



A systematic reappraisal of the Rufous Potoo *Nyctibius bracteatus* (Nyctibiidae) and description of a new genus

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Abstract

The Rufous Potoo (*Nyctibius bracteatus* Gould, 1846) is the smallest member of the family Nyctibiidae, which comprises seven species endemic to the Neotropical region. Morphologically, it is highly distinct from its congeners, not only in its smaller size, but also in possessing a strange marking on its iris and having entirely rufous plumage, which is lightly vermiculated and has pronounced white spots on the wing coverts, breast, belly, flanks and undertail coverts. Molecular studies have shown extraordinarily high levels of genetic divergence amongst potoo species, and a recent genome-scale molecular phylogeny of potoo species placed *N. bracteatus* as sister to all other potoos with high confidence. Similarly, osteological data reveal that the species has several unique and plesiomorphic characters. Therefore, its distinctive morphology, in combination with unique behavioral traits, and its recurrent placement as the earliest branching terminal in phylogenetic treatments of the family, convinced us to erect a new genus for the species, *Phyllaemulor*.

Keywords Nyctibiidae · Molecular phylogeny · Genetic divergence · Osteology · Plesiomorphy

Zusammenfassung

Eine systematische Neubewertung des Tropfentagschläfers *Nyctibius bracteatus* (Nyctibiidae) und die Beschreibung einer neuen Gattung

Der Tropfentagschläfer (*Nyctibius bracteatus* Gould, 1846) ist das kleinste Mitglied der Familie der Tagschläfer (Nyctibiidae), welche sieben für die Neotropis endemische Arten umfasst. Morphologisch unterscheidet er sich stark von den anderen Arten der Gattung, nicht nur durch seine geringere Größe sondern auch durch das Vorhandensein einer eigenartigen Musterung der Iris sowie durch sein gänzlich rötlichbraunes Gefieder, das eine leichte Wellenzeichnung und deutliche weiße Flecken auf Flügeldecken, Brust, Bauch, Flanken und Unterschwanzdecken aufweist. Molekulare Studien zeigen einen ungewöhnlich hohen Grad genetischer Divergenz bei den Tagschläferarten und eine neuere molekulare Phylogenie auf Genomebene stuft *N. bracteatus* mit hoher Konfidenz als basal zu allen übrigen Tagschläfern ein. Parallel dazu belegen osteologische Daten, dass die Art verschiedene einzigartige und plesiomorphe Merkmale besitzt. Diese charakteristische Morphologie in Verbindung mit einzigartigen Verhaltensmerkmalen und der derzeitigen Platzierung auf dem basalen Zweig der Familie haben uns daher dazu bewogen, für diese Art eine neue Gattung einzuführen, *Phyllaemulor*.

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Introduction

The family Nyctibiidae comprises seven nocturnal species restricted to the Neotropical region, with the highest diversity occurring in the Amazon Basin (Cohn-Haft 1999). These species are characterized by their distinctive cryptic plumage, which act as camouflage whilst they are perched on vertical branch stubs, where they typically remain almost motionless during the day. Their nocturnal habits

and secretive behavior make them some of the most poorly known of all birds (Mariaux and Braun 1996; Brumfield et al. 1997; Cleere 1998; Holyoak 2001; Cohn-Haft 1999; Costa et al. 2010; Cleere 2010) and until recently, very little information existed on aspects such as their distribution, habitat preferences and behavior (Cohn-Haft 1999).

The first potoo species to be recognized under the accepted rules of zoological nomenclature were the Great Potoo *Nyctibius grandis*, the Common or Gray Potoo *Nyctibius griseus* and the Northern Potoo *Nyctibius jamaicensis*, which were described by Johann F. Gmelin in 1789 in the 13th edition of *Systema Naturae* of Carolus Linnaeus. At that time, the systematics of these mysterious birds had yet to be established and they were originally included within the genus *Caprimulgus* Linnaeus 1758, which currently comprises the majority of the Old World nightjars (Caprimulgidae). Prince Maximilian of Wied followed the same taxonomic treatment when describing the Long-tailed Potoo *Nyctibius aethereus* (published in 1820) and the White-winged Potoo *Nyctibius leucopterus* (published in 1821) from Bahia in northeastern Brazil. Louis J. P. Vieillot erected the genus *Nyctibius* in 1816, citing as its type species Georges-L. L. Buffon's "Grand Engoulevent de Cayenne," an early French name for Gmelin's *Caprimulgus grandis*. But it was not until the middle of the nineteenth century that Chenu and Des Murs (1851) established the family Nyctibiidae exclusively for the single genus *Nyctibius*, and this treatment has generally been followed ever since.

Nocturnal habits, cryptic plumage and upright posture make potoos highly similar in external morphology, which may explain why they have been traditionally treated within a single genus. Nevertheless, potoos show high degrees of genetic divergence (e.g., Braun and Huddleston 2009), and present remarkable variation in their internal morphology, habits and behavior. At the extremes are the bulky, pallid Great Potoo *Nyctibius grandis* weighing 450–640 g, and the sprightly, diminutive Rufous Potoo *Nyctibius bracteatus*, weighing less than 57 g (Cleere 1998; Cohn-Haft 1999).

Nyctibius bracteatus is the smallest (ca. 21–25 cm) member of the family and was the penultimate potoo species to be described, the most recent being the Andean Potoo, *Nyctibius maculosus* Ridgway, 1912. It was described by John Gould in 1846 based on a single specimen (the holotype) from Bogotá, Colombia, but it was probably a trade skin collected elsewhere at an Amazonian locality and erroneously labeled. Originally held in the collection of the Royal Institution of Liverpool, UK, the current whereabouts of the holotype is unknown. Nowadays, *N. bracteatus* is known to occur in scattered localities in Amazonian Ecuador, Peru, Bolivia, Colombia, Venezuela, Guyana, Surinam, French Guyana and Brazil (Cohn-Haft et al. 1997; Cleere 1998; Cohn-Haft 1999; Cleere and

