A new genus name for pygmy lorises, *Xanthonycticebus* gen. nov. (Mammalia, Primates)

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Abstract

Lorisiformes are nocturnal primates from Africa and Asia with four genera, with two (*Arctocebus* and *Loris*), three (*Perodicticus*) and nine (*Nycticebus*) recognised species. Their cryptic lifestyle and lack of study have resulted in an underappreciation of the variation at the species and genus level. There are marked differences between the pygmy slow loris *Nycticebus pygmaeus* and the other *Nycticebus* species and, in the past, several authors have suggested that these may warrant recognition at the generic level. We here combine morphological, behavioural, karyotypical and genetic data to show that these contrasts are, indeed, significantly large and consistent. We propose *Xanthonycticebus* gen. nov. as a new genus name for the pygmy slow lorises and suggest a common name of pygmy lorises. Based on analysis of complete mitochondrial DNA sequences, we calculate the divergence of pygmy from slow lorises at 9.9–10.0%. The median date, calculated for the divergence between *Xanthonycticebus* and *Nycticebus*, is 10.5 Mya (range 4.9–21.0 Mya). *Xanthonycticebus* differs from *Nycticebus* by showing sympatry with other slow loris species, by habitually giving birth to twins, by showing seasonal body mass and whole body coat colour changes (absent in other species living at similar latitudes) and a multi-male, multi-female social system. Pygmy lorises are easily recognisable by the absence of hair on their ears and more protruding premaxilla. *Xanthonycticebus* is threatened by habitat loss and illegal trade despite legal protection across their range and all slow lorises are listed on appendix 1 of CITES. The suggested nomenclatural changes should not affect their legal status.

Key Words

conservation, cytotaxonomy, Lorisidae, Lorisiformes, primate taxonomy, Strepsirrhini

Background

Lorisiformes are a group of nocturnal primates with two genera, *Perodicticus* Bennett, 1831 (three species) and *Arctocebus* Gray, 1863 (two species) occurring in west and equatorial Africa and two, *Loris* É. Geoffroy, 1796 (two species) and *Nycticebus*, É. Geoffroy, 1812 (nine species) occurring in south, east and southeast Asia (Groves 2001; Nekaris 2013; Rowe and Meyers 2016). In west-central Africa, *Perodicticus edwardsi* Bouvier, 1979 and *Arctocebus* occur in sympatry and in eastern Indochina, *Nycticebus bengalensis* (Lacépède, 1800) and *N. pygmaeus* Bonhote, 1907 occur in sympathy. All other species have allopatric distributions.

At a major international conference on nocturnal primates in 1993, Schwartz and Beutel (1995: 189), at a time when only two species of *Nycticebus* were recognised, commented that “*N. coucang* and *N. pygmaeus* are species that are remarkable for their variability”. Since then, a considerable amount of comparative research has been conducted on the slow lorises, including morphologically (e.g. Ravosa 1998; Groves 2001; Nekaris and Jaffe 2007; Munds et al. 2013; Xie et al. 2013 7), behaviourally (e.g. Fitch-Snyder and Ehrlich 2003; Nekaris et al. 2008; Nekaris et al. 2010; Streicher et al. 2012; Ni et al. 2020; Poindexter and Nekaris 2020) and genetically (e.g. Chen et al. 2006; Perelman et al. 2011; Pozzi et al. 2015; Munds et al. 2018; Munds et al. 2021). Combined, these studies
allow us to gain a better understanding of the species and higher-level taxonomy. Recent molecular phylogenetic research has revealed the divergence between genera and between species and, from this, it is evident that one species, the pygmy slow loris *Nycticebus pygmaeus* is anomalous. In combination with karyotypical, behavioural and morphological data, this supports the conclusion that this species is best placed in its own genus.

Although under the Code (International Commission on Zoological Nomenclature 1999), Art. 13.1, we are not obliged to provide a description of a new taxon (it would suffice to provide a bibliographic reference to earlier descriptions), we feel that, in this instance, it may be opportune to give a generic diagnosis.

**Order Primates Linnaeus, 1758**

Suborder Strepsirhini É. Geoffroy Saint-Hilaire, 1812
Family Lorisidae Gray, 1821

*Xanthonycticebus* gen. nov.

