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Hidden in the Dark: A Review of Galagid Systematics and Phylogenetics

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Abstract

An accurate representation of species diversity is critical in primatology; most of the questions in evolutionary biology, ecology, and conservation hinge on species as a fundamental unit of analysis. Galagos are among the least-known primates. Because of their cryptic morphology, broad distribution, and sampling challenges arising from elusive habits and political instability, substantial knowledge gaps about their taxonomy, evolutionary history, and biogeography remain. Despite these limitations, recent research that integrated field surveys, acoustic, morphological, and genetic analyses helped us to better understand the taxonomic diversity of this primate group. In this paper, we (1) review the current status of galagid taxonomy; (2) synthesize our current understanding of their phylogenetics, origins, and biogeography; and (3) explore current and future approaches to elucidate galagid cryptic species diversity. The onset of galago systematics dates back to the early 19th century, with taxonomic descriptions following natural history expeditions and comparative anatomy studies. Although morphology has historically dominated systematic research on galagos, the coupling of acoustic analyses with genetic data has revolutionized the field. Taxonomic rearrangements include the discovery of new species in the wild (e.g., *Galagoides kumbirensis*) and the description of a new genus (*Paragalago*). Technological advances have allowed the collection of acoustic data in remote areas, and molecular techniques have the potential to help researchers fill important geographic gaps. Improving the resolution of galago species diversity also has implications for the conservation of wild populations, as a better understanding of species boundaries and ranges can aid in the implementation of conservation strategies.

Keywords Galago · Bushbaby · Taxonomy · Systematics · Phylogenetics · Africa

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In memory of Drs. Judith Masters and Fabien Genin.

"—lest our enchantment with nucleotide sequences leads us to believe that all the important questions have been answered."
Masters et al. (2013)

Introduction

Ensuring an accurate characterization of species diversity among primates is vital, because most inquiries about their evolutionary biology, ecology, and conservation rely on species as the fundamental analytical unit (Isaac *et al.*, 2004; Bickford *et al.*, 2007; Ceballos & Ehrlich, 2009). Members of the family Galagidae, also known as galagos or bushbabies, are relatively small nocturnal primates with wooly fur, long tails, and elongated hind limbs that inhabit various ecosystems across sub-Saharan Africa. They are phylogenetically related to African and Asian lorises (family Lorisidae) and together are classified within the infraorder Lorisiformes, the sister group to Malagasy lemurs (Groves, 2001a, 2001b; Nekaris & Bearder, 2007; Nekaris, 2013). Galagids are likely "the least known of all primates," and their classification and phylogeny is one of the most long-standing problems in primate systematics (Ellison *et al.*, 2021; Nekaris & Bearder 2007; Pozzi *et al.*, 2014). In the 1970s, when Dorst and Dandelot published their field guide on African mammals (Dorst & Dandelot, 1970), only five species of galagos (or bushbabies) were recognized, all part of the genus *Galago*: *Galago alleni*, *Galago crassicaudatus*, *Galago demidoff*, *Galago elegantulus*, and *Galago senegalensis*. More recently, in a similar field guide on African mammals published by Kingdon (2015), each of these species was regarded as a distinct genus (*Sciurocheirus*, *Otolemur*, *Galagoides*, *Euoticus*, and *Galago*, respectively), and the species diversity within each genus has dramatically increased over the past few decades to more than 20 species (Kingdon, 1997, 2015; Masters *et al.*, 2017; Nekaris & Bearder, 2007; Nekaris, 2013; Svensson *et al.*, 2017; Table 1).

A clear understanding of galago diversity has been affected by the limited degree of morphological differences among species (Masters & Bragg, 2000; Nekaris & Bearder, 2007). Being nocturnal, galagos are highly cryptic and closely related species often show limited morphological differences (Butynski *et al.*, 2006; Masters *et al.*, 2017; Masters & Bragg, 2000; Nekaris & Bearder, 2007). More recently, the description of species diversity within galagids has relied mostly on bioacoustic data, leading to a large—but still debated—increase in species number during the past decade (Pozzi *et al.* 2019).

The rationale behind the taxonomic use of loud calls is explained by the Recognition Species Concept, which defines a species as a group of organisms characterized by a shared Specific Mate Recognition System (Paterson, 1978, 1985). Different species-specific signals may be involved in mate recognition and can consequently restrict gene flow with other species (Paterson, 1985; Paterson & McEvey, 1993). Speciation occurs when the fertilization system of the daughter population is no longer consistent with that of its parent and members of the two

Table 1 Overview of the main changes in Galagidae taxonomic classification since the 19th century

	Geoffroy Saint-Hilaire,(1812)	Gray, (1863)	Elliot, (1913)	Schwarz, (1931)	Hill, (1953)	Olson, (1979)	Kingdon, (1997)	Groves, (2001a, 2001b)	Grubb *et al.* (2003)	After Masters *et al.* (2017) and Svensson *et al.* (2017)
Otolemur		*(Otogale) crassicaudata* *garnetti* *senegalensis* *peli* *teng* *(Callotus) monteiri*				*crassicaudatus* *garnettii*	*crassicaudatus* *garnettii* *argentatus*	*crassicaudatus* *garnettii* *monteiri (?)*	*crassicaudatus* *garnettii* *monteiri (?)* *sp. nov. (mwera)*	*crassicaudatus* *garnettii*
Euoticus		*(Otogale) pallidus*		*elegantulus*	*elegantulus* *inustus*		*elegantulus* *pallidus*	*elegantulus* *pallidus*	*elegantulus* *pallidus*	*elegantulus* *pallidus*

Table 1 (continued)

	Geoffroy Saint-Hilaire,(1812)	Gray, (1863)	Elliot, (1913)	Schwarz, (1931)	Hill, (1953)	Olson, (1979)	Kingdon, (1997)	Groves, (2001a, 2001b)	Grubb *et al.* (2003)	After Masters *et al.* (2017) and Svensson *et al.* (2017)
Galago	*senegalensis* *demidoff* *alleni* *moholi* *madagascariensis*	*allenii* *maholi* *senegalensis* *sennariensis* *madagascariensis* *demidoff* *conspicillatus*	*(Otolemur)* *crassicaudatus* *zuluensis* *panganiensis* *garnettii* *badius* *monteiri* *kirki* *lasiotis* *hindsi* *kikuyuensis* *(Otolicnus)* *alleni* *zanzibaricus* *talboti* *(Otogale)* *gallarum* *braccatus* *dunni* *nyssae* *granti* *senegalensis* *sennariensis* *mosambicus* *pupulus* *elegantulus*	*crassicaudatus* *senegalensis* *alleni* *demidoff*	*senegalensis* *crassicaudatus* *alleni*	*moholi* *senegalensis* *matschiei* *gallarum* *elegantulus*	*moholi* *senegalensis* *matschiei* *gallarum* *alleni* *cameronensis (?)* *gabonenesis (?)*	*moholi* *senegalensis* *matschiei* *gallarum* *alleni* *cameronensis (?)* *gabonenesis* *demidoff* *thomasi* *zanzibaricus* *granti* *orinus* *rondoensis* *udzungwensis* *nyasae*	*moholi* *senegalensis* *matschiei* *gallarum*	*moholi* *senegalensis* *matschiei* *gallarum*

Table 1 (continued)

	Geoffroy Saint-Hilaire,(1812)	Gray, (1863)	Elliot, (1913)	Schwarz, (1931)	Hill, (1953)	Olson, (1979)	Kingdon, (1997)	Groves, (2001a, 2001b)	Grubb *et al.* (2003)	After Masters *et al.* (2017) and Svensson *et al.* (2017)
Sciurocheirus									*alleni* *gabonensis* *sp. nov. (makande)*	*alleni* *gabonensis* *makandensis (?)*
Galagoides			*(Hemigalago)* *demidoff* *anomurus* *thomasi*		*demidoff*	*demidoff* *thomasi* *zanzibaricus* *alleni*	*demidoff* *thomasi* *zanzibaricus* *granti* *orinus (?)* *rondoensis (?)*		*demidoff* *thomasi* *zanzibaricus* *granti* *orinus* *rondoensis* *cocos* *nyasae* *Kalwe Galago sp. nov. 1* *Mt. Thyolo Galago sp. nov. 2* *Ukinga Galago sp. nov. 3*	*demidoff* *thomasi* *kumbiranensis*

Table 1 (continued)

	Geoffroy Saint-Hilaire,(1812)	Gray, (1863)	Elliot, (1913)	Schwarz, (1931)	Hill, (1953)	Olson, (1979)	Kingdon, (1997)	Groves, (2001a, 2001b)	Grubb *et al.* (2003)	After Masters *et al.* (2017) and Svensson *et al.* (2017)
Paragalago										*zanzibaricus* *granti* *orinus* *rondoensis* *cocos* *nyasae*
Genera/Species	1/5	3/14	2/26	2/6	3/6	3/11	4/18	3/20	5/24	6/20

The species *demidoff* is often reported as *demidovii* in the literature; however, following Jenkins et al. (2018), we decided to use the term *demidoff* across the article groups no longer recognize each other as potential mates (Masters, 1988, 1998; Paterson, 1985; Paterson & McEvey, 1993). Among nocturnal species, such as the galagos, advertisement signals for mate recognition are unlikely to be visually mediated by morphological traits, and species cohesiveness is more likely to be maintained by chemical and/or vocal signals (Bearder *et al.*, 1995; Braune *et al.*, 2008; Masters, 1993; Paterson, 1985; Paterson & McEvey, 1993). Consequently, cryptic species complexes (i.e., groups of biological species with very similar morphologies; Henry, 1985) are likely to emerge (Masters, 1993; Masters & Spencer, 1989).

Within galagids, vocal signals are used to maintain contact with other members of the same species, attract mates, repel rivals, and warn off predators (Bearder *et al.*, 1995; Charles-Dominique, 1977). Thus, field researchers have used advertising calls to identify several new species in the wild (Ambrose, 2003; Butynski *et al.*, 2006; Grubb *et al.*, 2003; Honess & Bearder, 1996; Perkin *et al.*, 2002; Svensson *et al.*, 2017). These proposed taxonomic arrangements match the observed variations in soft tissues, such as penile morphology and hair structure (Anderson, 1998; Perkin, 2007), which can aid in field identifications. However, for many of the new species described over the past two or three decades, very limited data about their ecology, behavior, morphology, and genetics are available, making the validity of some of these taxa a subject requiring further study.

More recently, efforts have been made to integrate multiple lines of evidence to clarify the systematics of certain galago groups. A series of studies combined genetic and bioacoustic data to clarify the systematics of the *Paragalago zanzibaricus* species complex (*P. cocos, P. zanzibaricus*, and *P. granti*; Pozzi *et al.*, 2019, 2020). Similarly, the integration of morphological, acoustic, genetic, and biogeographical data has resulted in the description of a new genus, *Paragalago*, for the eastern species of dwarf galagos (Masters *et al.*, 2017). Despite recent work, a firm understanding of galagid systematics is likely hindered by substantial cryptic diversity (Svensson *et al.*, 2017). An underappreciation of cryptic diversity within galagids affects not only our understanding of primate biodiversity but also our ability to explore modes and patterns of speciation and species dispersal at a continental-scale. Moreover, it is likely that underestimating biodiversity within cryptic species complexes has negative consequences for species conservation and natural resource protection and management (Bickford *et al.*, 2007; Ceballos & Ehrlich, 2009). For example, species that are considered “least concern” or “vulnerable” might be composed of multiple cryptic species that are rarer than previously supposed or even restricted to smaller distribution ranges and that might require specific conservation strategies. The goal of this review paper is to (1) provide an overview of the current status of galagid taxonomy, (2) synthesize our current understanding of their phylogenetics and biogeography, and (3) explore current and future approaches that will help us to elucidate galagid cryptic diversity.

Historical Overview of Galagid Systematics

Over the past three decades, the taxonomy of the family Galagidae has dramatically changed thanks to new field surveys integrating bioacoustic, morphological, and genetic data (Table 1).

The first formal species description of a galagid specimen dates to Geoffroy Saint-Hilaire in 1796. Material collected in the French colonies of Senegal and Madagascar played a central role in these initial descriptions. Because of the morphological similarities between small-sized galagids and lemurids, the first taxonomic arrangement by Geoffroy Saint-Hilaire (1812) included *Galago madagascariensis*, which turned out to be *Microcebus murinus* (Table 1). At that time, there was no distinction between the strepsirrhine families, and all "lemur-like" primates were classified under the suborder Lemuroidea (Mivart, 1864), which also included the tarsiers. In 1918, Pocock adopted a classification system to distinguish the biogeographical constraints of the suborders Lorisiformes and Lemuriformes (Pocock, 1918). Elliot (1913) offered perhaps the first thoroughly illustrated species account with detailed geographic and taxonomic information for each galagid genus, species, and subspecies recognized at the time. He proposed separating galagos into two genera that could be distinguished based on the presence or absence of a cusp in the heel of the second upper molar (p. 46), suggesting that it was advantageous to maintain the forms within the subgenera level.

In the first "modern" taxonomic revision of galagids published in 1931, Schwarz (1931) recognized only five species grouped into two genera: *Euoticus* and *Galago.* Later, Hill (1953) recognized the existence of at least five main types based on body size: large forms of *crassicaudatus*; small forms of *senegalensis*; medium forms of elongated fingers *alleni*; very small forms of *demidoff*; and small forms of very specialized *elegantulus* (Table 1). The validity of the genus *Otolemur* is now well established; however, the taxonomic status of dwarf and squirrel galagos has been the focus of debate over the past few decades (Groves, 2001a, 2001b; Grubb *et al.*, 2003; Nash *et al.*, 1989; Nekaris & Bearder, 2007; Nekaris, 2013). Currently, Allen's squirrel galagos are classified within a separate genus, *Sciurocheirus,* based on acoustic, morphological, and (limited) molecular data. Finally, Masters *et al.* (2017) split the dwarf galagos genus *Galagoides* into two and proposed the name *Paragalago* for the eastern dwarf galagos to emphasize its closer phylogenetic affinity to the genus *Galago* rather than to the remaining dwarf forms of the genus *Galagoides* (Table 1).

