# Systematic revision and generic classification of a clade of New World nightjars (Caprimulgidae), with descriptions of new genera from South America

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ABSTRACT: The complex and cryptic plumage patterns of nightjars and allies (Caprimulgidae) have historically hindered our understanding of their phylogenetic relationships. However, recent advances in molecular methods have greatly enhanced our interpretation of their systematics, revealed novel phylogenetic arrangements, and documented the non-monophyly of several traditional genera, which has called for a major revision of some clades. In this paper, we use recent molecular studies as a framework for a comprehensive systematic revision of a diverse clade of South American nightjars (called NW3 by Han *et al.* 2010), marshalling phenotypic, behavioural, and vocal data to support systematic recommendations. We provide comments on the limits of genera, resurrect the previously used generic names *Nyctipolus*, *Setopagis, Systellura, Antiurus* and *Thermochalcis* (some already in use by some authorities), and introduce new genera for *Setopagis whitelyi* (Salvin, 1885) and *Systellura decussata* (von Tschudi, 1844). In this new arrangement, we follow a rationale grounded on reestablishing generic monophyly, reconciling the generic names with the phylogenetic trees, and providing diagnostic characters for the genera as clearly as possible. We also present a classification proposal with a recommended linear sequence that better reflects the tree topologies.

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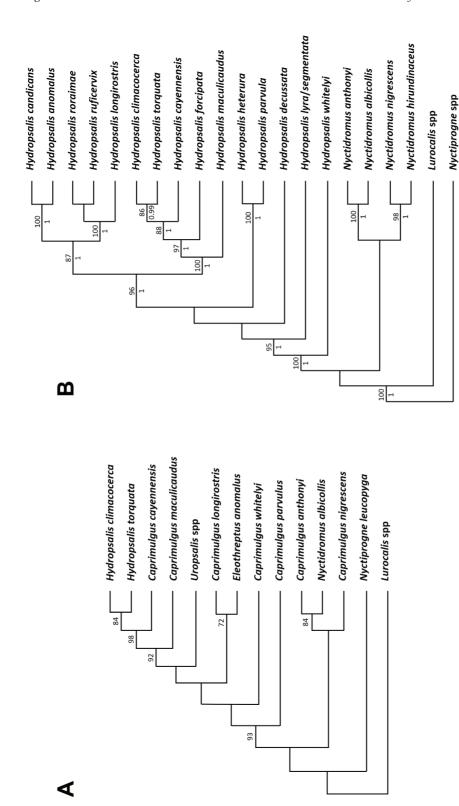
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#### INTRODUCTION

The family Caprimulgidae (nightjars and nighthawks) is a diverse cosmopolitan lineage comprising approximately 90 nocturnally adapted species (Cleere, 1999, 2010; Winkler *et al.*, 2020). They are found in virtually all environments and in a wide variety of habitats, reaching their highest diversity in the New World, especially in South America where 34 species are known to occur (Remsen *et al.*, 2023).

The complex and cryptic plumage patterns of caprimulgids have hindered our understanding of their phylogenetic relationships and complicated establishment of accurate systematics in the group. In recent decades, advances in molecular methods have greatly enhanced our interpretation of the phylogenetic relationships among nightjar species, and the systematics of the group has advanced significantly (Barrowclough et al., 2006; Larsen et al., 2007; Braun & Huddleston, 2009; Han et al., 2010; Sigurðsson & Cracraft, 2014). Overall, these studies have highlighted an extensive conservatism in the species' plumages across clades, revealing that most of the morphological characters used to diagnose early and traditional generic affinities represent parallel evolution, documenting the non-monophyly of the two traditional subfamilies Chordeilinae and Caprimulginae, and of several genera. For the New World nightjars, these studies were largely congruent in finding the existence of three major radiations: the Nighthawk clade, including the genera Podager Wagler, 1832, and Chordeiles Swainson, 1832; the Poorwill clade, including the genera Nyctiphrynus Bonaparte, 1857, Antrostomus Bonaparte, 1838, Siphonorhis P.L. Sclater, 1861 and Phalaenoptilus Ridgway, 1880; and the South American clade, the most diverse, including 10 genera and 23 species (Han et al., 2010; Sigurðsson & Cracraft, 2014). The South American clade (sensu Sigurðsson & Cracraft, 2014; named NW3 in Han et al. 2010 and hereafter, Figure 1) is almost entirely limited to South and Central America, with the exceptions of Hydropsalis maculicaudus (Lawrence, 1862) and Nyctidromus albicollis (J.F. Gmelin, 1789) that reach southern North America. The existence of this group and many of the new arrangements were unanticipated by traditional classifications. For a couple of examples, the presence in this clade of the genera Lurocalis Cassin, 1851 and Nyctiprogne Bonaparte, 1857, traditionally placed in Chordeilinae; and a close relationship between Nyctidromus albicollis and "Caprimulgus" anthonyi Chapman, 1923, as a sister clade to "C." nigrescens Cabanis, 1849 and "C." hirundinaceus von Spix, 1825.