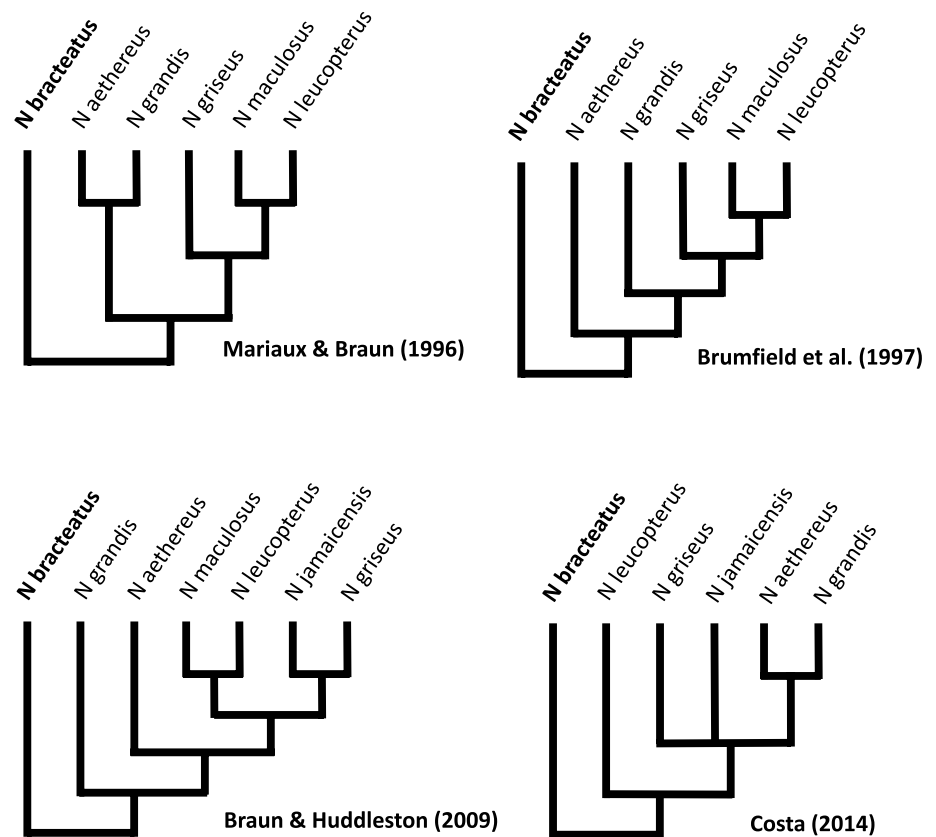
Ingels 2002; Cisneros-Heredia 2006; Restall et al. 2006; Ingels et al. 2008; Marantz et al. 2011). It is in many ways the most distinctive potoo, not only in size, but also in its habits, vocalizations and, most noticeably, its plumage, which consists of a faintly vermiculated, deep rufous pattern with marked white spots over the breast, belly, scapulars, wing coverts, flanks and undertail coverts.

Many authors have emphasized the need of a systematic review of the family Nyctibiidae (Cohn-Haft 1999; Brumfield et al. 1997; Braun and Huddleston 2009; Costa and Donatelli 2009; Costa 2014), in which all seven species are included in a single genus despite having very divergent lineages and distinctive morphological traits. Whilst more information on several taxa is needed to fully revise potoo phylogeny and classification, it is clear that establishment of new genera within the family would better reflect their evolutionary history. A recent genome-scale molecular phylogeny resolves the relationships of extant potoo species with high statistical support, providing a solid foundation to begin such a revision (White et al. 2017). Thus, based on its distinctive morphology, behavior, and voice, and its recurrent placement as the earliest branching lineage in phylogenetic treatments of the family (Fig. 1), we erect here a new genus for *N. bracteatus*.

Materials and methods

We analyzed 21 study skins and 246 skeleton specimens of *N. bracteatus* and other caprimulgidiform birds deposited in the following museums and institutions: Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG); Louisiana State University Museum of Natural Science, Baton Rouge, USA (LSUMNS); National Museum of Natural History, Smithsonian Institution, Washington DC, USA (NMNH); Field Museum of Natural History, Chicago, USA (FMNH); American Museum of Natural History, New York, USA (AMNH); Academy of Natural Sciences of Drexel University, Philadelphia, USA (ANSP); Carnegie Museum of Natural History, Pittsburgh, USA (CMNH); Florida Museum of Natural History, Gainesville, USA (FLMNH); Museum of Vertebrate Zoology, Berkeley, USA (MVZ); University of Michigan Museum of Zoology, Ann Arbor, USA (UMMZ); Museum of Comparative Zoology, Cambridge, USA (MCZ); Kansas University Museum of Natural History, Lawrence, USA (KUMNH); The Natural History Museum, Tring, UK (NHMUK); Forschungsinstitut Senckenberg, Frankfurt, Germany (SMF); Museum für Naturkunde, Berlin, Germany (ZMB); and Muséum National d'Histoire Naturelle, Paris, France (MNHN) (see Appendix 1). Plumage description follows Munsell (1994) soil color charts for coloration and granular and crumb structures. The osteology of

Fig. 1 Phylogenetic tree topologies of the family Nyctibiidae proposed in previous molecular (Mariaux and Braun 1996; Brumfield et al. 1997; Braun and Huddleston 2009) and morphological (Costa 2014) studies, recovering *Nyctibius bracteatus* as the earliest branching terminal in the family, sister to the remaining species



N. bracteatus was studied comparatively with the remaining species and described, in most cases, using Leica Wild M3B and Zeiss Stemi Mill stereomicroscopes. We studied all *Nyctibius* species (except *N. maculosus*) and the polarity of the characters presented were determined based either on comparisons with outgroups, representatives of other “caprimulgiform” and apodiform families, such as Caprimulgidae, Aegothelidae, Steatornithidae, Podargidae, Hemiprocidae and Apodidae (see Appendix 1), or on the information present in Mayr (2002). All osteological characters were studied in a comparative way and most of the relevant osteological structures were photographed or pointed out in illustrations. The osteological terminology follows Baumel and Witmer (1993) and the species nomenclature follows the South America Classification Committee (Remsen et al. 2017). The habits and behavior of the species described here are based on opportunistic field observations by the authors, especially B. M. W.