Traditional taxonomic revisions of galagids have relied almost exclusively on morphological data gathered from museum specimens (teeth, cranial, postcranial, and pelage). Recent research has incorporated ecological, genetic, and acoustic communication data. For instance, based on their long or advertisement calls, galago species can be categorized into different vocal groups (Bearder *et al.*, 1995; Grubb *et al.*, 2003; Svensson *et al.*, 2017): 1) click callers (*Euoticus* spp.); 2) croak callers (*Sciurocheirus* spp.); 3) repetitive callers (*G. senegalensis*, *G. moholi*, and *G. matschiei*); 4) trailing callers (*Otolemur* spp.); 5) rolling callers (*P. rondoensis* and *P. zanzibaricus*); 6) scaling callers (*P. orinus*); 7) incremental callers (*P. cocos* and *P. granti*); and 8) crescendo callers (Gd. *thomasi* and *Gd. demidoff*).

Currently, most authors recognize six genera (*Euoticus*, *Galagoides*, *Paragalago*, *Sciurocheirus*, *Otolemur*, and *Galago*) and at least 20 species of galagos. Herein, we briefly describe the taxonomy and biology of each genus.

Needle-clawed galagos (*Euoticus* – Gray, 1872)

The genus *Euoticus* includes medium-sized galagids (~300 g) with unique dietary and locomotive adaptations to gum feeding that likely make them the most enigmatic of all galagos. Their phylogenetic position, especially with respect to the genus *Galago,* has been widely debated. Gray (1872) and much later Kingdon (1997), however, recognized the needle-clawed species as a separate genus (*Euoticus*). Their advertisement calls are characterized by a series of brief and high-pitched clicks, very different from the calls emitted by any other galago, supporting the generic distinction between *Euoticus* and *Galago* (Bearder *et al.*, 1995). It is commonly accepted that *Euoticus* is a sister taxon of all other galagids (Pozzi *et al.*, 2014; Springer *et al.*, 2012; Stiner & Turmelle, 2003).

Two species of *Euoticus* are currently recognized: *E. elegantulus* and *E. pallidus* (Groves, 2001a, 2001b; Grubb *et al.*, 2003; Kingdon, 1997), but there is limited evidence to support their specific status. Studies on *Euoticus elegantulus* in Gabon and *E. pallidus* in Cameroon showed high similarities in their loud calls (Bearder *et al.*, 1995), and morphological investigations failed to discriminate between the two (Masters & Bragg, 2000). Needle-clawed galagos are restricted to forests in western-central Africa, ranging from Nigeria to Gabon, and the two proposed species are divided by the Sanaga River in Cameroon (Fig. 1).

Euoticus is a specialized gum feeder; more than 75% of its diet is based on exudates (gums and resins; Burrows & Nash, 2010). In the single long-term study conducted by Charles-Dominique (1977), 80% of gum was obtained from a single liana, *Entada gigas* (Fabaceae). Needle-clawed galagos have several unique morphological features that distinguish them from other galagids, including enlarged feet and hands (relative to body size), keels on fingernails ending in a sharp point, and a single pair of mammae (Kingdon, 1997). Interestingly, limb proportions and nail structure are similar to the only other galago species that strongly rely on gum feeding, the spectacled galago (*Galago matschiei*). From a biomechanical perspective, such similarity could be related to the fact that both species likely cling to trunks or branches while engaging in gumnivory, and the strong ridges and sharp ends in their nails enable them to generate more friction while clinging to the substrate.

Western dwarf galagos (*Galagoides* – A. Smith, 1833)

The genus *Galagoides* includes some of the smallest galago species (*Gd. demidoff* ~45 g; *Gd. thomasi* ~75 g). Because of their highly cryptic nature and small-bodied size, the taxonomic diversity of the dwarf forms has been long debated (Groves, 2001a, 2001b; Masters & Couette, 2015; Nekaris, 2013). Until recently, all dwarf forms from the western (*demidoff* and *thomasi*) and eastern (*zanzibaricus, cocos, granti, orinus,* and *rondoensis*) groups were included in

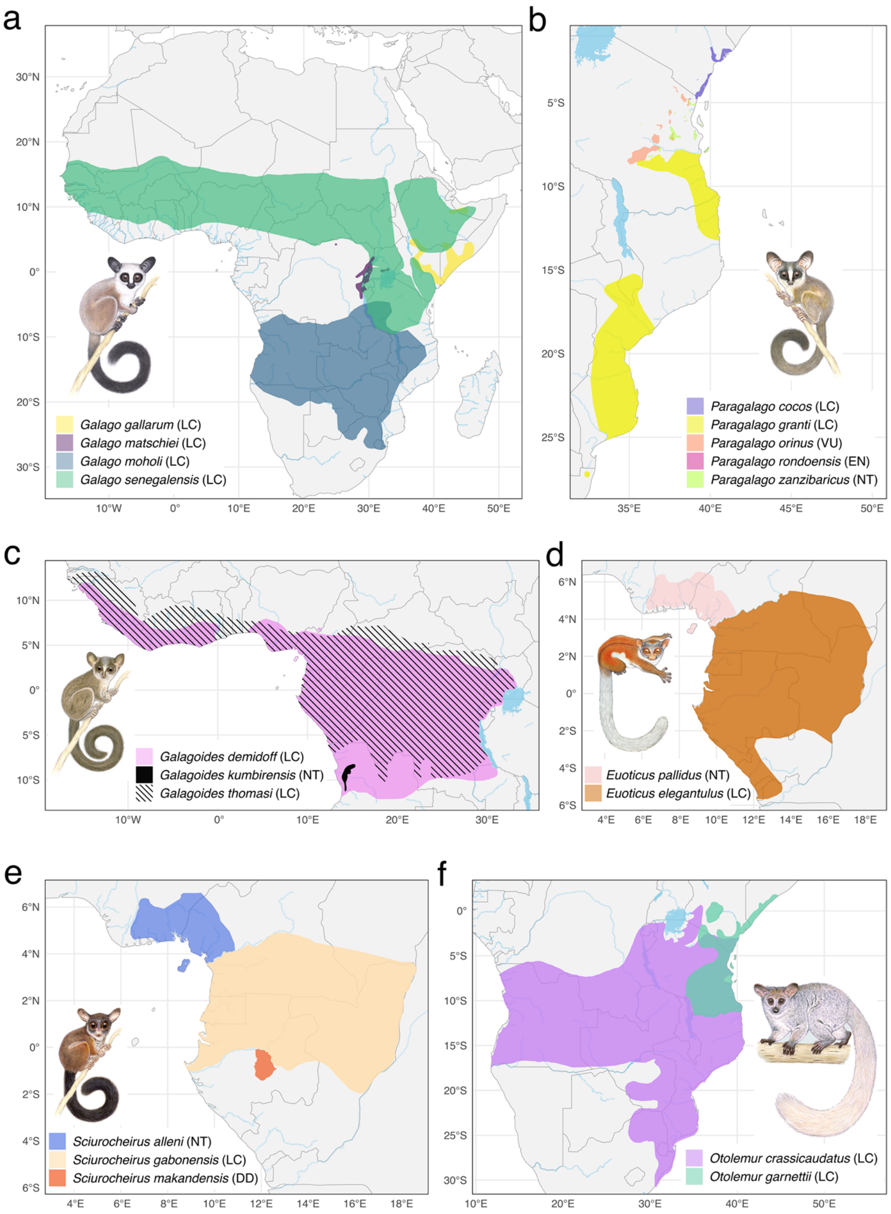

Fig. 1 Maps depicting galago species' distribution range according to the most recent IUCN Red List assessment (2020). The colors indicate different species, with panels organized by genera: (**a**) *Galago*, (**b**) *Paragalago*, (**c**) *Galagoides*, (**d**) *Euoticus*, (**e**) *Sciurocheirus*, and (**f**) *Otolemur*. Species conservation status is listed after their respective Latin binomials following the IUCN categories: Data Deficient (DD), Least Concern (LC), Near Threatened (NT), and Vulnerable (VU). Illustrations represent species listed in top of color caption, except for *Euoticus*. All drawings were provided by S. Nash and used with permission.

the "waste-basket" genus *Galagoides*; however, evidence from acoustic analyses demonstrates that these dwarf groups exhibit remarkable difference in their advertisement calls (Bearder *et al.*, 1995; Zimmermann, 1990). Based on morphological evidence, all dwarf galagos were grouped together with the squirrel galagos (*Sciurocheirus*), under the same genus *Galagoides* (Olson, 1979). Nash *et al.* (1989) and Kingdon (1997) differentiated the dwarf forms based on morphological distinctions, including unique limb proportions and craniodental features in *Galagoides* compared with lesser galagos (*Galago* spp.). In contrast, Groves (2001a, 2001b) merged all dwarf forms back into the genus *Galago*. A recent comprehensive taxonomic revision incorporating morphological, bioacoustic, biogeographical, and genetic data proposed the name *Paragalago* for eastern dwarf galagos (Masters *et al.*, 2017).

Species diversity within western dwarf forms remains the focus of intense debate. Currently, the genus *Galagoides* is thought to include three species found in a broad range of forest types in central and western Africa: two sympatric and broadly distributed *Gd. thomasi* and *Gd. demidoff* occurring as far west as Senegal and Guinea Bissau and the newly described *Gd. kumbirensis* limited to the western mountainous areas of Angola. Considerable levels of within-population variation in pelage color and body size have been reported in the literature (Bearder & Masters, 2013; Groves, 2001a, 2001b), making *Galagoides* one of the longest-lasting puzzles in primate taxonomy. Elliot (1907) was the first to distinguish (*Hemigalago*) *thomasi* as a separate species, although it has been considered a subspecies of *demidoff* by many later authors.

The two species were distinguished by Nash *et al.* (1989), mostly based on the *thomasi*'s larger body size and longer and denser fur. Field observations suggest habitat and behavioral differences when the two species occur in sympatry, with *Gd. demidoff* occupying the lower forest strata and preferring the understory, whereas *Gd. thomasi* is generally found in the upper strata of the canopy (Bearder & Masters, 2013). Their sympatric status, small size, and cryptic morphology increase the likelihood of one species being mistaken for another in the field; consequently, species identification in museum collections should be interpreted carefully (Cuozzo, 2001; Oates, 2011). Moreover, a comprehensive morphological analysis suggested that either *Gd. demidoff* displays more variation than *Gd. thomasi* or the species contains several cryptic taxa that disagree with the current subspecies arrangements (Masters & Couette, 2015).

The extensive variation within *Galagoides* specimens is reflected at the genetic level, as previous studies have indicated paraphyly of *Gd. demidoff* (Everson *et al.*, 2023; Pozzi *et al.*, 2015; Penna *et al.*, 2024) and multiple karyotypes within the same nominal taxa (Stanyon *et al.*, 1992). A third species, the Angolan dwarf galago (*Gd. kumbirensis*) was recently described based on species-specific differences in its loud crescendo call, larger body size, and differences in skull morphology, pelage color, and facial markings compared with members of sympatric *Gd. demidoff* (Svensson *et al.*, 2017).

Eastern dwarf galagos (*Paragalago* – Masters *et al.*, 2017)

The genus includes small galagid species, ranging from the tiny Rondo galago (*P. rondoensis*) at 60 g to a maximum of ~160 g for the Mozambique dwarf galago (*P. granti*). Because of their miniature size and similarities in their external morphology, eastern dwarf galagos were historically classified as *Galagoides*. In 1979, Olson recognized only two species of dwarf galago in eastern Africa (*Galagoides demidoff* and *"Galagoides" zanzibaricus*). Their taxonomy has been extensively revised over the past 20 years, particularly since the incorporation of acoustic communication data. Coupled with recent analyses of morphological, genetic, and biogeographic evidence, Masters & colleagues (Masters *et al.*, 2017) assigned them to the new genus *Paragalago* due to their closer phylogenetic relationship to lesser galagos. Therefore, dwarf galagos are a paraphyletic clade with more than 20-million-year-old divergence, suggesting that their diminutive size is an example of convergent dwarfism (Masters *et al.*, 2017).

At least five species are recognized, including *P. orinus*, *P. granti,* and *P. rondoensis* after Honess & Bearder (1996). Once considered a variant of *P. zanzibaricus*, *P. cocos*, from the coastal region of Kenya, has been resurrected as a full species based on the incremental structure of the advertisement call, which differs from both *P. zanzibaricus* and *P. granti* (Butynski *et al.*, 2006; Grubb *et al.*, 2003). This classification was later confirmed by molecular evidence (Pozzi *et al.*, 2019, 2020). Despite their similar size and morphology to western dwarf galagos (*Galagoides* spp.) (Masters & Couette, 2015), *P. orinus* and *P. rondoensis* are genetically more similar to the Zanzibar species complex galagos (Fabre *et al.*, 2009; Pozzi *et al.*, 2015; Springer *et al.*, 2012). While most species are restricted to small fragments of lowland and montane forests in East Africa (Fig. 1)*, P. granti* is the only widely and disjointly distributed species (found from the lowland coastal tropical forest and semi-arid woodland in Southern Tanzania to southern Malawi, Mozambique, and northeastern South Africa (Butynski *et al.*, 2006; de Jong *et al.*, 2019; Génin *et al.*, 2016; Pozzi *et al.*, 2020; Kingdon, 1997). *P. nyasae*, an additional species restricted to southern Malawi also has been proposed, but insufficient data prevents its recognition as a full species. Because of their small body size, dwarf galagos are highly insectivorous, with up to 70% of their diet composed of insects, such as beetles and orthopterans (Nekaris & Bearder, 2007). Their locomotion is variable, ranging from vertical clinging and leaping in *P. rondoensis* to quadrupedal running and walking in *P. cocos* and *P. zanzibaricus* (Harcourt & Nash, 1986; Nekaris & Bearder, 2007; Nekaris, 2013).