The novel phylogenetic arrangements revealed in the above-mentioned studies called for a major systematic revision of the group, in order to align classification with phylogeny. As a starting point, the inclusion of several species in a broad *Hydropsalis* Wagler, 1832 — a name that has priority over the other generic names — was advocated (Han *et al.*, 2010; Sigurðsson & Cracraft, 2014). Following this baseline, new systematic adjustments were proposed, including rearrangements and resurrections of several old generic names, such as *Nyctipolus* Ridgway, 1912, *Setopagis* Ridgway, 1912 and *Systellura* Ridgway, 1912 by some authors and classification committees (Dickinson & Remsen, 2013; Remsen *et al.*, 2023; Gill *et al.*, 2023). Nevertheless, alternative taxonomies are still adopted by some authorities, such as the use of more inclusive genera and broader groupings, like an expanded *Hydropsalis* and *Nyctidromus* Gould, 1838 (Piacentini *et al.*, 2015; Pacheco *et al.*, 2021), a rationale that sometimes leads to phenotypically diverse and undiagnosable genera. However, regardless of the view adopted — i.e., the use of broader genera that preserve traditional genera and do not require new names, or the



igure 1. Summary of the molecular phylogenetic studies for the New World nightiar clade NW3. (A) maximum-likelihood of three nuclear markers (MT-CYB, MYC, GH) adapted from Han et al. (2010), with values in branches indicating ML bootstrap >50% (B) maximum-likelihood of four genetic markers (ND2, CYTB, RAG-1, ACO1 19) adapted from Sigurðsson and Cracraft (2014), with values in branches indicating ML bootstrap >60% and Bayesian posterior probability higher than 0.95 Species nomenclature follows the respective studies.

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resurrection or introduction of new generic names — some adjustments in the systematics of this radiation of South American nightjars are still mandatory due to the paraphyly of multiple groups revealed by the molecular studies.

In this paper, we use the studies of Han *et al.* (2010) and Sigurðsson and Cracraft (2014) as a solid framework for a comprehensive systematic revision and proposal of generic reclassification of this clade of South American nightjars. These studies are the most extensive to date in terms of taxon sampling and represent the best estimates of the phylogenetic relationships of this clade. From this baseline, we aimed to reconcile the generic names with those trees, producing a classification that emphasizes both monophyly and diagnosability. To achieve this objective, we marshalled phenotypic, behavioural, and vocal data to support systematic recommendations. We believe that taxonomy should not blindly follow molecular phylogeny in this case, but that it is better served by recognizing morphological, ecological and vocal disparities in the group in conjunction with genetic patterns, because: i) subclade boundaries in the group are clearly congruent with these disparities; ii) supporting most rearrangements, genus names are already available; and iii) monotypy should not be an argument to avoid genus-level recognition.

#### **METHODS**

We use the classification and generic-level systematics of the Howard & Moore Checklist of Birds of the World (Dickinson & Remsen, 2013) as our baseline classification for species and subspecies-level treatment of taxa studied by Han et al. (2010) and Sigurðsson & Cracraft (2014). For morphological studies, we analysed 96 study skins and 255 skeletons specimens of 49 species of nightjars, including the NW3 clade (sensu Han et al., 2010), 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 (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), Carnegie Museum of Natural History, Pittsburgh, USA (CMNH), Florida Museum of Natural History, Gainesville, USA (FLMNH), Museum of Vertebrate Zoology, Berkeley, USA (MVZ), Museum of Comparative Zoology, Cambridge, USA (MCZ), Kansas University Museum of Natural History, Lawrence, USA (KUMNH), The Natural History Museum, Tring, UK (NHMUK), and Muséum National d'Histoire Naturelle, Paris, France (MNHN) (see Appendices 1 and 2). The osteological terminology follows Baumel and Witmer (1993). For measurements and an average size of species, we follow Cleere (2010). For the molecular diagnoses of new genera, we use the methodology proposed by Burns et al. (2016). For the classification proposal, the linear sequence follows Sigurðsson and Cracraft's (2014) tree, for being the most complete study in terms of surveyed taxa, and the rationale used in the Howard & Moore Checklist of Birds of the World, according to which the least taxon-diverse lineage comes before the more diverse lineage. The habits and behaviour of the species described here are based on field observations by the authors.