Results

Systematics

Order Caprimulgiformes (sensu Cracraft 2013).

Family Nyctibiidae.

Phyllaemulor Costa, Whitney, Braun, White, Silveira and Cleere gen. nov.

Type species

By original designation and monotypy *Nyctibius bracteatus* Gould, 1846.

Included species

Phyllaemulor bracteatus (Gould, 1846) comb. nov. Rufous Potoo.

Diagnosis

A small potoo measuring 21–25 cm in length and weighing 46–57 g. Sexes similar. Rufous-tawny plumage, paler on throat and undertail coverts, with marked white spots narrowly bordered black on the wing coverts, scapulars, lower breast, belly, flanks and undertail coverts (Figs. 2, 3). Dark brown primary and secondary feathers, and rufescent-tawny rectrices barred in dark brown. Immatures and subadults duller, with fewer white spots and boldly spotted black in crown, back, breast and belly caused by the dusky tips of the feathers. Long rectal bristles. Iris bright yellow with a dark wedge in the lowest portion.



Fig. 2 Adult (a, c and d) and chick (b) *Phyllaemulor bracteatus*, in the understory of Amazonian terra firme forests in Peru and Brazil. Photos by B. M. W. (a–c) and Francine Brondex (d)



Fig. 3 Dorsal (top) and ventral (bottom) views of *P. bracteatus* NHMUK 1888.8.1.25, showing the rufous brown plumage, with white spots on the breast, belly, flanks, scapulars and wing coverts. Copyright The Natural History Museum, Tring, UK

Etymology

The genus name *Phyllaemulor* is a masculine noun formed of the two Greek words *Phyllo* (leaf, foliage) and *aemulor* (like, strive to equal, emulate), calling attention to the highly developed leaf mimicry of the species, which is unique in Nyctibiidae (see “[Ecology and Behavior](#)”, below).

Plumage, external morphology and bare parts

Adult male—forehead, crown and nape rufescent-tawny (close to 7.5Y 4/6), very finely (less than 1 mm) barred and spotted blackish-brown (close to 7.5Y 3/4). No collar around hindneck. Mantle and back rufescent-tawny (close to 7.5Y 4/6), indistinctly barred or vermiculated dark brown. Rump and upper tail coverts also rufescent-tawny or tawny, indistinctly vermiculated dark brown. Alula and primary coverts brownish. Rest of wing coverts rufescent-tawny, speckled and vermiculated dark brown. Scapulars rufescent-tawny (close to 7.5Y 4/6) speckled brown, boldly spotted whitish towards tips of outer webs, spots bordered blackish-brown (close to 7.5Y 2.5/1) and often rather square-shaped. Ten primaries brown (close to 5YR 2.5/2); P10–P5 (numbered in descending order) buffish on outer webs (close to 7.5YR 5/8), slightly darker on P10; P4–P1 entirely dark brown (close to 5YR 2.5/2). Nine secondaries; S1–S6 dark brown (close to 5YR 2.5/2), edged rufescent-tawny (close to 7.5YR 4/6) along outer webs; S7–S9 rufescent-tawny (close to 7.5YR 4/6). Tertials rufescent-tawny (close to 7.5YR 4/6) speckled brown, broadly tipped whitish with a dark brown subterminal band. Ten retrices rufescent-tawny (close to 7.5YR 5/6), very finely (less than 1 mm) and finely (1–2 mm) barred in dark brown (close to 7.5Y 3/4) on R2–R4; R1 (the outermost tail feather) broadly barred (medium to coarse) dark brown (close to 7.5Y 2.5/2). Lores and ear coverts rufescent-tawny (close to 7.5YR 4/6), speckled or very finely barred brown (7.5Y 2.5/2). Chin and throat rufescent-tawny, thinly barred brown. Breast rufescent-tawny, barred and vermiculated brown, boldly spotted whitish, with spots (medium, 2–5 mm) edged or bordered blackish-brown. Belly, flanks and undertail-coverts tawny or buff, boldly spotted (medium 2–5 mm to coarse 5–10 mm) whitish with no blackish-brown margins. Underwing coverts brown, lightly barred tawny. Female similar to the male. Immature similar to the adults but more heavily spotted blackish-brown on both upperparts and underparts, and with paler, buffier scapulars and wing coverts. Juvenile paler, more cinnamon than adult, with upperparts heavily spotted blackish brown. Downy chick brown. Bare parts—iris yellowish with dark mark in lower portion; bill blackish; gape yellowish-brown; legs and feet brownish. Facial bristles—at least four elongated rictal bristles and several guard bristles below the eye. Measurements: wing of male (1) 162 mm, of

female—no data, unsexed (3) 159–168 mm; tail of male (1) 119 mm, of female—no data, unsexed (3) 121–136 mm; bill of unsexed adult (3) 18.4–19.3 mm; tarsus—no data. Weight of male (1) 57 g, unsexed (1) 48 g.

Within Nyctibiidae, only *P. bracteatus* has unmarked remiges; all other species show conspicuous barring or spotting along the flight feathers. The primary molt of this species is serially descendant.

Osteology

Phyllaemulor bracteatus possesses unique osteological traits, as pointed out in Costa and Donatelli (2009) and Costa (2014) and summarized in Table 1. Many of these characters are plesiomorphic within the family, as follows: dorsoventrally flattened nostril; thin *pilla supranasalis*; the presence of a curved crest in the ventral face of the maxillary bone; a short interpalatin bridge; a tapering cranial end of the vomer bone, without any process; presence of a slightly curved *rostrum maxillae* and *rostrum mandibulae*; accentuated *depressio frontalis*; short *processus spinosus* on the

axis and 3rd vertebrae; and *tarsometatarsus* less hollowed laterally (Figs. 4, 5, 6 and 7). Some osteological traits are found to be autapomorphic, as follows: in dorsal view, a larger distance between the caudal face of the maxillary and the ectethmoid bone; a more laterally expanded ectethmoid bone; narrower frontal region; pterygoid bones enlarged in their rostral half part; lack of the lacrimal bone; post-orbital region showing a small fenestra and a pointed process; a more slim and downward curved maxillary jugal projection (“tooth-like” projection); thin and long *trabecula lateralis* at the caudal margin of the *sternum*; and typical pattern of the tarsometatarsus proximal end.