Lesser galagos (*Galago* – É. Geoffroy Saint-Hilaire, 1796)

The genus *Galago* was the first generic name to be recognized for the members of the family Galagidae. However, the number of species assigned to this genus has been extremely variable over time, and several authors used this genus to group species of unclear phylogenetic position (Groves, 2001a, 2001b; Grubb *et al.*, 2003; Table 1). Today, the generic name *Galago* is restricted to the lineage of most specialized galagos in terms of locomotion, showing active leaping and bipedal hopping (Nekaris & Bearder, 2007).

These medium-sized animals (~200 g) feed on a mix of animal prey (usually insects) and gum (Nekaris & Bearder, 2007). The genus includes at least four species: *G. senegalensis*, *G. moholi*, *G. matschiei*, and *G. gallarum*. Once identified as a subspecies of *senegalensis*, *G. moholi* was elevated to the species level based on morphological and acoustic data (Groves, 1974, 2001a, 2001b; Nash *et al.*, 1989; Zimmermann *et al.*, 1988). Olson (1979) first differentiated *G. gallarum* from *G. senegalensis*, a decision further confirmed by acoustics and morphological data (Bearder *et al.*, 1995; Grubb *et al.*, 2003; Kingdon, 1997; Masters & Bragg, 2000; Masters & Brothers, 2002; Nash *et al.*, 1989). Groves (2001a, 2001b) identified the main morphological differences between *G. gallarum* and G. *senegalensis*, including ear, hindlimb, hindfoot, and tail length. Additionally, Butynski & de Jong (2004) were the first to point out specific differences in *G. gallarum*'s loud calls and habitat preferences. This species remains one of the least known galagos, as very limited data regarding its morphology, behavior, ecology, and genetics are currently available (Butynski & Jong, 2004).

On the other side of the spectrum, *G. moholi* and *G. senegalensis* are probably the most studied galagos, because they are commonly found in captivity (Nekaris & Bearder, 2007). These two species are widely distributed across northern and southern Africa, respectively, but *G. gallarum and G. matschiei* are restricted to small geographic ranges in eastern Africa (Fig. 1). Whereas lesser galago species inhabit dry woodlands and savannahs, *G. matschiei* is the only galago restricted to closed forests in Eastern/Central Africa, representing either a secondary adaptation (Kingdon, 1997) or a relic of ancestral *Galago* distribution patterns (Pozzi, 2016).

Squirrel galagos (*Sciurocheirus* – Gray, 1872)

Squirrel galagos are medium-sized species (~280 g), highly frugivorous (up to 73% of total diet), and with a unique locomotion pattern within galagids to land hands first after leaping (Kingdon, 1997). The taxonomic status of squirrel galagos remains controversial. Studies have allocated the *alleni* taxon within either the genus *Galago* (Groves, 2001a, 2001b; Zimmermann, 1990) or *Galagoides* (Masters & Brothers, 2002; Nash *et al.*, 1989; Olson, 1979) based on morphological and acoustical data. However, molecular analyses have consistently supported a sister-group relationship with the greater galagos, *Otolemur* (Crovella *et al.*, 1994; DelPero *et al.*, 2000; Masters *et al.*, 2007; Pozzi *et al.*, 2014, 2015; Roos *et al.*, 2004). More recently, the generic name *Sciurocheirus* (Gray 1863) was resurrected for the Allen's squirrel galago (Ambrose, 2003; Grubb *et al.*, 2003).

Members of this genus show a distribution similar to that of *Euoticus*, being restricted to tropical forests between the Niger and Zaire Rivers. Originally described as a single species, *alleni* (Waterhouse, 1838), it was subsequently split into three subspecific taxa (*alleni, cameronensi*s, and *gabonensis*) by Eisentraut (1973). These subspecies were eventually elevated to species status by Groves (2001a, 2001b), but most authors consider *cameronensis* as a subspecies of *S. alleni*. The Sanaga

River in Cameroon acts as a biogeographical barrier between *S. alleni* (restricted to the North) and *S. gabonensis* (South and Bioko island) (Ambrose, 2003; Kingdon, 1997; Nekaris & Bearder, 2007). A third species, *S. makandensis,* found in the Forêt des Abeilles in Gabon was proposed based on a distinct loud-call repertoire and fur coloration (Ambrose, 2013). However, its taxonomic status remains unclear, and more data are required to clarify its validity.

Greater galagos (*Otolemur* – Coquerel, 1859)

Greater galagos were once included in the genus *Galago*, but Olson (1979) assigned them to their own genus, *Otolemur*, and most authors have now recognized the taxonomic validity at the genus level (Groves, 2001a, 2001b; Grubb *et al.*, 2003). Schwarz (1931) divided them into two groups within the species *Galago crassicaudatu*s. After extensive evaluation of thousands of museum specimens, Olson (1981) revised this taxonomic classification and recognized two species: *O. crassicaudatus* and *O. garnettii* based on distinctive morphological features, including forehead color, body, and ear size. Further differences between these two species include their body size, litter size, sexual dimorphism, locomotion, and karyotype (Masters, 1988).

The taxonomic status of other taxa recognized in this genus, such as *montieri* and *argentatus*, is still questionable (Groves, 2001a, 2001b; Grubb *et al.*, 2003) and often are maintained at the subspecific level. For instance, Groves (2001a, 2001b) argued that *monteiri* (silvery greater galago) may represent either a primary cline or a hybrid zone as first pointed out by Olson (1979). Little is known about the distribution and biology of *monteiri*, and preliminary acoustic analyses suggest a strong similarity with *O. crassicaudatus* (Bearder *et al.*, 1995). As the name suggests, greater galagos are the largest of all galagids ranging from 600 g in *O. garnettii* to up to 1.5–2 kg in *O. crassicaudatus* (Kingdon, 1997; Nekaris & Bearder, 2007). Because of their size, these are highly frugivorous animals (>50% of their diet) that exhibit limited leaping behavior (mainly quadrupedal runners). They inhabit diverse environments from coastal forests and thickets to more open savannas (Kingdon, 1997). *O. crassicaudatus* ranges across the southern part of the African continent from Angola and Namibia in the west to Somalia and Tanzania in the east, whereas *O. garnettii* is restricted to the coastal and mountain forests of eastern Africa (Harcourt & Perkin, 2013; Kingdon, 1997).

As Colin Groves suggested, there is no "official taxonomy," and every taxonomic decision should be seen as a scientific hypothesis (Groves, 2001a, 2001b). These taxonomic arrangements have the main purpose of aiding researchers in communicating about the specimens following a common classification system. Nevertheless, the categories and nomenclature used in classification go beyond just giving names to biological organisms; ultimately, evolutionary taxonomists are concerned about their evolutionary affinities. Therefore, the subdivision of animals in these nomenclature categories and taxonomic ranks (order, genera, and species) is based on the underlying assumption that all living representatives of these lineages can be traced back to a common and exclusive ancestor. These subdivisions may be entirely artificial; however, the discontinuities captured in such taxonomic categories may correspond to actual past geological or ecological events that led to such separation (Martin, 1968). For instance, Goodman *et al.* (1998) proposed standardizing the taxonomic ranks applied in primate classification by time depth, a scheme that was later refined by Groves (2001a, 2001b).

Galagid Phylogenetics and Biogeography

In the following section, we review the evolutionary history of galagos, with a focus on their phylogenetic relationships, divergence dates, and biogeographic patterns.

Historical perspective on galagid phylogeny

During the past three decades, multiple molecular studies have helped to clarify the relationships among different genera (Crovella *et al.*, 1994; DelPero *et al.*, 2000; Masters *et al.*, 2007; Pozzi *et al.*, 2014, 2015; Roos *et al.*, 2004); however, much work is needed at the intrageneric and intraspecific levels.

A major source of disagreement in early galagid phylogenetic studies has been the position of the enigmatic needle-clawed galago (*Euoticus* spp.; Fig. 2a–c). Early work based on morphology or short fragments of mitochondrial DNA found *Euoticus elegantulus* to be more closely related to members of the genus *Galago* and, more specifically, the sister taxon of *Galago matschiei* (Chatterjee *et al.*, 2009; Fabre *et al.*, 2009; Masters *et al.*, 2007; Roos *et al.*, 2004) (Fig. 2b). Other studies that combined morphological data with genetic (Masters *et al.*, 2007) and behavioral (Groves, 2001a, 2001b) data also supported this hypothesis (Fig. 2a). Interestingly, these gum-feeding species are the most specialized among galagids, suggesting that their morphological affinities may be attributed to convergence to a similar ecological niche instead of phylogenetic relatedness (Pozzi *et al.*, 2014). The first proponents of an alternative placement of needle-clawed galagos were Stiner and Turmelle (2003). In their analysis of partial mitochondrial DNA sequences (cytochrome b, 12S, and 16S rRNAs), *Euoticus* was identified as the first lineage to emerge within the family Galagidae, and sister taxon of all other galagids, with no particular relationship to any of the lesser galagos (genus *Galago*). This hypothesis was further supported by more recent and comprehensive molecular studies (Everson *et al.*, 2023; Pozzi *et al.*, 2014; Springer *et al.*, 2012; Penna *et al.*, 2024; Fig. 2c).

Another outstanding challenge in resolving the galago tree-of-life was the monophyletic status of dwarf galagos (Figs. 2a–c). Although morphologically similar, the systematics of dwarf galagos has historically been a major source of uncertainty. Early studies favored the grouping of the western and eastern dwarf forms within the same genus, *Galagoides*. However, with the advent of molecular data, the polyphyletic status of the genus *Galagoides* has become more evident (DelPero *et al.*, 2000; Fabre *et al.*, 2009; Masters *et al.*, 2007; Roos *et al.*, 2004; Springer *et al.*, 2012) (Figs. 2a–c). Although most of these studies used only partial mitochondrial DNA, a series of more recent studies, which combined mitochondrial and nuclear data,

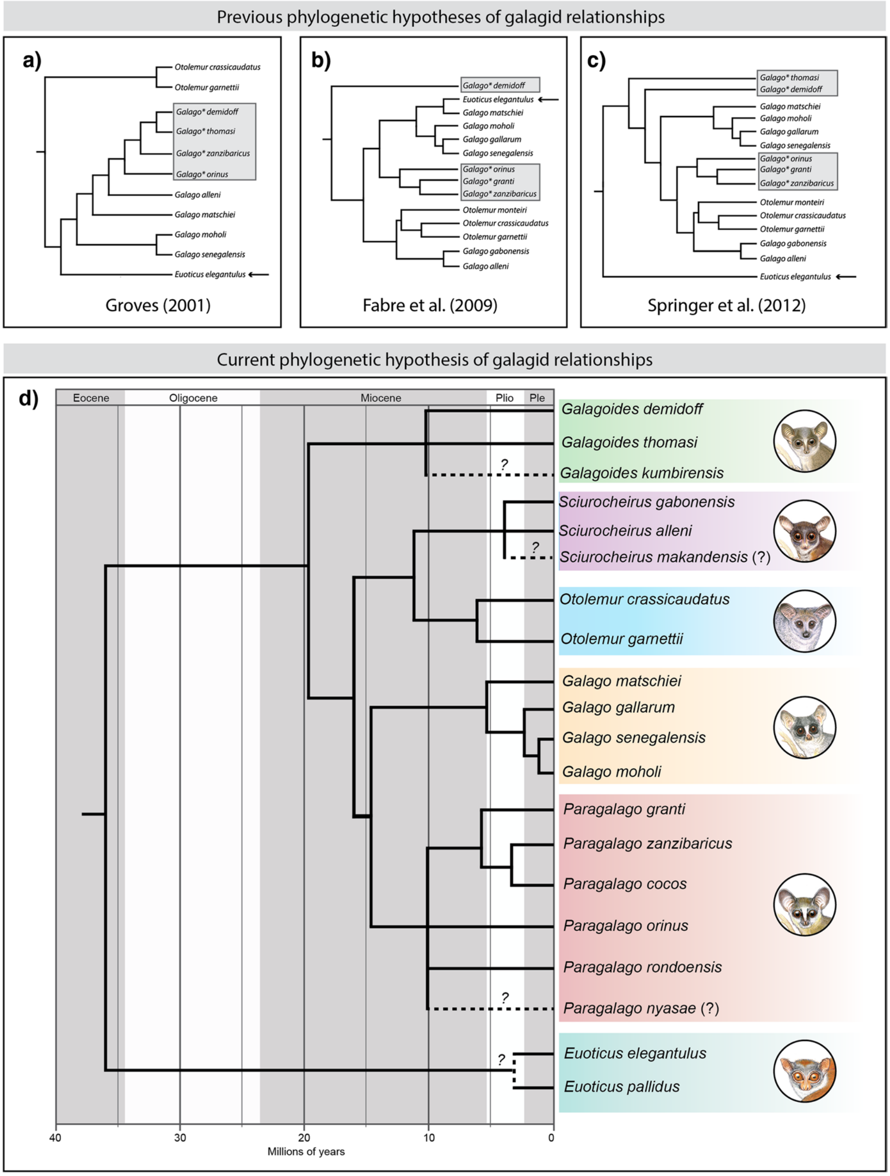

Fig. 2 Phylogenetic hypotheses of galagid relationships. Grey boxes indicate the position of members of the genus *Galagoides* and arrows indicate the position of *Euoticus*. (**a**) Galagid phylogeny based on 40 characters, including morphology, reproductive, and vocal behavior from Groves (2001a, 2001b). (**b**) Phylogeny based on a supermatrix of mitochondrial and nuclear DNA from Fabre *et al.* (2009). (**c**) Phylogenetic reconstruction based on a concatenation of nuclear gene segments and mitochondrial gene sequences from Springer *et al.* (2012). (**d**) Summary of our current understanding of relationships among the galagids based on both nuclear and mitochondrial sequence data, derived from the studies of Pozzi *et al.* (2014, 2015) and Pozzi (2016). Dashed lines indicate lineages for which no information about their phylogenetic relationships is currently available. Note: *The authors did not recognize the genus *Galagoides*, which is subsumed within the genus *Galago*.

confirmed the polyphyletic status of the genus *Galagoides* (Pozzi, 2016; Pozzi *et al.*, 2014). This phylogenetic hypothesis is now reflected in the new taxonomic arrangement proposed by Masters *et al.* (2017), who assigned the eastern dwarf galagos to the genus *Paragalago* due to its close phylogenetic relatedness to the lesser galagos (genus *Galago*).