#### RESULTS AND DISCUSSION

We provide below comments on limits of genera and make a new proposal of generic-level classification of the NW3 clade, following a rationale grounded on reestablishing generic monophyly and providing diagnostic characters for the genera as clearly as possible. To this end,

we resurrect previously used generic names (some currently in use by some authorities), introduce two new genera, and include diagnoses for each genus. We also present a classification with a recommended linear sequence that better reflects the tree topologies.

## Nyctiprogne Bonaparte, 1857

Riv. Contemp. Turin, 9, p. 215.

Type species, by monotypy, *Caprimulgus leucopygus* von Spix, 1825, currently *Nyctiprogne leucopyga* (von Spix, 1825).

As clarified by Whitney et al. (2003), the genus Nyctiprogne currently comprises two South American species, N. leucopyga (von Spix, 1825) and N. vielliardi (Lencioni-Neto, 1994). They are small nightjars with remarkably short bills, semi-concealed nostrils, and with unmarked wings (Friedmann, 1945; Cleere, 1998; Whitney et al., 2003). Nyctiprogne leucopyga presents a white band in the medial portion of the tail, which is absent in N. vielliardi (Figure 2). The short bill and lack of elongated rictal bristles have been used to include *Nyctiprogne* in the traditional subfamily Chordeilinae, alongside other superficially similar genera such as Lurocalis, Chordeiles, Podager and sometimes Eurostopodus (Cleere, 1999; Holyoak, 2001; see also Oberholser, 1914). However, phylogenetic studies have shown that Nyctiprogne belongs to the NW3 radiation, a position previously postulated by Whitney et al. (2003), representing either the first (Sigurðsson & Cracraft, 2014) or the second (Han et al., 2010) branching lineage in that clade. Thus, based on these results, several morphological traits shared by Nyctiprogne and Chordeiles are probably best regarded as homoplastic. Whitney et al. (2003) provided detailed discussion of vocal and behavioural traits characterizing the genus Nyctiprogne. All foraging is done on the wing and usually commences around sunset and ceases when it becomes too dark for the birds to see prey items. They spend the night roosting in the same area as the diurnal roost site. There is another feeding bout before dawn, with birds going to roost shortly after sunrise. Roost sites are thin (about 25–75 mm diameter) roughly horizontal branches about 0.5–2 metres above water or near water, and are loosely communal concentrations in structurally ideal vegetation. Birds roost singly, or huddled in groups of 2–10, usually all facing the same direction, and perpendicular to the branch. Flight characteristics are distinctive, with shallow, fluttery wingbeats interspersed with occasionally slightly deeper strokes, and much short-distance gliding with the wings held in a dihedral position. Individuals frequently bank abruptly to roughly retrace their route as they pursue tiny arthropod prey.

The study of Sigurðsson and Cracraft (2014) also exposed overlooked taxonomic diversity within *Nyctiprogne*, confirming previous original observations of two distinctly divergent song types breeding syntopically and at the same season on the lower Rio Negro above Manaus, Amazonas, Brazil (BMW & M. Cohn-Haft, pers. obs.), revealing that more than one species is included in *N. leucopyga*. The genetic analysis showed that the genus comprises three lineages probably best considered separate species, the nomenclature of which is remarkably complicated. This case is under study and will be resolved in the near future as analyses of specimens collected after voice-recording are matched to type material with provenance as well-established as is possible.

**Included species:** *Nyctiprogne leucopyga* (von Spix, 1825), *Nyctiprogne vielliardi* (Lencioni-Neto, 1994).

**Diagnosis:** small (160–200 mm), sexually monomorphic nightjar species, diagnosable by the combination of the following characters: short bill with semi-concealed nostrils; dark brown or blackish plumage overall; small white patches on either side of the throat; long, pointed wings with no white in the remiges; notched tail which is unmarked (*vielliardi*) or presents a transverse, medial white band on the outer approximately three rectrices (all other populations).



