of primate diversification inferred from a species supermatrix. *PLoS*
34
35 575 *ONE* 7: e49521.
36
37
38 576 Thomas O, Wroughton RC. 1907. The Rudd exploration of South Africa. VII. List of
39
40 577 mammals obtained by Mr. Grant at Coguno, Inhambane. *Proceedings of the Zoological*
41
42 578 *Society of London* 1907: 285-299.
43
44
45
46 579 Warton DI, Duursma RA, Falster, DS, Taskinen S. 2012. smatr 3 - an R package for
47
48 580 estimation and inference about allometric lines. *Methods in Ecology and Evolution* 3: 257-
49
50 581 259.
51
52
53
54 582 Wesselman HB. 1984. The Omo micromammals: systematics and paleoecology of early man
55
56 583 sites from Ethiopia. *Contributions to Vertebrate Evolution* 7:1-219.
57
58
59
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- 1
2
3 584 Wickings EJ, Ambrose L, Bearder SK. 1998. Sympatric populations of *Galagoides demidoff*
4
5 585 and *Galagoides thomasi* in the Haut-Ogooué Region of Gabon. *Folia Primatologica* 69
6
7 586 (suppl. 1): 389-393.
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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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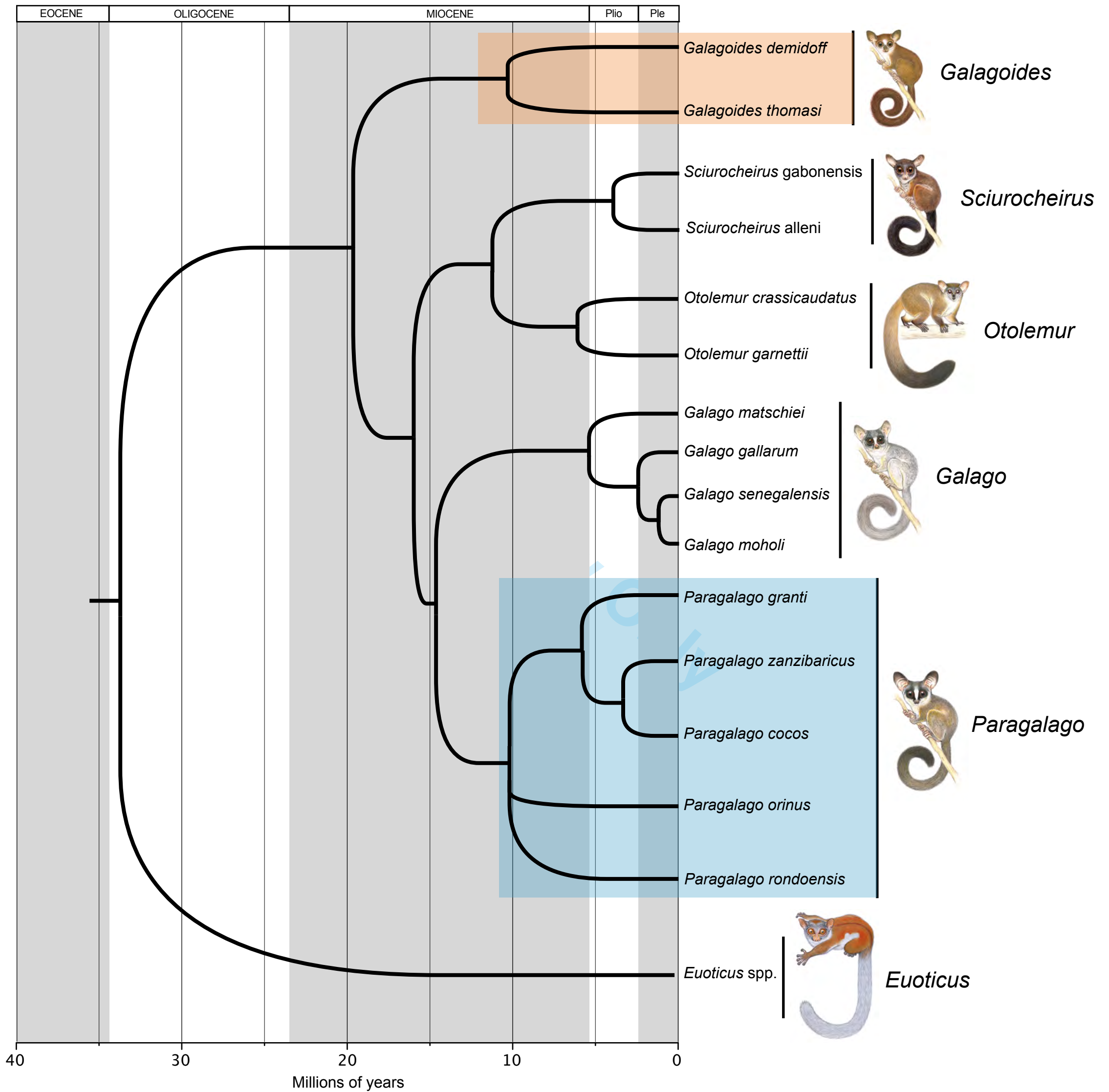
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3 611 among genera. Specimens of the two smallest eastern taxa, *orinus* and *rondoensis*, are
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5 612 indicated.
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8 613 Figure 7: Allometric trajectories for each genus described by the linear regression of
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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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14 616 allometry. Specimens of the two smallest eastern taxa, *orinus* and *rondoensis*, are indicated.
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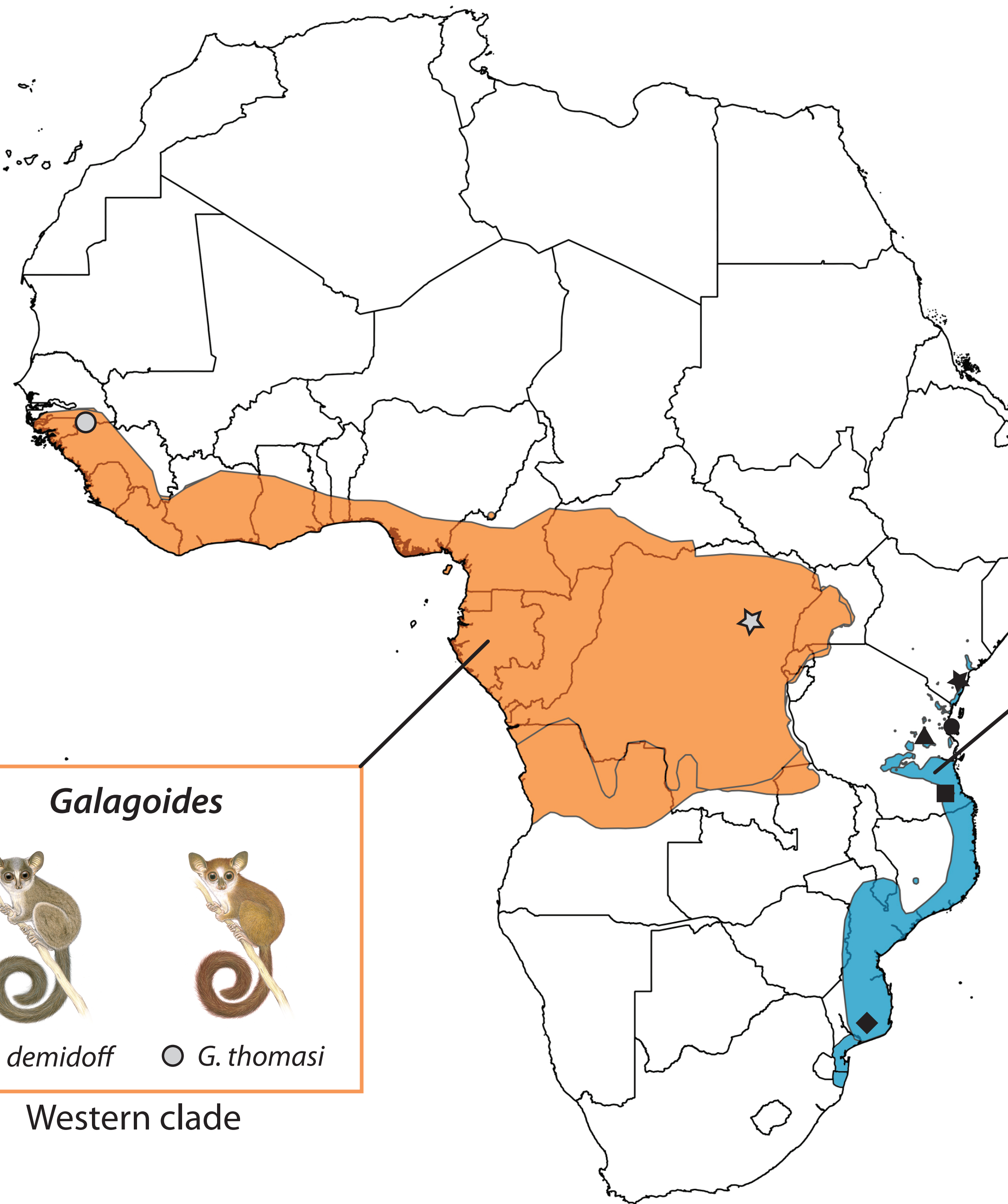
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21 618 Table 1: Cranial measurements used in the study (illustrated in figure 1)
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Paragalago