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**Diagnosis.** Morphological synapomorphies to *Xanthonycticebus* include: (i) skull length consistently less than 55 mm, (ii) diastema between P2 and P3, (iii) long black ears, hairless at the tips (iv) relatively narrow interorbital distance compared to *Nycticebus* and (v) full seasonal coat colour change including almost complete loss of dorsal stripe (Fig. 1). The species is furthermore distinguished from *Xanthonycticebus* species by giving birth habitually to twins, frequent sympatry with *N. bengalensis* (sensu lato) and more rapid locomotion. Regarding multiple births, this trait occurs with varying frequency in primates. Most of the marmosets and tamarins are polyovulatory and twins are the dominant litter size in the wild and most twins are considered dizygotic (Ward et al. 2014; Wåhåb et al. 2015). Old World monkeys, apes and humans are monovulatory species and while single births are the rule, multiple births do occasionally occur in various species, typically at a rate at, or below one percent (Geissmann 1990). Around two-thirds to three-quarters of these twins are estimated to be monozygotic (Geissmann 1990). This contrasts with twinning in strepsirrhines, as here all, or practically all, are dizygotic (Pasztor and Van Horn 1979).

No other species of slow lorises are known to be sympatric, with their distribution similar to gibbons *Hylobatidae* Gray, 1870 and langurs *Presbytina* Gray, 1825, which, even though having more recent evolutionary histories, contain multiple genera (Rowe and Meyers 2016). Where nocturnal primate genera or species are sympatric, different locomotor strategies have evolved, allowing reduced competition (Charles-Dominique 1977). Additional differences, as well as those from *Loris*, are summarised in Table 1.

**Eymology.** The genus name *Xanthonycticebus*, masculine, refers to the species orange/ish overall colouration and their nocturnal activity pattern; Xanto, Gr., Yellowish-orange; nykt-, Gr., night; kêbos, Gr., monkey (Gainsford 2020). Currently, the most frequently used common name of this genus is pygmy slow loris, followed by the rarely used slower slow loris or intermediary slow loris. For the common English name, we suggest pygmy loris in order to differentiate the new genus from

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**Table 1. Summary of key similarities and differences amongst the three Asian lorisiform genera.**

|                        | Loris               | Nycticebus          | Xanthonycticebus     | Reference                  |
|------------------------|---------------------|---------------------|----------------------|----------------------------|
| Lattitudinal range     | 6°N–20°N            | 8°S–28°N            | 10°N–25°N            | Rasova (1998)              |
| Altitudinal range (asl)| 0–2,000 m           | 0–2,400 m           | 50–1,500 m           | Nekaris (2013)             |
| Twins                  | Rare but occasional | Absent              | Present              | Fitch-Snyder and Ehrlich (2003) |
| Torpor                | Absent              | Present, 68 volatile| Present, 200 volatile| Streicher and Reinhart (2020) |
| Venomous              | Absent              | Present, 68 volatile| Present, 200 volatile| Hagel et al. (2007)        |
| Seasonal body mass change | Absent             | Absent              | Present              | Streicher (2004)           |
| Seasonal coat colour change | Absent            | Dorsal stripe shorter in some species | Present, dorsal stripe change | Streicher (2004); Nekaris, unpubl. data |
| Species                | Two                 | Nine                | One, possibly two    | Rowe and Meyers (2016)     |
| Body size, range       | 120–330 g           | 265–2200 g          | 360–580 g            | Nekaris (2013)             |
| Ears                   | Haired, larger than in Nycticebus | Haired and small often with tufts | Ear length intermediate and naked at tips | Osman Hill (1953)          |
| Multimale, multimale female social system | Present            | Absent              | Present              | Poindexter and Nekaris (2020) |
| Gestation              | 160–170 d           | 184–197 d           | 184–200 d            | Fitch-Snyder (2020)        |
| Molar size             | M1 larger than M2   | M1 larger than M2   | M1 larger than M2    | Osman Hill (1953)          |
| Karyotype and nucleolus organiser regions (NORs) | 2n = 62            | 2n = 50; NORs on chromosome 1, 6, 9, 15 and 23 | 2n = 50; NORs on chromosome 6, 9 and 15 | Chen et al. (1993); Goonan et al. (1995) |
| Third hand pad         | Smallest            | Intermediate or small | Largest              | Osman Hill (1953); Nekaris, unpubl. data |
| Snout                  | Narrow and pointy   | Broader and more rounded | Broader than Loris, but longer premaxilla than Nycticebus | Osman Hill (1953)          |
| Interorbit             | Narrowest           | Widest              | Intermediate         | Rasova (1998)              |
| Ocular axial and corneal diameter | AD – 14.0 mm; CD – 12.0 mm | AD – 15.7 mm; CD – 12.1 mm | AD – 15.5 mm; CD – 12.3 mm | Ross and Kirk (2007)       |
the two other loris genera (slow and slender lorises). We acknowledge, however, that with the recognition of \textit{N. menagensis} Munds, Nekaris and Ford 2013, from Bor - neo, with a minimum adult body mass of 265 g, the small size is no longer a unique feature of the pygmy loris. The most commonly-used name for pygmy lorises in Vietnamese is Cu li nhỏ, in Mnong, it is Tau kless, in Lao, it is Linh lom and in Chinese, it is \textit{Xiao lan hou} (Nijman and Nekaris 2016; Thach et al. 2018).