Phylogenetic analyses based on osteological data support the position of *P. bracteatus* as sister taxon of the remaining species within the family (Costa 2014), and all the plesiomorphic osteological characters mentioned are found also in the family Caprimulgidae, as follows: dorsoventrally flattened nostril; the presence of a curved crest in the ventral face of the maxillary bone (also observed in Apodidae and Aegothelidae); a short interpalatin bridge; tapering cranial end of the vomer bone; presence of a slightly curved *rostrum*

Table 1 Osteological characters of *Phyllaemulor bracteatus*, with their character states and polarity

Character	Polarity	Notes
Cranium		
Narrower frontal region	Autapomorphic	Wider in <i>Nyctibius</i> spp. and variable in the other groups
Accentuated <i>depressio frontalis</i>	Autapomorphic	Smooth in <i>Nyctibius</i> spp. and variable in the other groups
Larger distance between the maxillary and ectethmoid bones	Autapomorphic	
Ectethmoid more laterally expanded	Autapomorphic	
Slightly curved <i>rostrum maxillae</i> and <i>mandibulae</i>	Plesiomorphic	Similar to Caprimulgidae spp.; very curved in the remaining <i>Nyctibius</i>
Thin <i>pilla supranasalis</i>	Plesiomorphic	Similar to Caprimulgidae spp., as well as in Aegothelidae and Apodidae spp.
Narial opening dorsoventrally flattened	Plesiomorphic	Similar to Caprimulgidae spp.
Curved crest in the ventral face of the maxillary bone	Plesiomorphic	Similar to Caprimulgidae spp., as well as Aegothelidae and Apodidae spp.
A fenestra and a thin process in the post-orbital region	Autapomorphic	Distinct from any other group
Very short interpalatin bridge	Plesiomorphic	Very short in Caprimulgidae, medium in <i>Nyctibius leucopterus</i> and long in the remaining <i>Nyctibius</i> spp.
Tapering rostral end of the vomer bone	Plesiomorphic	Similar to Caprimulgidae; variable rostral processes in <i>Nyctibius</i> spp.
Very wide rostral end of the pterygoid bone	Autapomorphic	Distinct from any other group
Slimmer and downward curved maxillary jugal projection	Autapomorphic	
Absence of lacrimal bone	Autapomorphic?	Present but poorly developed in <i>Nyctibius</i> spp., well developed in Caprimulgidae
Vertebrae		
Short <i>processus spinosus</i> in axis and 3rd vertebrae	Plesiomorphic	
Sternum		
Thin and long <i>trabecula lateralis</i>	Autapomorphic	Short and wider in <i>Nyctibius</i>
Tarsometatarsus		
Less hollowed laterally	Plesiomorphic	Intermediate condition between a straight margin in Caprimulgidae and very hollowed in <i>Nyctibius</i> spp.

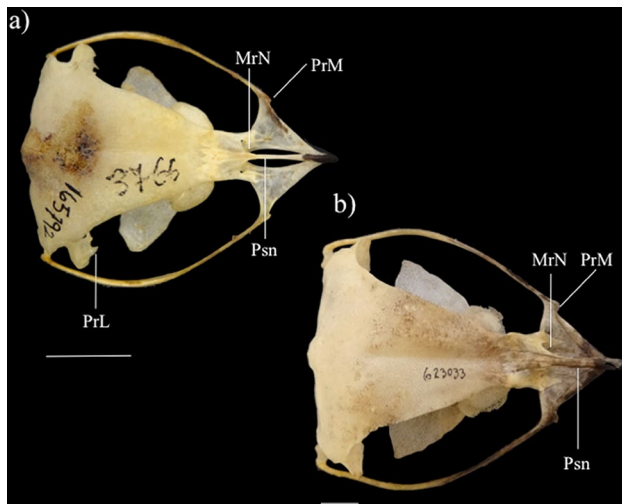


Fig. 4 Dorsal views of the skulls of **a** *P. bracteatus* LSUMZ 165792 and **b** *Nyctibius griseus* USNM 623033. *MrN* medial ramus of the nasal bone, *PrL* process in the laterosphenoid region, *PrM* projection in the maxillary jugal region, *Psn* Pilla supranasalis. Scale bars indicate 1 cm

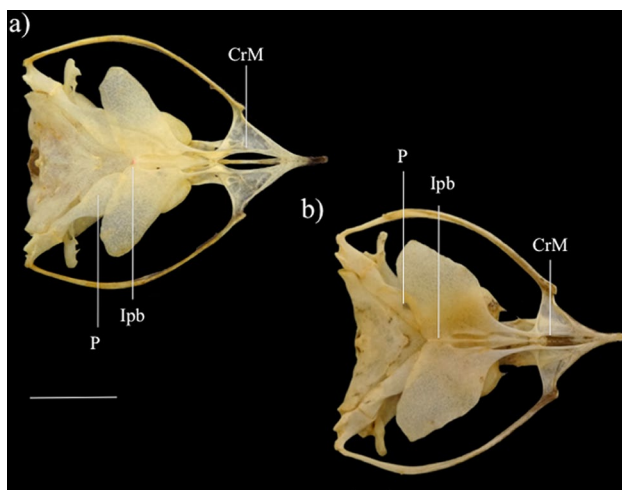


Fig. 5 Ventral views of the skulls of **a** *P. bracteatus* LSUMZ 165792 and **b** *Nyctibius grandis* USNM 623085. *CrM* ventral crest in the maxillary region, *P* pterygoid bone, *Ipb* interpalatin bridge. Scale bars indicate 1 cm

maxillae and *rostrum mandibulae*; accentuated *depressio frontalis* (which is also variable in Caprimulgidae); short *processus spinosus* on the axis and 3rd vertebrae (except in *Eurostopodus* spp.); and *tarsometatarsus* less hollowed laterally.