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

▲ *P. orinus* ■ *P. rondoensis*

Galagoides

★ *G. demidoff* ○ *G. thomasi*

Eastern clade

Western clade

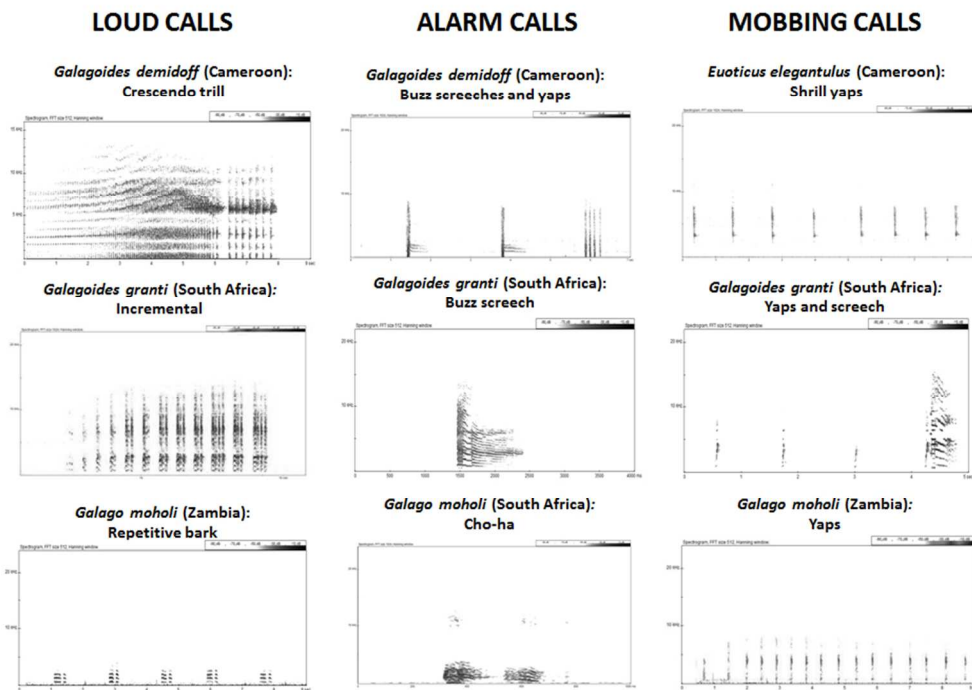


Figure 3: Sonograms of vocalisations emitted by small-bodied galagid species. Calls of *Eutoticus* (Cameroon) and *Galagoides granti* (Tshanini, South Africa) were recorded by FG. All other sonograms were downloaded from the East African Primate Diversity and Conservation website (<http://www.wildsolutions.nl/vocal-profiles>).