\textbf{Contents.} a single species, \textit{Xanthonycticebus pygmaeus} (Bonhote, 1907) is currently recognised and \textit{Nycticebus intermedius} Dao Van Tien, 1960 and the not formally described \textit{N. chinensis} are treated as synonyms. There is clear clinal latitudinal variation in body size and craniofacial size (smaller in the north) (Ravosa 1998). Variation in pelage colourations, coupled with a considerable amount of genetic divergence between available sequences deposited in GenBank (e.g. up to 2.0\% in \textit{cytb}; Fig. 1), largely from specimens without exact geographic locality data, may lead to the recognition of additional species in the future. Pozzi et al. (2020), based on monophyletic northern and southern populations of pygmy lorises from Laos PDR, Cambodia and Vietnam, advocate more research to confirm if these are, indeed, two species.

Mein and Ginsburg (1997) tentatively described a single third upper molar M3 (T Li 41) from Li Mae Long in Lamphum Province, Thailand dated to the early Miocene, 17–18 Mya, as \textit{?Nycticebus linglom} Mein & Ginsburg, 1997. The small size (1.29 × 1.82 mm) shows affini - ties with \textit{X. pygmaeus}, but absence of a hypocone and a metaconule on M3 on T Li 41 aligns it closer to \textit{N. bengalensis} than to \textit{X. pygmaeus} and Li Mae Long is situated west of the Mekong River, outside the current distribution range of \textit{X. pygmaeus}. We suggest to retain \textit{?Nycticebus linglom} within the genus \textit{Nycticebus}.

The holotype of \textit{X. pygmaeus} is a juvenile male collect - ed by J. Vassal on 13 November 1905 in Nha Thrang Vietnam \{12.24, 109.19\}, that is currently stored in the Natural History Museum London under registration number 1906.11.6.2. It is described in detail by Bonhote (1907).

\textbf{Divergence and molecular clock dates.} Several molecular phylogenetic studies have been conducted that included samples of \textit{X. pygmaeus} and two or more other \textit{Nycticebus} species; in all analyses, \textit{X. pygmaeus} is the first

\begin{figure}
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\includegraphics[width=\textwidth]{figure1.png}
\caption{Characteristics of pygmy loris \textit{Xanthonycticebus pygmaeus} gen. nov. A. Photograph of wild adult male \textit{X. pygmaeus} from Mondulkiri District, Cambodia and skull from Li Chau, Vietnam (FMNH 32499), compared with \textit{Nycticebus javanicus} from Garut Regency, Indonesia and skull (RMNH14563) from South Java, Indonesia; and with \textit{Loris lydekkerianus nordicus} from Trincomalee District, Sri Lanka and skull (FMNH95029) from Jaffna District, Sri Lanka. Features distinctive to \textit{Xanthonycticebus} include yellowish-orange colour, mid-broad snout with long premaxilla, M2 larger than M1 and ears hairless at the tips; B. Neighbour-joining tree of 175 cytochrome b sequences (alignment 1,068 bp) of \textit{Nycticebus}, \textit{Xanthonycticebus} and \textit{Loris}; C. Neighbour-joining tree of complete mtDNA sequences of \textit{Nycticebus}, \textit{Xanthonycticebus} and \textit{Loris}, with \textit{Perodicticus} as outgroup, showing considerable divergence of \textit{Xanthonycticebus} from \textit{Nycticebus}. All photographs courtesy of K.A.I. Nekaris.}
\end{figure}
group to split, thus forming two distinct reciprocal monophyletic groups. Our own analysis, based on the complete mitochondrial genome sequences of *Xanthonycticebus* (*X. pygmaeus* GenBank Accession #: KX397281), two species of Loris (*L. lydekkerianus* KC757402 from India and *L. tardigradus* AB371094 from Sri Lanka), three *Nycticebus* (*N. bengalensis* KY436589 from China, *N. c. insularis* MG515246 from Malaysia and *N. coucang* AB371094 from an unknown location) with *P. edwardsi* KC757407 from Cameroon as an outgroup, likewise shows a genetic distance of 9.9–10.0% between *X. pygmaeus* and the three other *Nycticebus* species (Fig. 1).