Today, phylogenetic relationships at the generic level are well established, and multiple studies have confirmed the same topology (Fig. 2d). Needle-clawed galagos (*Euoticus* spp.) are the sister lineage to all galagos, followed by western dwarf galagos (*Galagoides* spp.). The eastern dwarf galagos (*Paragalago* spp.*)* are closely related to lesser galagos (*Galago* spp.), and this clade is a sister taxon of a lineage that includes both the greater (*Otolemur* ssp.) and squirrel galagos (*Sciurocheirus* spp.).

Galagid fossil record

Answering questions about the time of origin of the galagids, morphological and genetic divergence from other African and Asian lorisiforms, and underlying environmental and historical causes of their current distribution patterns requires an appreciation of the fossil record. In contrast to the closely related lemurs for which no fossil record is present, several galagid fossils have been found in northern and eastern Africa (Harrison, 2010, 2011). Fossils are usually grouped into two hierarchical categories: a) stem species (any extinct taxa more closely related to a given crown group than any other living radiation), or b) crown group (the group represented by the node of the last common ancestor of all living forms and all its descendants) (Table 2).

Stem galagids

The two oldest putative stem galagid species were found in Late Eocene sediments in Fayum, Egypt. The first, *Saharagalago mirrensis* (~36.9–42 Ma), was originally assigned to the family Galagidae based on remarkable similarities of upper molar morphology to those of modern galagids (Seiffert *et al.*, 2003). Because *Saharagalago* is twice as old as any other crown lorisid, the classification of *Saharagalago* as a stem galagid dramatically shifts the time estimate for the lorisid-galagid split to a much older divergence around the late Eocene (Seiffert *et al.*, 2003). This hypothesis seems to match the divergence time estimates based on the molecular clock (Pozzi *et al.*, 2015).

However, recent studies that have applied a total evidence approach (e.g., molecular data integrated with morphological evidence) to reconstruct the phylogeny of strepsirrhine primates have recovered *Saharagalago* as sister to all Lorisiformes, not as a stem Galagidae (Gunnell *et al.*, 2018; Herrera & Dávalos, 2016; Seiffert *et al.*, 2018). Moreover, a couple of studies conducted by Phillips (2016) and Phillips & Fruciano (2018) pointed out that the use of *Saharagalago* to calibrate the lorisid-galagid split results in an apparent discrepancy in molecular rates, suggesting that this fossil taxon might not be a crown lorisiform and, thus, inappropriate

Table 2 Fossil species relevant for the understanding of galagid biogeography and divergence times with their classification assignment and geographic location

Species	Reference	Age	Localities
Stem galagids			
Komba minor	Le Gros Clark and Thomas, 1952; Simpson, 1967	Early Miocene, ~17–20 Ma	Songhor, Rusmga Island, Legetet and Chamtwara, Kenya and Napak and Moroto, Uganda
Komba robustus	Le Gros Clark and Thomas, 1952; Simpson, 1967	Early Miocene, ~19–20 Ma	Songhor, Rusinga Island, Koru and Mfangano, Kenya and Napak, Uganda
Komba walkeri sp. nov.	Le Gros Clark and Thomas, 1952; Simpson, 1967	Early Miocene, ~16.5–18.0 Ma	Rusinga (Wayondo, Hiwegi, Kulu Fm.) and Mfangano (Makira Beds), Kenya
Komba sp.	Pickford and Mein, 2006	Early Miocene, ~17.0–17.5 Ma	Moroto II, Uganda
Komba winamensis	McCrossin, 1992	Middle Miocene, ~15 Ma	Maboko Island, Kenya
Progalago dorae	MacInnes, 1943; Simpson, 1967; Walker 1969	Early Miocene, ~19 Ma	Koru, Songhor, and Mlangano. Kenya and Napak. Uganda
Progalago songhorensis	Simpson, 1967	Early Miocene, ~19–18 Ma	Songhor and Rusinga Island, Kenya
Saharagalago misrensis	Seiffert *et al.*, 2003	Late Eocene, ~37Ma	Bartonian Birket Qarun Formation, Fayum, northern Egypt, locality BQ-2
Wadilemur elegans	Simons, 1997; Seiffert *et al.*, 2005	Late Eocene, ~35 Ma	Quarry L-41, Lower Sequence of Jebel Qatrani Formation, Fayum Depression, northern Egypt
gen. et sp. indet.	Kunimatsu *et al.*, 2017	Late Miocene, 10-9.8 Ma	Nakali site NA60, Kenya.
Crown galagids			
Galago farafraensis	Pickford, *et al.*, 2006	Late Miocene 10-11 Ma	Sheikh Abdallah, Western Desert, Egypt
Otolemur howelli	Wesselman, 1984	Pliocene, ~3.0–3.2 Ma	Omo, Ethiopia
Galago sadimanensis	Walker, 1987	Pliocene, ~3.5–5.0 Ma	Laetoli, Tanzania and Kapchebrit, Kenya
Galagoides cf. zanzibaricus	Wesselman, 1984	Pliocene, ~3.0 Ma	Omo, Ethiopia
Galago senegalensis	Simpson, 1965	Early Pleistocene, ~1.8 Ma	Bed I, Olduvai Gorge, Tanzania
Galagidae indet.	Pickford and Senut, 2001	Late Miocene, ~6 Ma	Kapsomin, Lukeino Fm, Kenya
Galagidae indet.	Harris *et al.*, 2003	Early Pliocene, ~4.1–4.2 Ma	Kanapoi, Kenya
Galagidae indet.	Wesselman, 1984	Late Pliocene, ~2.0 Ma.	Lower Mb. G, Shungura Fm., Omo, Ethiopia
Galagidae indet.	Denys, 1987	Early Pleistocene, ~1.3–1.7 Ma	Humbu Fm., Peninj, Tanzania

for calibrating the lorisid-galagid split. *Saharagalago mirrensis* is known from only two molars, and it is possible that there might be some doubts in the interpretation of these supposed galagid traits (López-Torres & Silcox, 2020). Moreover, total evidence analyses can be prone to debatable phylogenetic reconstructions because of the way morphological data are treated in the analyses (Pozzi & Penna, 2022). Nevertheless, this fossil is well accepted as a lorisiform, making it useful to date the age of crown Strepsirrhine (Vries & Beck, 2023).

Another lorisiform taxon from the late Eocene of Egypt, *Wadilemur elegans*, has been classified as a stem galagid due to its similarity in dental features (Seiffert *et al.*, 2005, 2018). Less controversial than *Saharagalago*, *Wadilemur* is more often recovered as a stem galagid (Gunnell *et al.*, 2018; Herrera & Dávalos, 2016, Wisniewski *et al.*, 2022), but some analyses have recovered them outside the crown lorisiforms (Lopés-Torres & Silcox, 2020). A late Oligocene (25.2MY) lorisiform from Rukwa Rift Basin in Tanzania has been excavated and pointed as a potential stem galagid (Stevens, 2017; Stevens *et al.*, 2013), but its taxonomic affinity remains unclear as the material has yet to be described and fully analyzed.

More recently dated (Miocene to Pliocene) fossils include members of the genera *Progalago* (~19 Ma; MacInnes, 1943; Simpson, 1967), *Komba* (15–20 Ma; Le Gros Clark & Thomas, 1952; Pickford *et al.*, 2016; Simpson, 1967), and *Laetolia* (~3.5–5.0 Ma; Harrison, 2011). The phylogenetic position of *Progalago* is still controversial, and although several authors classify it as a stem galagid (Harrison, 2010, 2011), others consider it a crown lorisiform with uncertain affinities (Rasmussen & Nekaris, 1998; Seiffert, 2007a). *Komba*, on the other hand, has been consistently recovered as a stem galagid in most phylogenetic analyses (Gunnell *et al.*, 2018; Seiffert *et al.*, 2018; Wisniewski *et al.*, 2022), and for that reason it has recently been recommended as a more solid calibration point to date the lorisid-galagid split than either *Saharagalago* or *Wadilemur* (Vries & Beck, 2023).

Crown galagids

The paleontological record of crown galagids is unfortunately quite sparse. The oldest putative crown galago is most likely *Galago farafraensis* found in Sheikh Abdallah (11–10 Ma) in Egypt (Pickford *et al.*, 2006). This species is known from several isolated teeth and postcranial elements that are similar in morphology to *Galago senegalensis*, but more similar in size to *Galagoides demidoff*. Other Miocene galagids of ambiguous classification include two isolated upper molars found in Namibia (Harasib 3a; 10-9 Ma; Conroy *et al.*, 1993; Rasmussen & Nekaris, 1998) and a mandibular fragment recovered from the Lukeino Formation in the Tugen Hills, Kenya (6-5 Ma; Mein & Pickford, 2006; Pickford & Senut, 2001).

More recently, a fossilized right maxillary fragment with M^1–M^2 excavated in Nakali (Kenya) and dated to the early Late Miocene was assigned to the family Galagidae (Kunimatsu *et al.*, 2017); however, its placement within this family remains unclear. Additional fossil remains are restricted to a few Pliocene-Pleistocene species in eastern Africa, including *Otolemur howelli* (Shungura formation, Omo, Ethiopia, ~3.0–3.2 Ma; Wesselman, 1984), and possibly some specimens belonging to *Galago senegalensis* (Olduvai Gorge, Tanzania, ~1.8 Ma; Simpson, 1965) and "Galagoides" (*Paragalago*) cf. *zanzibaricus* (Omo, Ethiopia, ~3.0 Ma; Wesselman, 1984).

Origins and biogeography of the galagids

The presence of multiple putative stem galagid species (*Saharagalago* and *Wadilemur*) in the Late Eocene suggests that the Galagidae-Lorisidae split probably occurred before 38–40 million years ago. Molecular studies have also estimated remarkable ancient divergences among galagids (Everson *et al.*, 2023; Pozzi, 2016; Pozzi *et al.*, 2014, 2015; Springer *et al.*, 2012) that date back to the mid-Miocene. The majority of biogeographic studies have focused on the unique disjunct geographic distribution of lorisiforms: living lorisids are found in both tropical Africa (pottos and angwantibos) and South and Southeast Asia (slow and slender lorises), whereas galagids are restricted to continental sub-Saharan Africa (Masters *et al.*, 2017; Nekaris & Bearder, 2007; Rowe & Myers, 2016).

A few studies have aimed at elucidating the biogeography of galagids, mostly focusing on the diversification patterns at the intrageneric level. For example, speciation events within both greater (*Otolemur* ssp.) and lesser (*Galago* spp.) species seem to be associated with the expansion of more arid savanna-like environments in the Early-Middle Pleistocene (Masters, 1988, 1998), whereas the diversification of eastern dwarf galagos (*Paragalago zanzibaricus* species complex) seems to be linked with forest contraction and expansion during the Middle Miocene (Miller *et al.*, 2023; Pozzi *et al.*, 2019). However, only one study has explicitly conducted a detailed biogeographical analysis at the family level (Pozzi, 2016).

Although no living galago species is found to the North of the Sahara Desert, the fossil record indicates that stem galagids occurred as North as Egypt (e.g., El Fayum; Pickford *et al.*, 2006; Seiffert *et al.*, 2003, 2005). The occurrence of *Galago farafraensis* in Egypt in the Middle Miocene suggests that members of the extant radiation once inhabited that area, which was possibly characterized by a more humid climate than today (Pickford *et al.*, 2006). However, the taxonomic assignment of this specimen to the genus *Galago,* and therefore to the crown group, remains unclear. A comprehensive biogeographical reconstruction of African galagids identified three major phases in their historical biogeography (Pozzi, 2016; Fig. 3).

Phase 1 - Early Oligocene: origins in central Africa

*S*everal molecular studies have indicated relatively old origins for the common ancestor of the radiation of living galagids, dating back to the beginning of the Oligocene (Pozzi, 2016; Pozzi *et al.*, 2014). Interestingly, the first two lineages to diverge within the family are two genera that are currently confined to central-western Africa: *Euoticus* and *Galagoides* (Pozzi *et al.*, 2014). Based on this phylogenetic pattern and biogeographic analyses, Pozzi (2016) suggested that the early evolution of extant galagids may have been restricted to central-western Africa, where rain forests were still present at that time (Fig. 3). The beginning of the Oligocene was

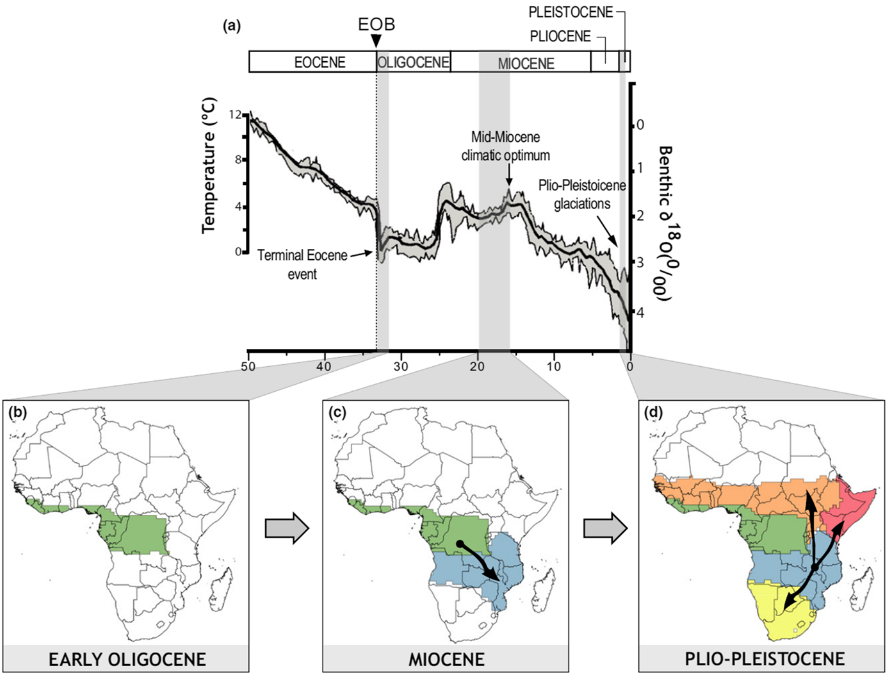

Fig. 3 Proposed biogeographical scenario for African galagids. (**a**) Summary of important climatic events throughout the Cenozoic is presented. Benthic $\mathrm{d}^{18}\mathrm{O}$ ($^{0}/_{00}$) is a proxy for global ocean temperatures, with lower values corresponding to warmer temperatures (climate figure redrawn from Morley & Kingdon, 2013). Maps summarizing the three main events that characterized galagid biogeography: (**b**) origins in central Africa, (**c**) expansion towards eastern Africa in the Miocene, and (**d**) expansion into northern and southern savannas in the Plio-Pleistocene (Adapted from Pozzi, 2016).

in fact characterized by a dramatic decrease in temperature, which likely resulted in increased aridity in the north and the contraction of rainforest habitat to the equatorial region (Morley, 2000; Seiffert, 2007a, 2007b; Zachos *et al.*, 2001). Early galagids likely persisted in sub-Saharan Africa because of the presence of tropical refugia (Morley & Kingdon, 2013).