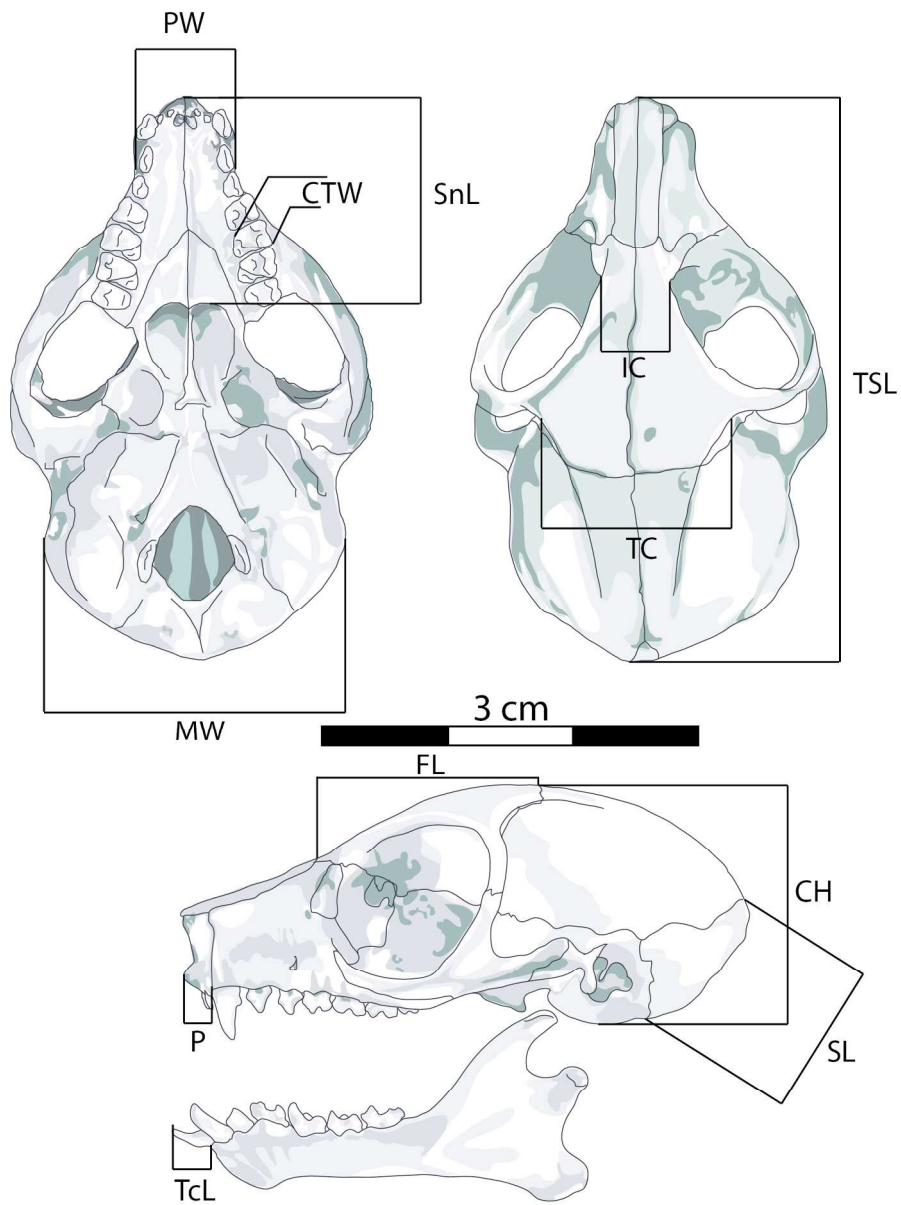


Figure 4: Schematic depiction of an eastern dwarf galago skull showing the 12 craniodental measurements included in the multivariate morphometric analyses. Descriptions of the variables are presented in Table 1.

163x220mm (300 x 300 DPI)

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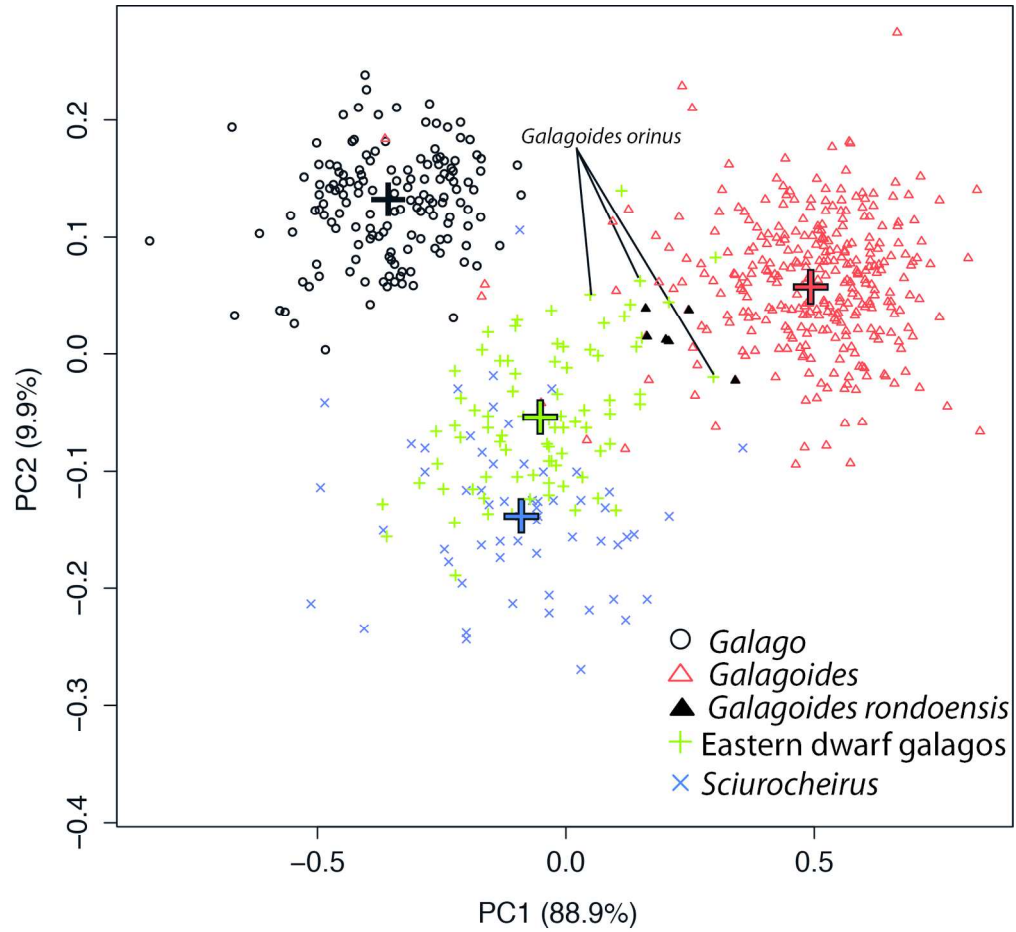