The divergence time between *X. pygmaeus* and the other *Nycticebus* species was estimated at between 6.4 Mya and 26.4 Mya (Table 2). Pozzi et al. (2015) commented that the gap of around six million years between the divergence of *X. pygmaeus* and the radiation of the other *Nycticebus* species may lend support to the distinction of *Nycticebus* and any of the other species. Both *Nycticebus* and *Xanthonycticebus* have *n* = 30 chromosomes, but karyotypically, the former differs from the latter by having a secondary constriction in the short arm of chromosome 1 and the additional presence of nucleolus organiser regions on chromosome 1 (Stanyon et al. 1987; Chen et al. 1993).

**Status.** *Xanthonycticebus pygmaeus* occurs naturally in Vietnam (historically south to the vicinity of Ho Chi Minh City [10.75, 106.66]), Laos PDR (west to Phongsali [21.59, 102.25]), Cambodia (east of the Mekong River), China (historically north to Lîuchun County [23.00, 104.67]) (Nekaris 2013). The species may have established itself in Thailand, west of the Mekong River, as a result of poorly planned release efforts (Osterberg and Nekaris 2015). *Xanthonycticebus pygmaeus* has been assessed as Endangered according to IUCN Red List Criteria, with the trade for medicinal purposes and as pets and habitat loss recognised as the main threats (Starr et al. 2011; Blair et al. 2020). The species is protected in all four of its range countries, but active enforcement of these laws is far from optimal (Nekaris and Starr 2015; Thã¢ch et al. 2018; Ni et al. 2020). The species is the most common loris kept in accredited zoological association and European Association of Zoos and Aquariums breeding programmes, but birth rates are low.

The genus *Xanthonycticebus* is listed in appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), precluding all commercial international trade (Nekaris and Nijman 2007).

| Type (bp) | Nycticebus species included in calculation | Split (mean, range), Mya | Reference |
|----------|------------------------------------------|--------------------------|-----------|
| Mitochondrial genes | | | |
| Cytochrome b (1140) | javancus / bengalensis / coucang / menagensis | 10.9 (7.6–14.5) | Pozzi et al. (2015) |
| Cytochrome b + cytochrome oxidase subunit 1 (536) | coucang | 26.4 (13.1–39.7) | Munds et al. (2018) |
| Nuclear genes | | | |
| 18 gene regions (9,500) | coucang | 6.4 (3.5–10.1) | Horvath et al. (2008) |
| 54 gene regions (34,927) | bengalensis / coucang | 10.2 (5.4–15.1) | Perelman et al. (2011) |
| Melanocortin 1 receptor (729) | bengalensis / coucang | 12.0 | Munds et al. (2021) |
| Recombinant activation gene 2 intron (716) | coucang | 14.5 (6.0–24.9) | Munds et al. (2018) |
| Mitochondrial and nuclear genes | | | |
| 4 genes (cytb, col, rag2, MC1R (1983)) | coucang | 18.4 (10.2–26.9) | Munds et al. (2018) |
In the proposal, submitted by Cambodia in 2007, which was accepted by consensus, three species names were singled out, including Nycticebus pygmaeus (with N. intermedius and N. chinensis listed as synonyms). As such, with respect to international trade, there is no doubt that Xanthonycticebus gen. nov. continues to receive the same level of protection and regulation as other slow lorises.

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