Ecology and behavior

Phyllaemulor bracteatus differs from other members of the family in several aspects of its behavior and ecology. All

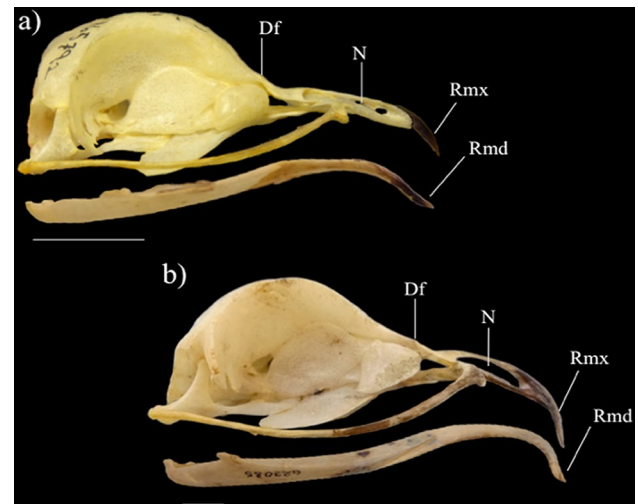


Fig. 6 Lateral views of the skulls of **a** *P. bracteatus* LSUMZ 165792 and **b** *N. grandis* USNM 623085. *Df* *Depressio frontalis*, *N* narial opening, *Rmd* *Rostrum mandibulae*, *Rmx* *Rostrum maxillae*. Scale bars indicate 1 cm

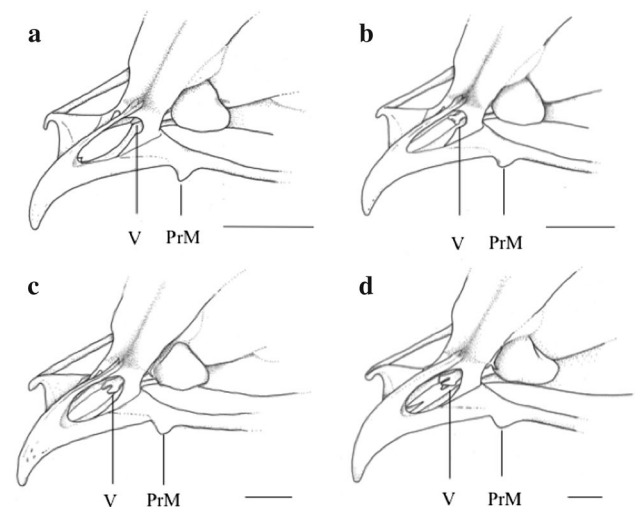


Fig. 7 Rostrolateral views of the skulls of **a** *P. bracteatus*, **b** *Nyctibius leucopterus*, **c** *Nyctibius griseus*, and **d** *Nyctibius grandis*. *V* Vomer, *PrM* projection in the maxillary jugal region. Scale bars indicate 1 cm

potoos have evolved remarkably camouflaged plumage to avoid attack by diurnal predators, but unlike other species' resemblance to tree bark (including dead stubs, fungus, and lichens), the unique, strongly rufous plumage of *P. bracteatus* blends with dead foliage, even to the extent of numerous white dots appearing as superficial flecks of sunlight (Cohn-Haft 1999) or holes with light coming through them. Strongly rufous plumage with white dots appears occasionally in other nocturnal families of Strisores, including Podargidae, Caprimulgidae, Aegothelidae, and, perhaps most notably, in Steatornithidae, which may be the sister group to Nyctibiidae (Hackett et al. 2008; Prum et al. 2015).

Also unique in Nyctibiidae, diurnal roosts of *P. bracteatus* are on roughly horizontal branches about 2 cm in diameter and often in the fork of a bare branch, thus emulating the appearance of an isolated dead leaf suspended in the forest understory (Fig. 2d); the birds perch perpendicular to the substrate, not generally aligned with it as in all other species.

Potoos remain almost motionless during the daytime. When disturbed or after detecting a potential predator, they reinforce their camouflage by adopting a “frozen” posture. This remarkable behavior involves the bird closing its eyes, slowly stretching the neck upwards to point the bill toward the sky while appressing the body plumage and, in some species, including *P. bracteatus* erecting short feathers above the eyes to resemble horns which interrupt the bulbous outline of the head. They then remain motionless in the well-known “dead stub” posture. During this morph in shape, any threat is kept under observation through two slits or notches in the upper eyelid. In a significant departure from the day-roosting behavior of all other potoos, *P. bracteatus* does not stretch the neck up to point the bill upward, instead remaining in a “normal” (more hunched) perching posture. Then, if the threat approaches, during the day or night, leaf mimicry is taken to the next level as the bird begins a slow, rocking oscillation, mostly on the vertical axis and perpendicular to the substrate that emulates the swing of a hanging leaf in a light breeze, or an isolated leaf trapped in vine tangles or suspended in spider web (Online Resource 1). This behavior is presented by the bird with both open or almost closed eyes. Conspicuous movement in response to a threat is highly unusual for any animal that depends on camouflaged appearance for avoiding detection by predators, but even as the rocking motion could initially attract attention, the rhythmic nature of it in conjunction with the dead-leaf plumage pattern must be especially effective in evading recognition as a potential prey item. *Phyllaemulor bracteatus* invariably performed the rocking motion when stimulated by our presence within about 7 m, and even chicks at the nest do it, but the behavior is not used exclusively in the presence of a threat; rocking may be performed at almost any time. Rocking is, however, most often associated with movements in the surrounding foliage caused by air currents in the forest understory and wind in the canopy. Thus, *P. bracteatus* takes advantage of disruptive motion in nearby foliage to perform necessary preening and stretching motions without calling attention to itself, and the effort put into rocking seems to roughly accompany the amount of movement in surrounding foliage. The elaborate leaf mimicry of *P. bracteatus*, involving both plumage and behavioral differentiation from other members of Nyctibiidae, is perhaps its most distinctive external trait. Notably, *Steatornis*, which may be the sister group of Nyctibiidae, seems to perform a similar rocking motion when perched in foliage. A more familiar case of avian movement enhancing foliage mimicry

occurs in bitterns of the genus *Botaurus*, whose vertically striped plumage and slow undulating movements make them remarkably cryptic in marsh grass waving in a gentle breeze.