Figure 5: Between Group Principle Component Analysis (BGPCA) calculated on the twelve shape variables. Crosses indicate the mean values of each group that defined the principle component axes to analyse inter-group variation. Specimen data were back-projected in this space. Specimens of the two smallest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

174x161mm (300 x 300 DPI)

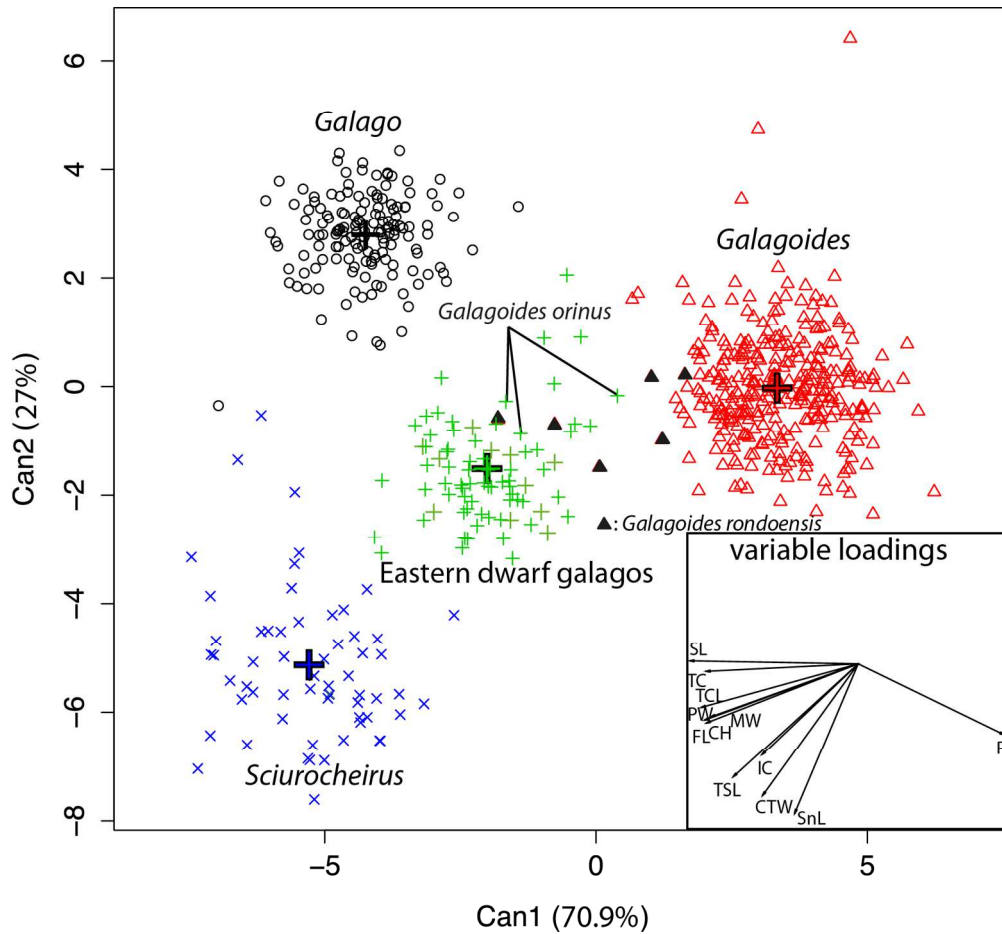


Figure 6: Canonical Variate Analysis of the twelve shape variables. Crosses indicate the centroid of each group. The first two roots illustrate significant differences in skull shape among genera. Specimens of the two smallest eastern taxa, *orinus* and *rondoensis*, are indicated.