Phase 2 – Oligo-Miocene: dispersal to the East

Temperatures started increasing at the end of the Oligocene and beginning of the Miocene, reaching a maximum during the so-called Mid-Miocene climatic optimum (Zachos *et al.*, 2001). Higher temperatures resulted in the expansion of rain forests, which eventually covered most of tropical and subtropical Africa from the West to the East (Andrews & Van Couvering, 1975; Morley, 2000). This forest expansion probably allowed forest-dwelling galagos to expand their ranges, colonizing regions in the east (Fig. 3).

Another critical factor that likely affected the biogeography of galagids in the Oligo-Miocene was the volcanic and geological activity that characterized Africa at this time (Livingstone & Kingdon, 2013). The formation of the African rift created several biogeographical barriers that limited the faunal connectivity between eastern and western Africa. Much of the diversity in galagid eastern clades, such as *Paragalago* and *Otolemur*, started to emerge at this time (Pozzi, 2016). Recent work supports this idea: studies based on mitochondrial DNA suggested that *Paragalago* originated in the Late Miocene (~10–11 mya; Pozzi *et al.*, 2015, 2019) and greater galagos are only slightly younger and dated at approximately 8 mya (Penna *et al.*, 2023).

Phase 3 - Plio-Pleistocene: expansion to the northern and southern savannas

Toward the end of the Pliocene (3–3.2 mya), drier environments started to spread in the Afrotropics (Morley & Kingdon, 2013). At this time, large savanna habitats expanded both north and south of the continent, creating ideal conditions for the evolution of novel adaptations. Pozzi (2016) suggested that lesser galagos (*Galago* spp.) likely started to colonize drier environments at this time. *Galago matschiei* was the first lineage to emerge within the genus and is the only living species of lesser galagos inhabiting wet forested areas. Its distribution probably represents a relic of the original distribution of the ancestors of all lesser galagos; however, other authors have suggested that this unique distribution of *G. matschiei* might be the consequence of secondary adaptation to wet environments (Kingdon, 1997). The other three species, *G. gallarum, G.moholi*, and *G. senegalensis*, are all adapted to dry habitats that were colonized during the aridification phases between the Late Pliocene and the Pleistocene (Masters, 1998; Masters *et al.*, 2007; Pozzi, 2016; Pozzi *et al.*, 2014).

Future Directions in Galago Systematics

The sections above illustrate the central role of systematics in our understanding of species diversity and the evolutionary and biogeographic history of galagids. Further refinements of species diversity within the family will require resolution of species boundaries, broad-scale geographic sampling, and integration of multiple lines of evidence (genetics, morphology, ecology, behavior, etc.). In turn, improved systematic and taxonomic knowledge will allow the elucidation of evolutionary patterns and improve the implementation of biodiversity monitoring strategies needed for the conservation of wild populations.

Expanding genetic resources to improve galago systematics

An accurate account of species diversity is pivotal to primatology, not only for inventory or classification purposes. Most questions in evolutionary biology (speciation dynamics), ecology (relationship between species and the environment), biogeography (diversification and distribution), and conservation (priorities for management of preserved areas) rely on species counts and the delimitation of "species" as an operational unit (Bickford *et al.*, 2007; Ceballos & Ehrlich, 2009).

The delimitation of species boundaries within small and nocturnal mammals has been particularly challenging because variation in their external morphology often is highly limited (Mayr, 1963; Sites Jr & Marshall, 2004). The incorporation of genetic data has proven to be effective in elucidating cryptic species diversity in these cases. Within galagids, the application of molecular techniques and phylogenetic methods improves the resolution of the Galagidae tree of life at both deep (i.e., above species level; Masters *et al.*, 2017; Pozzi *et al.*, 2014) and shallower scales (within populations of a same species; Penna *et al.*, 2023; Phukuntsi *et al.*, 2020, 2021; Pozzi *et al.*, 2020). However, very few studies have incorporated genetic information to delimit lineages in galagos.

Increased access to genetic data from other nocturnal primates at the population level has led to the description of several new species, suggesting that biological diversity among cryptic groups is much higher than expected based on morphology alone. In recent decades, the most extreme increase in the number of recognized species has occurred in mouse lemurs (*Microcebus* spp.) and sportive lemurs (*Lepilemur* spp.; Andriaholinirina *et al.*, 2006; Craul *et al.*, 2007; Hotaling *et al.*, 2016; Olivieri *et al.*, 2007; Thiele *et al.*, 2013; Weisrock *et al.*, 2010). Some new species proposed within these groups were elevated from subspecies, others were remote populations sampled for the first time and defined based on mitochondrial DNA alone.

Multiple authors criticized this practice suggesting that such dramatic increase in species might be an artifact of so called "taxonomic inflation" (Isaac *et al.*, 2004; Markolf *et al.*, 2011; Tattersall, 2007, 2012), as they were reclassified based on very limited molecular data. More importantly, these studies have suffered from a lack of integration of molecular analyses with other sources of evidence to propose new species. Later studies have found support for some of these lineages in cytogenetics, morphology, and more robust genetic analyses incorporating multiple nuclear loci, but some of these proposed new species seem to represent only mitochondrial haplotypes that are geographically structured due to differences in male and female dispersal (Andriaholinirina *et al.*, 2006; Weisrock *et al.*, 2010; Yoder *et al.*, 2016). Moreover, using a few genetic differences as diagnostic traits without associated morphological, behavioral, or ecological information has obvious implications for the identification of species in the field. Making matters more complex, most of these proposed new species have limited photographic records (if any) and often lack a designated type specimen voucher deposited in museum collections, making it difficult to maintain a correspondence between the genetic analyses and future comparisons with other specimens.

Incorporating multiple lines of evidence: the integrative taxonomy approach

The example above illustrates potential contributions of genetic evidence for delimiting species boundaries, not as the sole source of evidence, just as morphological evidence alone is often insufficient for species resolution. A more integrative taxonomic approach can incorporate multiple and complementary sources of evidence to better understand species dynamics (Padial & Miralles, 2010; Schlick-Steiner *et al.*, 2010; Zimmermann & Radespiel, 2014). Recent work with dwarf galagos has illustrated the advantages of this integrative approach when dealing with the challenges of cryptic species complexes. The description of the new genus *Paragalago* combined multiple lines of evidence to support the hypothesis that dwarf galagos do not represent a single evolutionary lineage but, in fact, two radiations of miniaturized primates (Masters *et al.*, 2017). More recently, a series of studies using genetics, bioacoustics, and ecological models to identify species boundaries within the *Paragalago zanzibaricus* species complex (Miller *et al.*, 2023; Pozzi *et al.*, 2019, 2020) showed more evidence for the distinction between the three species in the complex. Despite inherent challenges in collecting multiple lines of evidence, research is needed to apply this approach to other taxa within galagids.

Technological improvements to field data collection

One of the main challenges in studying wild galago populations is the ability of researchers to locate and identify cryptic, small, and fast-moving animals in their natural habitats. For this reason, the species-specific vocal repertoires used in different behaviors are among the most commonly used evidence of a species' presence in a given area (Bearder *et al.*, 1995; Génin, 2021; Svensson *et al.*, 2017). Among these, loud or advertisement calls are particularly important, because they are used by both males and females to attract potential mates and repel rivals from their territories and thus are extremely useful in species recognition (Bearder *et al.*, 1995; Masters, 1993; Paterson, 1985). Although most vocalization data come from opportunistic recordings during field surveys, the availability of passive acoustic monitoring (PAM) has the potential to be an effective way to study galago vocalizations in the wild. This new recording technique is a noninvasive and relatively inexpensive monitoring strategy that consists of employing stationary recorders throughout the study area to gather information about the species' presence, abundance, density, distribution, population status, and seasonal and geographical variability of vocal behavior (Ravaglia *et al.*, 2023).

PAM has been used in multiple primate species, including fork-marked lemur (*Phaner pallescens*; Markolf *et al.*, 2022), indris (*Indri indri*; Ravaglia *et al.*, 2023), gibbons (*Nomascus hainanus*; Dufourq *et al.*, 2021), and more recently galagos in Taita Hills, a remote mountainous area of Kenya (Rosti *et al.*, 2023). The galagos that inhabit this region potentially represent relictual populations of eastern dwarf galagos first recorded 20 years ago (Perkin *et al.*, 2002; Rosti *et al.*, 2023). PAM is likely to be a very effective strategy for obtaining novel information on galago diversity, distribution, and behavior. Specifically, recording multiple populations across the distributional range of various species can help researchers identify possible cryptic diversity or populations, a rich topic for future research.

Importance of museum collections to fill important geographic gaps and unveil cryptic diversity

Studies that have included multiple specimens across the distributional range of some species have indicated that the level of cryptic diversity within galagids might be underestimated (Everson *et al.*, 2023; Penna *et al.*, 2023, 2024; Pozzi *et al.*, 2019, 2020). However, another limitation hampering the collection of galago samples in the wild is the challenge of obtaining permits for broadly distributed taxa from multiple countries. These difficulties intensify in regions of political instability and epidemiological concerns, where research often is difficult to conduct. Consequently, our understanding of galago systematics and phylogenetics is likely limited to a small representation of the diversity within each taxon.

Fortunately, natural history museums house millions of specimens worldwide, and museum collections provide an irreplaceable source of data. There has been an increase in studies applying molecular techniques to a wide range of biological samples hosted in museum collections (Bi *et al.*, 2013; Green & Speller, 2017; Mason *et al.*, 2011; Raxworthy & Smith, 2021; Rowe *et al.*, 2011; Penna *et al.*, 2024). Various tissue sources, including teeth, bones, claws, nails, and skin, can be used to obtain genetic information from museum specimens. High-throughput sequencing and genomic technologies have recently unlocked museum collections, providing a new and exciting alternative to overcome the challenges of obtaining genetic data from wild populations. Several studies have shown that genomic data from museum specimens can be obtained using next-generation platforms from various tissues, including specimens more than 100 years old or even formalin-fixed (Burrell *et al.*, 2015; Hykin *et al.*, 2015; Lim & Braun, 2016; McCormack *et al.*, 2016; Ruane & Austin, 2017). In primates, full mitochondrial genomes have been obtained from museum specimens of guenons (Guschanski *et al.*, 2013), gorillas (van der Valk *et al.*, 2017), macaques (Liedigk *et al.*, 2015; Yao *et al.*, 2017), and marmosets (Porter *et al.*, 2021). Recently, multiple studies have used museum specimens to generate genomic-level data. For instance, reduced-representation genomic datasets have been generated from 40-year-old olive baboon skin (*Papio anubis*; Burrell *et al.*, 2015) and bald uakaris (*Cacajao* spp.; Ennes Silva *et al.*, 2022). van der Valk *et al.* (2019) obtained genomic data from museum samples to investigate population decline in eastern gorillas (*Gorilla beringei*).

Museum samples will be critical to increase the accessibility of genetic data for more specimens, thus obtaining population-level data from galagid species across their geographic ranges. Such data will allow researchers to understand how genetic variation within different genera is distributed in the landscape, thereby elucidating species boundaries and biogeographic patterns on a continental scale. Additionally, obtaining genetic data from museum specimens offers a unique opportunity to directly link genetic and morphological analyses when exploring the level of cryptic diversity across this primate family.

Bridging systematics and conservation

Primates are among the most endangered mammalian lineages, with approximately 65% of species and subspecies currently categorized as endangered or threatened by extinction (IUCN SSC Primate Specialist Group, 2021). Human-driven habitat loss and fragmentation are the main threats to primate populations (Estrada *et al.*, 2017) and are particularly critical for species with narrow distributions. Systematic investigations incorporating molecular data have often split taxa into species with more restricted ranges than previously thought (Weisrock *et al.*, 2010).

Although the vast majority of galago species are listed as Least Concern, they are among the least-known primate taxa, with extensive evidence of underestimated species diversity. All five galago species listed as Vulnerable or Endangered (Fig. 1) are geographically restricted. Careful investigation of genetic diversity across the distribution of galagos will likely reveal narrow-range genotypically and morphologically unique lineages that may require special protection or management. Moreover, galagos are becoming more common in the illegal pet trade (Svensson *et al.*, 2021), and broad characterization of spatial genetic variation can help track the geographic sources of smuggled animals and illegal networks (Blair *et al.*, 2023). Finally, genetic-based estimates of effective population sizes can be used to monitor demographic trends in response to environmental perturbations, and the use of historical museum samples has already provided crucial comparative genetic material (Roycroft *et al.*, 2021; van der Valk *et al.*, 2019). These examples support the idea that molecular systematic investigations will play a central role in the long-term conservation of this fascinating and relatively understudied branch of the Order Primates.