The nest site of *P. bracteatus* [$n = 6$ (Cohn-Haft 1999; Ingels et al. 2008; personal observation)] atop a broken (usually dead), vertical or near-vertical stub about 7–10 cm diameter in the forest understory is also unusual in the family, but not unique (see below). All other potoos generally nest higher above ground, particularly when breeding inside forest, and lay the egg in an indentation or crevice of a live tree branch or in a shallow knothole on the side of an angled trunk or branch (Cohn-Haft 1999). Occasionally, Common Potoo *Nyctibius griseus* will also nest low down, sometimes in rather open country, and lay its egg in a depression in the top of wooden fence posts (personal observation) or spiny stumps protruding from water (Cooper and Kay 2004). The clutch always contains a single egg, as in all potoos. The egg is also remarkably different from the wholly white eggs of other members of the family (M. Barreiros, in preparation). Unlike known nestling (downy) plumage of other potoo species, which are largely white or whitish, these plumages in *P. bracteatus* are entirely brown, with no gray or white feathering (Cohn-Haft 1999; Ingels et al. 2008; personal observation). Both parents take care of the chick and young, which are fed by regurgitation. Nestlings already have the dark mark in the lower portion of the iris. Nestlings, when threatened by especially close approach, perform a striking defense behavior in the form of a sudden lunge toward the intruder with mouth opened completely to show the pink lining and gape, sometimes accompanied by exaggerated rocking motions (Fig. 2b).

Foraging of *P. bracteatus* is almost always inside forest, sometimes close to tree-fall gaps, and seems to be done almost exclusively in the understory. Prey items recorded for *P. bracteatus* include cockroaches, moths, bugs and beetles (Cleere 1998; Holyoak 2001). This contrasts with the foraging behavior of the other potoos, which is concentrated in higher forest strata (often from canopy snags) and frequently at the forest edge or even well away from forest. These differing strategies appear to be extensions of substrate mimicry, in the case of *P. bracteatus*, of leaf mimicry, as dead leaves are concentrated in the understory where many become trapped in live vegetation after falling from higher strata, and of bark camouflage in the cases of other nyctibiids. Although it is unknown to what extent prey items of *P. bracteatus* and other potoos may overlap (*P. bracteatus* is widely syntopic with four other species of potoos), we agree with the implication of Cohn-Haft (1999) that all potoos probably pursue most flying insects, even small ones.

The vocal repertoire of the species includes a loudsong and short contact calls. The unique, bubbling song is far more complex and multi-syllabic than the song of any other nyctibiid. In this regard, it is a true outlier, recalling,

however, the Amazonian Pygmy-Owl (*Glaucidium hardyi*) or Marbled Frogmouth (*Podargus ocellatus*) of Australasia (or Australo-Papua). It consists of a series of hooting notes, the first note being slightly longer than the remaining hoots and the whole song decreasing in frequency. The call consists of single notes which may represent contact calls and are often given in response to playback, and agitated birds occasionally emit harsher, strident calls.

Discussion

Phylogenetic relationships among traditional “caprimulgi-form” families are very controversial. Some molecular data suggest a link between potoos and the Oilbird *Steatornis caripensis* (e.g., Hackett et al. 2008; Prum et al. 2015), while morphological data indicate a close relationship between potoos and nightjars (Mayr 2002; Costa 2014). The osteological divergence of Nyctibiidae from Steatornithidae and Podargidae is remarkable, even though some molecular studies indicate a link between the two former families. Full resolution of these familial relationships will likely require the much larger molecular datasets that are now achievable, employing next-generation sequencing. Thus, for the purposes of this study, the polarity of the osteological character states between *P. bracteatus* and *Nyctibius* species were established based mainly on comparisons with Caprimulgidae, and to Aegothelidae to some extent, to which homologies were possible to establish with confidence. The interspecific variation observed between the osteological characters of *P. bracteatus* and those of the remaining *Nyctibius* species is notable and equivalent to that observed between distinct genera of other related groups, e.g., *Hydropsalis* vs. *Macropsalis* vs. *Uropsalis*, *Antrostomus* vs. *Nyctiphrynus*, *Batrachostomus* vs. *Rigidipenna* vs. *Podargus*, and amongst many genera of Apodidae, Trochilidae, and so forth. In the same way, many other morphological aspects of *P. bracteatus* indicate a very deep divergence from the remaining species of the family, most noticeably the distinctive plumage and elaborate leaf mimicry described above. Its plumage resembles to some extent that of the South American Oilbird (*S. caripensis*), the Australasian Marbled Frogmouth (*Podargus ocellatus*), and the Neotropical Ocellated Poorwill (*Nyctiphrynus ocellatus*) which may also indicate that the typical plumage of *P. bracteatus* is plesiomorphic within Nyctibiidae. However, the overall similarities among these species can be more properly interpreted as a parallel evolution in birds that rely on dead-leaf camouflage at diurnal roosts.

The iris in *P. bracteatus* is bright yellow, similar in color to those of *N. griseus* and *N. leucopterus*. However, the dark wedge on the lower portion of the iris, which creates a “keyhole”-like appearance in conjunction with the pupil, is remarkable and unique, not only amongst the potoos but also

amongst all other birds. If this character plays some role in the camouflage of the bird, it has yet to be investigated, but perhaps it disguises the large, open eyes by “breaking” the perfect contour of the yellow ring, thus contributing somewhat to the bird’s camouflage. The species also benefits from the existence of two notches in the upper eyelids (the so-called “magic eyes”), a feature also present in other potoos (Borrero 1974), that allows roosting birds to observe potential threats in their surroundings whilst their eyes are closed.