160x152mm (300 x 300 DPI)

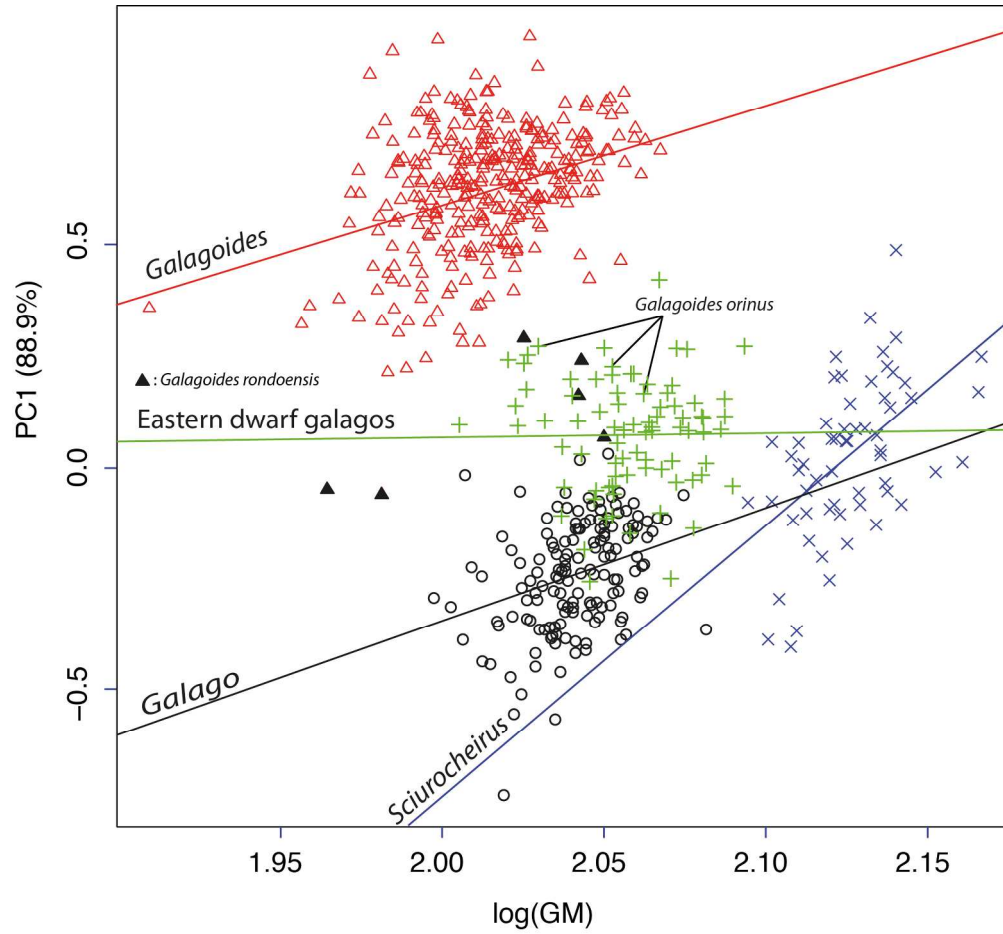


Figure 7: Allometric trajectories for each genus described by the linear regression of PC1 against the log-transformed centroid size. The allometric patterns are different among genera. Unlike the other genera, the eastern dwarf galago taxa do not show significant allometry. Specimens of the two smallest 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 ¹
PW	Palate width	Distance between labial margins of right and left P ²
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>
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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>
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22	NMK DM 4547	<i>Galagoides</i>	<i>zanzibaricus</i>	<i>cocos</i>
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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>	
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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
24 **TM: Ditsong Museum of Natural History (Transvaal Museum), Pretoria, South Africa**
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26 **USNM: United States National Museum of Natural History (Smithsonian Institution),**
27 **Washington DC, USA**
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29 **ZMB: Museum of Natural History, Berlin, Germany**
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