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References

Ambrose, Lesley. (2003). Three acoustic forms of Allen's galagos (Primates; Galagonidae) in the Central African region. *Primates, 44*(1), 25–39. https://doi.org/10.1007/s10329-002-0004-x

Ambrose, L. (2013). *Scirocheirus makandensis*—Makandé squirrel galago. *Mammals of Africa, 2*, 421–422.

Anderson, M. J. (1998). Comparative morphology and speciation in galagos. *Folia Primatologica, 69*(7), 325–331.

Andrews, P., & Van Couvering, J. A. (1975). Palaeoenvironments in the East African Miocene. *Approaches to Primate Paleobiology, 5*, 62–103.

Andriaholinirina, N., Fausser, J.-L., Roos, C., Zinner, D., Thalmann, U., Rabarivola, C., et al. (2006). Molecular phylogeny and taxonomic revision of the sportive lemurs (*Lepilemur*, Primates). *BMC Evolutionary Biology, 6*(1), 17. https://doi.org/10.1186/1471-2148-6-17

Bearder, S. K., Honess, P. E., & Ambrose, L. (1995). Species diversity among galagos with special reference to mate recognition. *Creatures of the Dark* (pp. 331–352). UK: Springer.

Bearder, S. K., & Masters, J. C. (2013). Family Galagidae. Galagids: galagos (bushbabies). In J. S. Kingdon, T. Butynski, & J. Kalina (Eds.), *The Mammals of Africa, Vol. 5: Primates* (pp. 404–407). London, UK: Bloomsbury Publishing.

Bi, K., Linderoth, T., Vanderpool, D., Good, J. M., Nielsen, R., & Moritz, C. (2013). Unlocking the vault: Next-generation museum population genomics. *Molecular Ecology, 22*(24), 6018–6032. https://doi.org/10.1111/mec.12516

Bickford, D., Lohman, D. J., Sodhi, N. S., Ng, P. K. L., Meier, R., Winker, K., et al. (2007). Cryptic species as a window on diversity and conservation. *Trends in Ecology & Evolution, 22*(3), 148–155. https://doi.org/10.1016/j.tree.2006.11.004

Blair, M. E., Cao, G. T. H., López-Nandam, E. H., Veronese-Paniagua, D. A., Birchette, M. G., Kenyon, M., et al. (2023). Molecular Phylogenetic Relationships and Unveiling Novel Genetic Diversity among Slow and Pygmy Lorises, including Resurrection of *Xanthonycticebus intermedius*. *Genes, 14*(3), 643. https://doi.org/10.3390/genes14030643

Braune, P., Schmidt, S., & Zimmermann, E. (2008). Acoustic divergence in the communication of cryptic species of nocturnal primates (Microcebus ssp.). *BMC Biology, 6*(1), 19. https://doi.org/10.1186/1741-7007-6-19

Burrell, A. S., Disotell, T. R., & Bergey, C. M. (2015). The use of museum specimens with high-throughput DNA sequencers. *Journal of Human Evolution, 79*, 35–44. https://doi.org/10.1016/j.jhevol.2014.10.015

Burrows, A. M., & Nash, L. T. (2010). *The evolution of exudativory in primates*. Springer Science & Business Media.

Butynski, T. M., & de Jong, Y. A. (2004). Natural History Of The Somali Lesser Galago (*Galago gallarum*). *Journal of East African Natural History, 93*(1), 23–38. https://doi.org/10.2982/0012-8317(2004)93[23:NHOTSL]2.0.CO;2

Butynski, T. M., de Jong, Y. A., Perkin, A. W., Bearder, S. K., & Honess, P. E. (2006). Taxonomy, distribution, and conservation status of three species of dwarf galagos (Galagoides) in Eastern Africa. *Primate Conservation, 83*(18), 63–80.

Ceballos, G., & Ehrlich, P. R. (2009). Discoveries of new mammal species and their implications for conservation and ecosystem services. *Proceedings of the National Academy of Sciences, 106*(10), 3841–3846.

Charles-Dominique, P. (1977). *Ecology and behaviour of nocturnal primates: prosimians of equatorial West Africa*. Columbia University Press.

Chatterjee, H. J., Ho, S. Y., Barnes, I., & Groves, C. (2009). Estimating the phylogeny and divergence times of primates using a supermatrix approach. *BMC Evolutionary Biology, 9*(1), 259. https://doi.org/10.1186/1471-2148-9-259

Conroy, G. C., Pickford, M., Senut, B., & Mein, P. (1993). Diamonds in the desert: The discovery of *Otavipithecus namibiensis*. *Evolutionary Anthropology: Issues, News, and Reviews, 2*(2), 46–52. https://doi.org/10.1002/evan.1360020206

Craul, M., Zimmermann, E., Rasoloharijaona, S., Randrianambinina, B., & Radespiel, U. (2007). Unexpected species diversity of Malagasy primates (Lepilemur spp) in the same biogeographical zone: a morphological and molecular approach with the description of two new species. *BMC Evolutionary Biology, 7*(1), 83. https://doi.org/10.1186/1471-2148-7-83

Crovella, S., Masters, J. C., & Rumpler, Y. (1994). Highly repeated DNA sequences as phylogenetic markers among the galaginae. *American Journal of Primatology, 32*(3), 177–185. https://doi.org/10.1002/ajp.1350320304

Cuozzo, F. P. (2001). Craniodental body mass estimators in the dwarf bushbaby (*Galagoides*). *American Journal of Physical Anthropology, 115*(2), 187–190. https://doi.org/10.1002/ajpa.1068 de Jong, Y.A., Butynski, T.M. & Perkin, A. (2019). Paragalago granti. The IUCN Red List of Threatened Species 2019:e.T91970347A17962454. https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T91970347A17962454.en. Accessed on 05 April 2024.

de Vries, D., & Beck, R. M. D. (2023). Twenty-five well-justified fossil calibrations for primate divergences. *Palaeontologia Electronica, 26*(1), 1–52. https://doi.org/10.26879/1249

DelPero, M., Masters, J. C., Zuccon, D., Cervella, P., Crovella, S., & Ardito, G. (2000). Mitochondrial Sequences as Indicators of Genetic Classification in Bush Babies. *International Journal of Primatology, 21*(5), 889–904. https://doi.org/10.1023/A:1005502927658

Denys, C. (1987). Micromammals from the West Natron Pleistocene deposits (Tanzania). *Biostratigraphy and paleoecology. Sciences Géologiques Bulletin, 40*, 185–201.

Dorst, J., & Dandelot, P. (1970). *A field guide to the larger mammals of Africa*. Collins.

Dufourq, E., Durbach, I., Hansford, J. P., Hoepfner, A., Ma, H., Bryant, J. V., et al. (2021). Automated detection of Hainan gibbon calls for passive acoustic monitoring. *Remote Sensing in Ecology and Conservation, 7*(3), 475–487. https://doi.org/10.1002/rse2.201

Eisentraut, M. (1973). Die Wirbeltierfauna von Fernando Poo und Westkamerun. *Bonner zoologische Monographien, 3*, 1–428.

Elliot, D. (1907). XXVIII—Descriptions of apparently new species and subspecies of mammals belonging to the Families Lemuridæ, Cebidæ, Callitrichidæ, and Cercopithecidæ in the collection of the Natural History Museum. *Journal of Natural History, 20*(117), 185–196.

Elliot, D. (1913). A review of the primates. *American Museum of Natural History: Monograph Series, 3*, 227–254.

Ellison, G., Jones, M., Cain, B., & Bettridge, C. M. (2021). Taxonomic and geographic bias in 50 years of research on the behaviour and ecology of galagids. *PLoS ONE, 16*(12), e0261379. https://doi.org/10.1371/journal.pone.0261379

Ennes Silva, F., Valsecchi do Amaral, J., Roos, C., Bowler, M., Röhe, F., Sampaio, R., et al. (2022). Molecular phylogeny and systematics of bald uakaris, genus *Cacajao* Lesson, 1840 (Primates: Pitheciidae), with the description of a new species. *Molecular Phylogenetics and Evolution, 173*, 107509. https://doi.org/10.1016/j.ympev.2022.107509

Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di Fiore, A., et al. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances, 3*(1), e1600946. https://doi.org/10.1126/sciadv.1600946

Everson, K. M., Pozzi, L., Barrett, M. A., Blair, M. E., Donohue, M. E., Kappeler, P. M., Kitchener, A. C., Lemmon, A. R., Lemmon, E. M., Pavón-Vázquez, C. J., Radespiel, U., Randrianambinina, B., Rasoloarison, R. M., Rasoloharijaona, S., Roos, C., Salmona, J., Yoder, A. D., Zenil-Ferguson, R., Zinner, D., Weisrocket, D. W. (2023). Not one, but multiple radiations underlie the biodiversity of Madagascar's endangered lemurs. *bioRxiv*, 2023.04.26.537867. https://doi.org/10.1101/2023.04.26.537867

Fabre, P. H., Rodrigues, A., & Douzery, E. J. P. (2009). Patterns of macroevolution among Primates inferred from a supermatrix of mitochondrial and nuclear DNA. *Molecular Phylogenetics and Evolution, 53*(3), 808–825. https://doi.org/10.1016/j.ympev.2009.08.004

Génin, F. (2021). Speciation by Sensory Drive in the *Paragalago zanzibaricus* Species Complex. *International Journal of Primatology, 42*(3), 478–498. https://doi.org/10.1007/s10764-021-00213-7

Génin, F., Yokwana, A., Kom, N., Couette, S., Dieuleveut, T., Nash, S. D., & Masters, J. C. (2016). A new galago species for South Africa (Primates: Strepsirhini: Galagidae). *African Zoology, 51*(3), 135–143.

Geoffroy Saint-Hilaire, E. (1796). Mammifères. Mémoire sur les rapports naturels des makis Lemur, L. et description d'une espèce nouvelle de Mammifère. *Magasin Encyclopédique, 2*(1), 20–50.

Geoffroy Saint-Hilaire, E. (1812). Tableau des quadrumanes, ou des animaux composant le premier ordre de la classe des mammifères. *Annales du Muséum National d'Histoire Naturelle, Paris, 19*, 85–122.

Goodman, M., Porter, C. A., Czelusniak, J., Page, S. L., Schneider, H., Shoshani, J., et al. (1998). Toward a Phylogenetic Classification of Primates Based on DNA Evidence Complemented by Fossil Evidence. *Molecular Phylogenetics and Evolution, 9*(3), 585–598. https://doi.org/10.1006/mpev.1998.0495

Gray, J. E. (1863). Revision of the species of lemuroid animals, with the description of some new species. *Proceedings of the Zoological Society of London, 1863*(9), 129–152.

Gray, J. E. (1872). Notes on Propithecus, Indris, and other lemurs (Lemurina) in the British Museum. *Proceedings of the Zoological Society of London* (Vol. 1872, pp. 846–860).

Green, E. J., & Speller, C. F. (2017). Novel Substrates as Sources of Ancient DNA: Prospects and Hurdles. *Genes, 8*(7), 180. https://doi.org/10.3390/genes8070180

Groves, C. P. (2001a). *Primate Taxonomy*. Smithsonian Institution Press.

Groves, Colin. (2001b). Why taxonomic stability is a bad idea, or why are there so few species of primates (or are there?). *Evolutionary Anthropology: Issues, News, and Reviews, 10*(6), 192–198. https://doi.org/10.1002/evan.10005

Groves, C. P. (1974). Taxonomy and phylogeny of prosimians. In R. D. Martin, G. A. Doyle, & A. C. Walker (Eds.), *Prosimian Biology* (pp. 449–473). London: Duckworth.

Grubb, P., Butynski, T. M., Oates, J. F., Bearder, S. K., Disotell, T. R., Groves, C. P., & Struhsaker, T. T. (2003). Assessment of the Diversity of African Primates. *International Journal of Primatology, 24*(6), 1301–1357. https://doi.org/10.1023/B:IJOP.0000005994.86792.b9

Gunnell, G. F., Boyer, D. M., Friscia, A. R., Heritage, S., Manthi, F. K., Miller, E. R., et al. (2018). Fossil lemurs from Egypt and Kenya suggest an African origin for Madagascar's aye-aye. *Nature Communications, 9*(1), 3193. https://doi.org/10.1038/s41467-018-05648-w

Guschanski, K., Krause, J., Sawyer, S., Valente, L. M., Bailey, S., Finstermeier, K., et al. (2013). Next-Generation Museomics Disentangles One of the Largest Primate Radiations. *Systematic Biology, 62*(4), 539–554. https://doi.org/10.1093/sysbio/syt018

Harcourt, C. S., & Nash, L. T. (1986). Social organization of Galagos in Kenyan coastal forests: I. *Galago zanzibaricus*. *American Journal of Primatology, 10*(4), 339–355. https://doi.org/10.1002/ajp.1350100406

Harcourt, C., & Perkin, A. (2013). *Otolemur garnettii* Small-eared greater galago. *Mammals of Africa, 2*, 413–416.

Harrison, T. (2010). Later Tertiary Lorisiformes. In L. Werdelin (Ed.), *Cenozoic Mammals of Africa*. University of California Press. https://doi.org/10.1525/california/9780520257214.003.0020

Harrison, T. (2011). Galagidae (Lorisoidea, Primates). In T. Harrison (Ed.), *Paleontology and Geology of Laetoli: Human Evolution in Context: Fossil Hominins and the Associated Fauna* (2nd ed., pp. 75–81). Springer Netherlands. https://doi.org/10.1007/978-90-481-9962-4_5

Harris, J. M., Leakey, M. G., & Cerling, T. E. (2003). Early Pliocene tetrapod remains from Kanapoi, Lake Turkana Basin, Kenya. *Contributions in Science, 498*, 39–113.

Henry, C. S. (1985). Sibling Species, Call Differences, and Speciation in Green Lacewings (neuroptera: Chrysopidae: *Chrysoperla*). *Evolution, 39*(5), 965–984. https://doi.org/10.1111/j.1558-5646.1985.tb00441.x

Herrera, J. P., & Dávalos, L. M. (2016). Phylogeny and divergence times of lemurs inferred with recent and ancient fossils in the tree. *Systematic biology, 65*(5), 772–791.