Genome-based phylogenetic data suggest that the “caprimulgi-form” radiation dates back to the early Paleocene (Jarvis et al. 2014; Prum et al. 2015), and the oldest known Nyctibiidae fossils date back to the middle Eocene (Mayr 1999), indicating that the extant species may represent ancient phylogenetic splits. In the last few decades, several molecular studies have shown high genetic variation among *Nyctibius* species. Mariaux and Braun (1996) found genetic distance values between *Nyctibius* species notably higher than those typically found in other genera of birds in a molecular phylogeny using cytochrome *b* data. *Phyllaemulor bracteatus* was among the most divergent species, averaging 14.5% distance from other potoos. In subsequent work with allozyme electrophoresis, Brumfield et al. (1997) found extremely high levels of divergence among potoo species in the nuclear genome. The number of unique alleles and the level of divergence were again notable in *P. bracteatus*, indicating that either it is the earliest branching lineage within the family or has undergone an accelerated rate of evolution. Braun and Huddleston (2009) determined full-length cytochrome *b* sequences (1143 bp) from the mitochondrial DNA and 1131 bp of the nuclear *c-myc* gene and found *P. bracteatus* to be highly divergent from the remaining species. Finally, White et al. (2017) applied a genome-scale dataset of ultraconserved elements to the resolution of potoo species relationships. All maximum likelihood and coalescent-based trees based on multiple subsets of that matrix placed *P. bracteatus* as the earliest branching terminal in the family with high statistical support. Thus all molecular analyses are fully consistent with the idea that *bracteatus* deserves placement in a separate genus.

Apart from the molecular and morphological divergence, many aspects of the biology and natural history of *P. bracteatus* are also very distinctive. The leaf mimicry and rocking motion are remarkable aspects of the morphology and behavior of *P. bracteatus*. The rufous-brown plumage with white spots closely resembles the understory of a terra firme forest, where dead leaves frequently become trapped in vine tangles and spider webs, with the white spots resembling dappled light that penetrates the dark forest interior, small holes in dead leaves, or both. Solano-Ugalde (2011) also reported observations of individuals performing diurnal preening preferably while a breeze gently

moves the vegetation and nearby leaves of roosting sites tremble, which reinforces the hypothesis of leaf mimicry as the birds could benefit from the surrounding motion of foliage when they need to perform such movements (Online Resource 2). Many aspects of foraging, roosting, nesting and vocalizations are noticeably distinct from those of the remaining species, which suggests a long divergent history from the other potoos. It is hard to evaluate if some aspects of its behavior and natural history are primitive within the family or autapomorphic for its lineage.

The erection of a new genus for *P. bracteatus* makes sense at this point. In proposing systematic reviews within the potoos, it is crucial to adopt a taxonomy consistent with their phylogeny. The phylogenetic resolution and the delineation of monophyletic groups, based on both morphological and molecular data currently available, make it clear that the generic status of some other taxa also deserves more detailed evaluation.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical statement This article does not include any studies with human participants performed by any of the authors, and all procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

Appendix 1

Skin (*sk.*) and skeleton specimens of Caprimulgiformes and Apodiformes examined at the following institutions: Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG); Louisiana State University Museum of Natural Science, Baton Rouge, USA (LSUMNS, specimen acronym LSUMZ); National Museum of Natural History, Smithsonian Institution, Washington DC, USA (NMNH, specimen acronym USNM); Field Museum of Natural History, Chicago, USA (FMNH); American Museum of Natural History, New York, USA (AMNH); Academy of Natural Sciences of Drexel University, Philadelphia, USA (ANSP); Museum of Vertebrate Zoology, Berkeley, USA (MVZ); Carnegie Museum of Natural History, Pittsburgh, USA (CMNH); University of Michigan Museum of Zoology, Ann Arbor, USA (UMMZ); Florida Museum of Natural History, Gainesville, USA (FLMNH); Museum of Comparative Zoology, Cambridge, USA (MCZ); The Natural History Museum, Tring, UK (NHMUK); Forschungsinstitut Senckenberg, Frankfurt, Germany (SMF); Museum für Naturkunde, Berlin, Germany (ZMB); and Muséum National d'Histoire Naturelle, Paris, France (MNHN).

Nyctibius grandis USNM 615095, USNM 623085, UMMZ 208494, MVZ 165126, LSUMZ 109337, MPEG 952; *Nyctibius aethereus* USNM 321588, USNM 621717; *Nyctibius griseus* MZUSP 90514, MZUSP 90621, MZUSP 85895, MZUSP 85894, MZUSP 85896, USNM 344127, USNM 429776, USNM 502493, USNM 612299, USNM 559134, USNM 608918, USNM 227479, MVZ 123819, MVZ 126575, FMNH 317325, LSUMZ 63174, LSUMZ 86464; *Nyctibius jamaicensis* USNM 611744, USNM 288822, USNM 344903, USNM 556856, USNM 557530, MVZ 85696; *Nyctibius leucopterus* LSUMZ 165791, LSUMZ 165793; *Nyctibius bracteatus* MZUSP 92606 (*sk.*), MPEG 52954 (*sk.*), MPEG 62434 (*sk.*), MPEG 72300 (*sk.*), MPEG 72301 (*sk.*), MPEG 76511 (*sk.*), AMNH 231054 (*sk.*), ANSP 183091 (*sk.*), ANSP 187524 (*sk.*), ANSP 22016 (*sk.*), LSUMZ 71021 (*sk.*), LSUMZ 114641 (*sk.*), LSUMZ 87299 (*sk.*), LSUMZ 165792 (*sk.*), NHMUK 1888.8.1.25 (*sk.*), NHMUK 1888.8.1.26 (*sk.*), NHMUK 1888.8.1.27 (*sk.*), NHMUK 1890.2.18.70 (*sk.*), NHMUK 1890.2.18.71 (*sk.*), MNHN CG847.963 (*sk.*), SMF 29870 (*sk.*); *Steatornis caripensis* USNM 560206, USNM 560151, NHMUK 1900.7.6.39, LSUMZ 170392, AMNH 106720; *Podargus strigoides* NHMUK 1952.2.507, NHMUK 1955.9.4, USNM 492463, USNM 632131; *Podargus papuensis* USNM 614956, NHMUK 1900.7.9.53; *Rigidipenna inexpectata* FLMNH 40210, *Batrachostomus septimus* UMMZ 207453, *Batrachostomus auritus* USNM 530279; *Aegotheles cristatus* USNM 612708, USNM 620228, USNM 612637, USNM

632149, USNM 227841, UMMZ 214241; *Aegotheles crinifrons* USNM 560816; *Eurostopodus mystacalis* KUNHM 98274, *Eurostopodus guttatus* UMMZ 214242, *Lyncornis macrotis* USNM 431310, USNM 431311; *Chordeiles nacunda* MZUSP 90513, LSUMZ 151635, LSUMZ 169279, USNM 635857, USNM 635858; *Chordeiles minor* FMNH 452018, FMNH 428815, FMNH 467660, AMNH 29691, AMNH 26579, AMNH 29690; *Chordeiles gundlachii* FMNH 376624, USNM 555511, USNM 555514, USNM 555519, USNM 562472, USNM 555518, CMNH 14290; *Chordeiles acutipennis* AMNH 18303, AMNH 13245, USNM 226726, USNM 498931, CMNH 13083, LSUMZ 157235, LSUMZ 157236, LSUMZ 157237; *Chordeiles rupestris* MZUSP 90625, MZUSP 90626, MZUSP 90627, LSUMZ 48733, LSUMZ 118557; *Chordeiles pusillus* USNM 622336, USNM 622323, USNM 622249, KUNHM 91072, KUNHM 91107; *Lurocalis semitorquatus* MZUSP 90494, MZUSP 85902, LSUMZ 105663, AMNH 18303, USNM 488522, USNM 488523, USNM 622777; *Nyctiprogne leucopyga* USNM 632514, USNM 562195, USNM 562194, USNM 429363, USNM 429368; *Phalaenoptilus nuttallii* AMNH 26230, FMNH 342824, FMNH 291368, USNM 634988, USNM 554124, CMNH 14701; *Siphonorhis brewsteri* USNM 354527, KUNHM 95182, *Nyctiphrynus ocellatus* MZUSP 98497, USNM 345891, USNM 562200, USNM 562201, FMNH 433075, FMNH 320460; *Antrostomus carolinensis* AMNH 27976, FMNH 379200, FMNH 443592, FMNH 396925, *Antrostomus vociferus* AMNH 26392, CMNH 16108, USNM 499185, USNM 502467, USNM 499488, USNM 432586, LSUMZ 104889; *Antrostomus ridgwayi* AMNH 14196, MCZ 342974, FLMNH 33870; *Antrostomus rufus* USNM 347720, USNM 347730; *Antrostomus saturatus* LSUMZ 138599, USNM 429774, USNM 488517; *Nyctipolus nigrescens* MZUSP 98498, USNM 621718, FMNH 318684, LSUMZ 118174, LSUMZ 118175; *Systellura longirostris* USNM 322960, LSUMZ 169587, LSUMZ 114249; *Nyctidromus albigollis*, MZUSP 90624, MZUSP 85897, FMNH 376562, FMNH 376559, FMNH 376561, CMNH 9075, CMNH 9066, NHMUK 1974.11.20; *Nyctidromus anthonyi* LSUMZ 75600; *Eleothreptus anomalus* KUNHM 91797; *Uropsalis segmentata* FMNH 433080, LSUMZ 89704, LSUMZ 89705, LSUMZ 106948; *Uropsalis lyra* UMMZ 207243, LSUMZ 170391; *Setopagis parvula* FMNH 334393, USNM 555943, USNM 555944, USNM 620758, LSUMZ 151639; *Hydropsalis cayennensis* USNM 621954, USNM 622317, USNM 622382, USNM 498901; *Hydropsalis maculicaudus* USNM 344129, USNM 623217; *Hydropsalis torquata* FMNH 334973, FMNH 334974, LSUMZ 64992, LSUMZ 65298, USNM 227818; *Hydropsalis climacocerca* USNM 562201, USNM 562202, USNM 621955, USNM 621956, USNM 637265, LSUMZ 120980; *Macropsalis forcipata* MZUSP 85903; *Caprimulgus aegyptius* NHMUK 1986.71.5, NHMUK


188.12.6.145; *Caprimulgus affinis* USNM 20311, USNM 225822, USNM 223983; *Caprimulgus batesi* USNM 622984, USNM 623010, *Caprimulgus climacurus* USNM 347442, USNM 322580, USNM 431698, USNM 347443; *Gactornis enarratus* FMNH 352811, MCZ 343119, NHMUK 1897.5.10.1; *Caprimulgus fossii* USNM 430459, USNM 430801, USNM 430799; *Caprimulgus inornatus* USNM 319984, USNM 431697; *Caprimulgus madagascariensis* FMNH 436501, USNM 432198, USNM 432227; *Caprimulgus natalensis* USNM 313071; *Caprimulgus poliocephalus* FMNH 357952, LSUMZ 153210; *Caprimulgus fraenatus* FMNH 28022, USM 499379, FLMNH 38713; *Caprimulgus tristigma* USNM 558539, USNM 430800; *Caprimulgus ruficollis* NHMUK 1997.1133; *Caprimulgus europaeus* USNM 431701, USNM 490326, USNM 552944, USNM 552945; *Macrodipteryx longipennis* FMNH 319987, NHMUK 1976.43.1, NHMUK 1976.43.2; *Macrodipteryx vexillarius* FMNH 444039, USNM 431637, USNM 430848, USNM 439471, USNM 490183; *Streptoprogne zonaris* MZUSP 90688, MZUSP 85904, USNM 614120; *Cypseloides niger* USNM 614120; *Cypseloides phelpsi* USNM 622775; *Chaetura brachyura* USNM 561593; *Chaetura cinereiventris* USNM 632429; *Hemiprocne comata* USNM 488940, USNM 607338; *Hemiprocne longipennis* MVZ 131166, USNM 560827; *Hemiprocne mystacea* USNM 560827, USNM 560828; *Phaethornis superciliosus* USNM 632344; *Ramphodon naevius* USNM 562759; *Ensifera ensifera* USNM 428880; *Campylopterus hyperythrus* USNM 622808; *Heliothryx aurita* USNM 621731.

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