Honess, P., & Bearder, S. (1996). Descriptions of the dwarf galago species of Tanzania. *African Primates, 2*(2), 75–79.

Hotaling, S., Foley, M. E., Lawrence, N. M., Bocanegra, J., Blanco, M. B., Rasoloarison, R., et al. (2016). Species discovery and validation in a cryptic radiation of endangered primates: coalescent-based species delimitation in Madagascar's mouse lemurs. *Molecular Ecology, 25*(9), 2029–2045.

Hykin, S. M., Bi, K., & McGuire, J. A. (2015). Fixing Formalin: A Method to Recover Genomic-Scale DNA Sequence Data from Formalin-Fixed Museum Specimens Using High-Throughput Sequencing. *PLOS ONE, 10*(10), e0141579. https://doi.org/10.1371/journal.pone.0141579

Isaac, N. J. B., Mallet, J., & Mace, G. M. (2004). Taxonomic inflation: its influence on macroecology and conservation. *Trends in Ecology & Evolution, 19*(9), 464–469. https://doi.org/10.1016/j.tree.2004.06.004

Jenkins, P., Masters, J. C., Groves, C., & Couette, S. (2018). Case 3742 — *Galago demidoff* Fischer, 1806 (currently *Galagoides*; Mammalia, Primates, Galagidae): proposed conservation of the specific name and designation of a neotype. *Lemur minutus* Cuvier, 1797: proposed designation of a neotype. *The Bulletin of Zoological Nomenclature, 75*(1), 21–31. https://doi.org/10.21805/bzn.v75.a008

Kingdon, J. (1997). *The Kingdon field guide to African mammals*. A&C Black.

Kingdon, J. (2015). *The Kingdon Field Guide to African Mammals* (2nd ed.). Bloomsbury Publishing.

Kunimatsu, Y., Nakatsukasa, M., Sakai, T., Saneyoshi, M., Sawada, Y., & Nakaya, H. (2017). A newly discovered galagid fossil from Nakali, an early Late Miocene locality of East Africa. *Journal of Human Evolution, 105*, 123–126. https://doi.org/10.1016/j.jhevol.2017.02.003

Le Gros Clark, W. E., & Thomas, D. P. (1952). The Miocene lemuroids of East Africa. *Fossil Mammals of Africa, 5*, 1–20.

Liedigk, R., Kolleck, J., Böker, K. O., Meijaard, E., Md-Zain, B. M., Abdul-Latiff, M. A. B., et al. (2015). Mitogenomic phylogeny of the common long-tailed macaque (*Macaca fascicularis fascicularis*). *BMC Genomics, 16*(1), 222. https://doi.org/10.1186/s12864-015-1437-0

Lim, H. C., & Braun, M. J. (2016). High-throughput SNP genotyping of historical and modern samples of five bird species via sequence capture of ultraconserved elements. *Molecular Ecology Resources, 16*(5), 1204–1223. https://doi.org/10.1111/1755-0998.12568

Livingstone, D., & Kingdon, J. (2013). The evolution of a continent: geography and geology. *Mammals of Africa, 1*, 27–42.

López-Torres, S., & Silcox, M. T. (2020). What We Know (and Don't Know) About the Fossil Records of Lorisids. In A. M. Burrows & K. A. I. Nekaris (Eds.), *Evolution, Ecology and Conservation of Lorises and Pottos* (pp. 33–46). Cambridge University Press. https://doi.org/10.1017/9781108676526.005

MacInnes, D. (1943). Notes on the east African Miocene primates. *Journal of the East Africa and Uganda Natural History Society, 17*(3–4), 141–181.

Markolf, M., Brameier, M., & Kappeler, P. M. (2011). On species delimitation: Yet another lemur species or just genetic variation? *BMC Evolutionary Biology, 11*(1), 216.

Markolf, M., Zinowsky, M., Keller, J. K., Borys, J., Cillov, A., & Schülke, O. (2022). Toward Passive Acoustic Monitoring of Lemurs: Using an Affordable Open-Source System to Monitor *Phaner* Vocal Activity and Density. *International Journal of Primatology, 43*(3), 409–433. https://doi.org/10.1007/s10764-022-00285-z

Martin, R. D. (1968). Towards a new definition of primates. *Man, 3*(3), 377–401. https://doi.org/10.2307/2798876

Mason, V. C., Li, G., Helgen, K. M., & Murphy, W. J. (2011). Efficient cross-species capture hybridization and next-generation sequencing of mitochondrial genomes from noninvasively sampled museum specimens. *Genome Research, 21*(10), 1695–1704. https://doi.org/10.1101/gr.120196.111

Masters, J. C. (1993). Primates and Paradigms. In W. H. Kimbel & L. B. Martin (Eds.), *Species, Species Concepts and Primate Evolution* (pp. 43–64). Springer, US. https://doi.org/10.1007/978-1-4899-3745-2_3

Masters, J. C. (1998). Speciation in the Lesser Galagos. *Folia Primatologica, 69*(Suppl. 1), 357–370. https://doi.org/10.1159/000052724

Masters, Judith C., & Bragg, N. P. (2000). Morphological correlates of speciation in bush babies. *International Journal of Primatology, 21*(5), 793–813.

Masters, J. C., & Brothers, D. J. (2002). Lack of congruence between morphological and molecular data in reconstructing the phylogeny of the galagonidae. *American Journal of Physical Anthropology, 117*(1), 79–93. https://doi.org/10.1002/ajpa.10001

Masters, J. C., & Couette, S. (2015). Characterizing cryptic species: A morphometric analysis of craniodental characters in the dwarf galago genus *Galagoides*. *American Journal of Physical Anthropology, 158*(2), 288–299. https://doi.org/10.1002/ajpa.22792

Masters, J. C., & Spencer, H. G. (1989). Why We Need a New Genetic Species Concept. *Systematic Zoology, 38*(3), 270–279. https://doi.org/10.2307/2992287

Masters, J. C., Boniotto, M., Crovella, S., Roos, C., Pozzi, L., & Delpero, M. (2007). Phylogenetic relationships among the Lorisoidea as indicated by craniodental morphology and mitochondrial sequence data. *American Journal of Primatology, 69*(1), 6–15. https://doi.org/10.1002/ajp.20322

Masters, J. C., Gamba, M., & Génin, F. (2013). What's in a Name? Higher Level Taxonomy of the Prosimian Primates. *Leaping Ahead: Advances in Prosimian Biology, 2013*, 3–9.

Masters, J. C., Génin, F., Couette, S., Groves, C. P., Nash, S. D., Delpero, M., & Pozzi, L. (2017). A new genus for the eastern dwarf galagos (Primates: Galagidae). *Zoological Journal of the Linnean Society, 181*(1), 229–241. https://doi.org/10.1093/zoolinnean/zlw028

Masters, J. C. (1988). Speciation in the greater galagos (Prosimii: Galaginae): review and synthesis. *Biological journal of the Linnean Society.* https://doi.org/10.1111/j.1095-8312.1988.tb01954.x

Mayr, E. (1963). Animal species and evolution. *Animal species and evolution.* Harvard University Press.

McCormack, J. E., Tsai, W. L. E., & Faircloth, B. C. (2016). Sequence capture of ultraconserved elements from bird museum specimens. *Molecular Ecology Resources, 16*(5), 1189–1203. https://doi.org/10.1111/1755-0998.12466

McCrossin, M. L. (1992). New species of bushbaby from the middle Miocene of Maboko Island, Kenya. *American Journal of Physical Anthropology, 89*(2), 215–233.

Mein, P., & Pickford, M. (2006). Late Miocene micromammals from the Lukeino Formation (6.1 to 58 M.a), Kenya. *Publications de la Société Linnéenne de Lyon, 75*(4), 183–223. https://doi.org/10.3406/linly.2006.13628

Miller, E., Luhrs, A., Mancini, A., Blair, M. E., & Pozzi, L. (2023). Assessing Ecological Divergence and Speciation Scenarios of the *Paragalago zanzibaricus* Species Complex Through Climatic Niche Modeling. *International Journal of Primatology.* https://doi.org/10.1007/s10764-023-00374-7

Mivart, S. G. (1864). Notes on the crania and dentition of the Lemuridae. In: Presented at the Proceedings of the Zoological Society London, (vol. 1865, pp. 836–844)

Morley, R. J. (2000). *Origin and evolution of tropical rain forests*. John Wiley & Sons.

Morley, R., & Kingdon, J. (2013). Africa's environmental and climatic past. *Mammals of Africa, 1*, 43–56.

Nash, L., Bearder, S., & Olson, T. (1989). Synopsis of Galago species characteristics. *International Journal of Primatology, 10*, 57–80. https://doi.org/10.1007/BF02735704

Nekaris, K.A.-I. (2013). Family Galagidae (galagos). In R. A. Mittermeier, A. B. Rylands, & D. E. Wilson (Eds.), *Handbook of the mammals of the world-volume III Primates* (pp. 184–209). Lynx Edicions.

Nekaris, K. A. I., & Bearder, S. K. (2007). *The Lorisiform primates of Asia and mainland Africa* (pp. 24–45). Primates in Perspective. Oxford University Press.

Oates, J. F. (2011). *Primates of West Africa: a field guide and natural history*. Conservation International.

Olivieri, G., Zimmermann, E., Randrianambinina, B., Rasoloharijaona, S., Rakotondravony, D., Guschanski, K., & Radespiel, U. (2007). The ever-increasing diversity in mouse lemurs: Three new species in north and northwestern Madagascar. *Molecular Phylogenetics and Evolution, 43*(1), 309–327. https://doi.org/10.1016/j.ympev.2006.10.026

Olson, T. R. (1979). *Studies on aspects of the morphology of the genus Otolemur Coquerel, 1859 (Primates: Galagidae)*. University of London.

Olson, T. (1981). Systematics and zoogeography of the greater galagos. *Presented at the American Journal of Physical Anthropology* (54th ed., pp. 259–259). Wiley & Sons INC.

Hill, W. C. O. (1953). *Primates: comparative anatomy and taxonomy. Volume I. Strepsirhini*. Edinburgh: Edinburgh University Press.

Padial, J. M., & Miralles, A. (2010). The integrative future of taxonomy. *Frontiers in Zoology, 7*, 16.

Paterson, H. (1978). More evidence against speciation by reinforcement. *South African Journal of Science, 74*(10), 369.

Paterson, H. E., & McEvey, Shane F. (1993). *Evolution and the recognition concept of species: collected writings*. Johns Hopkins University Press Baltimore.

Paterson, H. E. (1985). The recognition concept of species. In S. Vrba (Ed.), *Species and speciation* (pp. 21–29). Transvaal Museum.

Penna, A., Dillon, R., Bearder, S. K., Karlsson, J., Perkin, A., & Pozzi, L. (2023). Phylogeography and evolutionary lineage diversity in the small-eared greater galago, *Otolemur garnettii* (Primates: Galagidae). *Zoological Journal of the Linnean Society, 198*(1), 131–148. https://doi.org/10.1093/zoolinnean/zlac079

Penna, A., Blair, E., Lui, M., Peters, H. L., Kistler, L., & Pozzi, L. (2024). Unlocking the potential of natural history collections to support galago evolutionary research and conservation. *International Journal of Primatology*. https://doi.org/10.1007/s10764-024-00429-3

Perkin, A. (2007). Comparative penile morphology of East African galagos of the genus Galagoides (family Galagidae): implications for taxonomy. *American Journal of Primatology: Official Journal of the American Society of Primatologists, 69*(1), 16–26.

Perkin, A., Bearder, S., Butynski, T. M., Agwanda, B., & Bytebier, B. (2002). The Taita Mountain Dwarf Galago Galagoides sp.: A new primate for Kenya. *Journal of East African Natural History, 91*(1), 1–13. https://doi.org/10.2982/0012-8317(2002)91[1:TTMDGG]2.0.CO;2

Phillips, M. J. (2016). Geomolecular Dating and the Origin of Placental Mammals. *Systematic Biology, 65*(3), 546–557. https://doi.org/10.1093/sysbio/syv115

Phillips, M. J., & Fruciano, C. (2018). The soft explosive model of placental mammal evolution. *BMC Evolutionary Biology, 18*(1), 104. https://doi.org/10.1186/s12862-018-1218-x

Phukuntsi, Metlholo Andries, Du Plessis, M., Dalton, D. L., Jansen, R., Cuozzo, F. P., Sauther, M. L., & Kotze, A. (2020). Population genetic structure of the thick-tailed bushbaby (*Otolemur crassicaudatus*) from the Soutpansberg Mountain range, Northern South Africa, based on four mitochondrial DNA regions. *Mitochondrial DNA Part A, 31*(1), 1–10. https://doi.org/10.1080/24701394.2019.1694015

Phukuntsi, Metlholo A., Du Plessis, M., Dalton, D. L., Jansen, R., Sauther, M. L., Cuozzo, F. P., & Kotze, A. (2021). Population and genetic structure of a male-dispersing strepsirrhine, *Galago moholi* (Primates, Galagidae), from northern South Africa, inferred from mitochondrial DNA. *Primates, 62*(4), 667–675. https://doi.org/10.1007/s10329-021-00912-y

Pickford, M., & Senut, B. (2001). The geological and faunal context of Late Miocene hominid remains from Lukeino, Kenya. *Comptes Rendus de l'Académie des Sciences - Series IIA - Earth and Planetary Science, 332*(2), 145–152. https://doi.org/10.1016/S1251-8050(01)01528-2

Pickford, M., Wanas, H., & Soliman, H. (2006). Indications for a humid climate in the Western Desert of Egypt 11–10 Myr ago: evidence from Galagidae (Primates, Mammalia). *Comptes Rendus Palevol, 5*(8), 935–943. https://doi.org/10.1016/j.crpv.2006.09.001

Pickford, M., Mocke, H., Ségalen, L., & Senut, B. (2016). Update of the Pliocene fauna of the Ekuma Valley, Etosha, Namibia. *Communications of the Geological Survey of Namibia, 17*, 115–144.

Pocock, R. I. (1918). On the external characters of the lemurs and of *Tarsius*. *Presented at the Proceedings of the Zoological Society of London* (88th ed., pp. 19–53). Wiley Online Library.

Porter, L. M., de la Torre, S., Pérez-Peña, P., & Cortés-Ortiz, L. (2021). Taxonomic diversity of *Cebuella* in the western Amazon: Molecular, morphological and pelage diversity of museum and free-ranging specimens. *American Journal of Physical Anthropology, 175*(1), 251–267. https://doi.org/10.1002/ajpa.24266

Pozzi, L. (2016). The role of forest expansion and contraction in species diversification among galagos (Primates: Galagidae). *Journal of Biogeography, 43*(10), 1930–1941. https://doi.org/10.1111/jbi.12846

Pozzi, L., & Penna, A. (2022). Rocks and clocks revised: New promises and challenges in dating the primate tree of life. *Evolutionary Anthropology: Issues, News, and Reviews, 31*(3), 138–153. https://doi.org/10.1002/evan.21940

Pozzi, L., Disotell, T. R., & Masters, J. C. (2014). A multilocus phylogeny reveals deep lineages within African galagids (Primates: Galagidae). *BMC Evolutionary Biology, 14*(1), 72. https://doi.org/10.1186/1471-2148-14-72

Pozzi, L., Nekaris, K.A.-I., Perkin, A., Bearder, S. K., Pimley, E. R., Schulze, H., et al. (2015). Remarkable ancient divergences amongst neglected lorisiform primates: Phylogeny of Lorisiform Primates. *Zoological Journal of the Linnean Society, 175*(3), 661–674. https://doi.org/10.1111/zoj.12286

Pozzi, L., Disotell, T. R., Bearder, S. K., Karlsson, J., Perkin, A., & Gamba, M. (2019). Species Boundaries within Morphologically Cryptic Galagos: Evidence from Acoustic and Genetic Data. *Folia Primatologica, 90*(Suppl. 5), 279–299. https://doi.org/10.1159/000496972

Pozzi, L., Penna, A., Bearder, S. K., Karlsson, J., Perkin, A., & Disotell, T. R. (2020). Cryptic diversity and species boundaries within the *Paragalago zanzibaricus* species complex. *Molecular Phylogenetics and Evolution, 150*, 106887. https://doi.org/10.1016/j.ympev.2020.106887

Rasmussen, D. T., & Nekaris, K. A. (1998). Evolutionary History of Lorisiform Primates. *Folia Primatologica, 69*(7), 250–285. https://doi.org/10.1159/000052716

Ravaglia, D., Ferrario, V., De Gregorio, C., Carugati, F., Raimondi, T., Cristiano, W., et al. (2023). There You Are! Automated Detection of Indris' Songs on Features Extracted from Passive Acoustic Recordings. *Animals, 13*(2), 241. https://doi.org/10.3390/ani13020241

Raxworthy, C. J., & Smith, B. T. (2021). Mining museums for historical DNA: advances and challenges in museomics. *Trends in Ecology & Evolution, 36*(11), 1049–1060. https://doi.org/10.1016/j.tree.2021.07.009

Roos, C., Schmitz, J., & Zischler, H. (2004). Primate jumping genes elucidate strepsirrhine phylogeny. *Proceedings of the National Academy of Sciences, 101*(29), 10650–10654. https://doi.org/10.1073/pnas.0403852101

Rosti, H., Heiskanen, J., Bearder, S., Lombo, B., Pihlström, H., Pellikka, P., & Rikkinen, J. (2023). Distribution, Population Density, and Behavior of Dwarf Galagos (*Paragalago* sp.) in Taita Hills, Kenya. *International Journal of Primatology*. https://doi.org/10.1007/s10764-023-00390-7

Rowe, N., & Myers, M. (Eds.). (2016). *All the world's primates*. Pogonias Press.

Rowe, K. C., Singhal, S., Macmanes, M. D., Ayroles, J. F., Morelli, T. L., Rubidge, E. M., et al. (2011). Museum genomics: low-cost and high-accuracy genetic data from historical specimens. *Molecular Ecology Resources, 11*(6), 1082–1092. https://doi.org/10.1111/j.1755-0998.2011.03052.x

Roycroft, E., MacDonald, A. J., Moritz, C., Moussalli, A., Portela Miguez, R., & Rowe, K. C. (2021). Museum genomics reveals the rapid decline and extinction of Australian rodents since European settlement. *Proceedings of the National Academy of Sciences, 118*(27), e2021390118. https://doi.org/10.1073/pnas.2021390118

Ruane, S., & Austin, C. C. (2017). Phylogenomics using formalin-fixed and 100+ year-old intractable natural history specimens. *Molecular Ecology Resources, 17*(5), 1003–1008. https://doi.org/10.1111/1755-0998.12655

Schlick-Steiner, B. C., Steiner, F. M., Seifert, B., Stauffer, C., Christian, E., & Crozier, R. H. (2010). Integrative Taxonomy: A Multisource Approach to Exploring Biodiversity. *Annual Review of Entomology, 55*(1), 421–438. https://doi.org/10.1146/annurev-ento-112408-085432

Schwarz, E. (1931). IV.— On the African long-tailed Lemurs or Galagos. *Annals and Magazine of Natural History, 7*(37), 41–66. https://doi.org/10.1080/00222933108673281

Seiffert, Erik R. (2007a). Evolution and Extinction of Afro-Arabian Primates Near the Eocene-Oligocene Boundary. *Folia Primatologica, 78*(5–6), 314–327. https://doi.org/10.1159/000105147

Seiffert, Erik R. (2007b). Early evolution and biogeography of lorisiform strepsirrhines. *American Journal of Primatology, 69*(1), 27–35. https://doi.org/10.1002/ajp.20324

Seiffert, Erik R., Simons, E. L., & Attia, Y. (2003). Fossil evidence for an ancient divergence of lorises and galagos. *Nature, 422*(6930), 421–424. https://doi.org/10.1038/nature01489

Seiffert, E. R., Simons, E. L., Ryan, T. M., & Attia, Y. (2005). Additional remains of *Wadilemur elegans*, a primitive stem galagid from the late Eocene of Egypt. *Proceedings of the National Academy of Sciences, 102*(32), 11396–11401. https://doi.org/10.1073/pnas.0505310102

Seiffert, Erik R., Boyer, D. M., Fleagle, J. G., Gunnell, G. F., Heesy, C. P., Perry, J. M. G., & Sallam, H. M. (2018). New adapiform primate fossils from the late Eocene of Egypt. *Historical Biology, 30*(1–2), 204–226. https://doi.org/10.1080/08912963.2017.1306522

Simpson, G. G. (1965). Family: Galagidae. In L. Leakey (Ed.), *Olduvai Gorge 1951–61: A preliminary report on the geology and fauna* (1st ed., pp. 15–16). Cambridge University Press.

Simpson, G. G. (1967). The Tertiary lorisiform primates of Africa. *Bulletin of the Museum of Comparative Zoology, 136*, 39–61.

Simons, E. L. (1997). Discovery of the smallest Fayum Egyptian primates (Anchomomyini, Adapidae). *Proceedings of the National Academy of Sciences, 94*(1), 180–184.

Sites, J. W., Jr., & Marshall, J. C. (2004). Operational criteria for delimiting species. *Annual Review of Ecology, Evolution, and Systematics, 35*, 199–227.

Springer, M. S., Meredith, R. W., Gatesy, J., Emerling, C. A., Park, J., Rabosky, D. L., et al. (2012). Macroevolutionary Dynamics and Historical Biogeography of Primate Diversification Inferred from a Species Supermatrix. *PLoS ONE, 7*(11), e49521. https://doi.org/10.1371/journal.pone.0049521

Stanyon, R., Wienberg, J., Simons, E. L., & Izard, M. K. (1992). A Third Karyotype for *Galago demidovii* Suggests the Existence of Multiple Species. *Folia Primatologica, 59*(1), 33–38. https://doi.org/10.1159/000156639

Stevens, N. (2017). Oligocene primates. In M. Bezanson, K. C. MacKinnon, E. Riley, C. J. Campbell, K. A. I. Nekaris, A. Estrada, A. F. Di Fiore, S. Ross, L. E. Jones-Engel, B. Thierry, R. W. Sussman, C. Sanz, J. Loudon, S. Elton, & A. Fuentes (Eds.), *The international encyclopedia of primatology* https://doiorg.libweb.lib.utsa.edu/10.1002/9781119179313.wbprim0432

Stevens, N. J., Seiffert, E. R., O'Connor, P. M., Roberts, E. M., Schmitz, M. D., Krause, C., Gorscak, E., Ngasala, S., Hieronymus, T. L., & Temu, J. (2013). Palaeontological evidence for an oligocene divergence between old world monkeys and apes. *Nature, 497*, 611–614. https://doi.org/10.1038/nature12161

Stiner, E., & Turmelle, A. (2003). Galagid taxonomy and the placement of the needle-clawed galago (*Euoticus*): based on cytochrome b, 12S and 16S partial sequences. *African Primates, 6*(1–2), 3–10.

Svensson, M. S., Bersacola, E., Mills, M. S., Munds, R. A., Nijman, V., Perkin, A., et al. (2017). A giant among dwarfs: a new species of galago (Primates: Galagidae) from Angola. *American Journal of Physical Anthropology, 163*(1), 30–43.

Svensson, M. S., Morcatty, T. Q., Nijman, V., & Shepherd, C. R. (2021). Shedding Light on the Trade in Nocturnal Galagos. *Primate Conservation, 35*, 157–168.

Tattersall, I. (2007). Madagascar's lemurs: cryptic diversity or taxonomic inflation? *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews, 16*(1), 12–23.

Tattersall, I. (2012). Species-level diversity among Malagasy lemurs. *Leaping Ahead* (pp. 11–20). Springer.

Thiele, D., Razafimahatratra, E., & Hapke, A. (2013). Discrepant partitioning of genetic diversity in mouse lemurs and dwarf lemurs – Biological reality or taxonomic bias? *Molecular Phylogenetics and Evolution, 69*(3), 593–609. https://doi.org/10.1016/j.ympev.2013.07.019

van der Valk, T., Lona Durazo, F., Dalén, L., & Guschanski, K. (2017). Whole mitochondrial genome capture from faecal samples and museum-preserved specimens. *Molecular Ecology Resources, 17*(6), e111–e121. https://doi.org/10.1111/1755-0998.12699

van der Valk, T., Díez-del-Molino, D., Marques-Bonet, T., Guschanski, K., & Dalén, L. (2019). Historical Genomes Reveal the Genomic Consequences of Recent Population Decline in Eastern Gorillas. *Current Biology, 29*(1), 165-170.e6. https://doi.org/10.1016/j.cub.2018.11.055

Walker. (1987). Fossil Galaginae from Laetoli. In M. D. Leakey & J. M. Harris (Eds.), *Laetoli: A Pliocene site in Northern Tanzania* (pp. 88–90). Clarendon Press.

Walker, A. C. (1969). True affinities of Propotto leakeyi Simpson 1967. *Nature, 223*, 647–648.

Waterhouse, G. R. (1838). *Catalogue of the Mammalia Preserved in the Museum of the Zoological Society of London*. Taylor.

Weisrock, D. W., Rasoloarison, R. M., Fiorentino, I., Ralison, J. M., Goodman, S. M., Kappeler, P. M., & Yoder, A. D. (2010). Delimiting species without nuclear monophyly in Madagascar's mouse lemurs. *PLoS One, 5*(3), e9883.

Wesselman, H. B. (1984). The Omo Micromammals: Systematics and Paleo-Ecology of Early Man Sites from Ethiopia. *Contributions to Vertebrate Evolution* (Vol. 7, p. 165). Basel, Switzerland: Karger.

Wisniewski, A. L., Lloyd, G. T., & Slater, G. J. (2022). Extant species fail to estimate ancestral geographical ranges at older nodes in primate phylogeny. *Proceedings of the Royal Society B: Biological Sciences, 289*(1975), 20212535. https://doi.org/10.1098/rspb.2021.2535

Yao, L., Li, H., Martin, R. D., Moreau, C. S., & Malhi, R. S. (2017). Tracing the phylogeographic history of Southeast Asian long-tailed macaques through mitogenomes of museum specimens. *Molecular Phylogenetics and Evolution, 116*, 227–238. https://doi.org/10.1016/j.ympev.2017.08.006

Yoder, A. D., Campbell, C. R., Blanco, M. B., dos Reis, M., Ganzhorn, J. U., Goodman, S. M., et al. (2016). Geogenetic patterns in mouse lemurs (genus *Microcebus*) reveal the ghosts of Madagascar's forests past. *Proceedings of the National Academy of Sciences, 113*(29), 8049–8056. https://doi.org/10.1073/pnas.1601081113

Zachos, J., Pagani, M., Sloan, L., Thomas, E., & Billups, K. (2001). Trends, Rhythms, and Aberrations in Global Climate 65 Ma to Present. *Science, 292*(5517), 686–693. https://doi.org/10.1126/science.1059412

Zimmermann, E. (1990). Differentiation of vocalizations in bushbabies (Galaginae, Prosimiae, Primates) and the significance for assessing phylogenetic relationships. *Journal of Zoological Systematics and Evolutionary Research, 28*(3), 217–239. https://doi.org/10.1111/j.1439-0469.1990.tb00377.x

Zimmermann, E., & Radespiel, U. (2014). Species concepts, diversity, and evolution in primates: Lessons to be learned from mouse lemurs. *Evolutionary Anthropology: Issues, News, and Reviews, 23*(1), 11–14. https://doi.org/10.1002/evan.213

Zimmermann, E., Bearder, S. K., Doyle, G. A., & Andersson, A. B. (1988). Variations in Vocal Patterns of Senegal and South African Lesser Bushbabies and Their Implications for Taxonomic Relationships. *Folia Primatologica, 51*(2–3), 87–105. https://doi.org/10.1159/000156360