**Figure 2.** Ventral views of *Nyctiprogne leucopyga* (top, MZUSP 92610), and *Nyctiprogne vielliardi* (bottom, holotype MZUSP 74687).

#### Lurocalis Cassin, 1851

Proc. Acad. Nat. Sci. Philadelphia, 5, p. 189.

Type species, by subsequent designation (G.R. Gray, 1855, p. 12.), *Caprimulgus nattererii* Temminck, 1822, currently *Lurocalis semitorquatus nattererii* (Temminck, 1822).

The genus *Lurocalis* was introduced in 1851 by John Cassin and currently includes two species, *L. semitorquatus* (J.F. Gmelin, 1789) and *L. rufiventris* Taczanowski, 1884, which are morphologically readily characterized by a short tail and long, pointed wings (Figure 3), as well as a short bill and the absence of elongated rictal bristles. Some of these traits have been considered indications for placement of *Lurocalis* in the subfamily "Chordeilinae", as in the case of *Nyctiprogne* (see above). However, phylogenetic studies have converged in showing that this genus represents either the first or second branching lineage in the NW3 radiation (changing position in respect to *Nyctiprogne*, see Figure 1), also indicating that morphological traits traditionally used to include it in Chordeilinae are plesiomorphic characters. The suite of morphological traits in external morphology, plumage, and osteology, regardless of being either plesiomorphic or derived, render *Lurocalis* highly divergent and clearly diagnosable.

Concerning their ecological aspects, species of *Lurocalis* are substantially distinct from other nightjars of this clade, mainly regarding flight behaviour, foraging and breeding. They are fairly common birds throughout their range, but are seldom seen perched and most of the records are

birds seen in fast flights during crepuscular foraging periods. They forage over humid forest canopy and clearings, markedly different from most of the remaining NW3 species that generally sally from the ground or from low perches (Cleere, 1999; Holyoak, 2001). The genus is also unique for its tree-nesting behaviour; *Lurocalis semitorquatus* is known to lay one egg in a shallow depression on a horizontal tree branch (Seutin & Letzer, 1995; Simon & Bustamante, 1999), and *L. rufiventris* is also expected to do so, with the nest still undescribed. This represents a notable exception to the widespread ground nesting behaviour of nightjars. *Lurocalis rufiventris* is monotypic and occurs from western Venezuela to central Bolivia (Cleere, 2010). *Lurocalis semitorquatus* (type locality Cayenne) currently comprises five subspecies: two in Central America and three in South America (Cleere, 1999, 2010). Morphological and vocal distinctions among them, and seasonally overlapping distributions for some of them, have been documented and a reanalysis of species limits in the genus is in progress.

Included species: Lurocalis semitorquatus (J.F. Gmelin, 1789), L. rufiventris Taczanowski, 1884.

**Diagnosis:** medium-sized (190–290 mm), sexually monomorphic species, diagnosable by the combination of the following characters: short tail with unmarked rectrices; long, pointed wings with unmarked remiges; plain (*L. rufiventris*) or barred (*L. semitorquatus*) belly varying from rufous to pale orange, contrasting with dark breast; "V"-shaped white patch in the throat; scapulars mottled in grey (Figure 3).



**Figure 3.** Ventral views of *Lurocalis semitorquatus* (top, MZUSP 92608) and *Lurocalis rufiventris* (bottom, LSUMZ 105663).

## Nyctipolus Ridgway, 1912

Proc. Biol. Soc. Wash., 25, p. 98.

Type species, by original designation, *Caprimulgus nigrescens* Cabanis, 1849, currently *Nyctipolus nigrescens* (Cabanis, 1849).

The genus *Nyctipolus* was introduced by R. Ridgway (1912) to accommodate *Caprimulgus nigrescens* Cabanis, 1849 and *C. whitelyi* (Salvin, 1885). That author specified the diagnostic characters for the genus in comparison to *Antrostomus* Bonaparte, 1838, as follows: presence of a feathered tarsus; narrow nostrils, longitudinal and opening laterally; primaries either uniform black or with a white spot on the inner web of seventh and eighth, or seventh, eighth and ninth primaries. This arrangement, proposed by Ridgway, was followed by most authors for three decades, until the two species were transferred back to *Caprimulgus* by Peters (1940), an arrangement in use until recently. The molecular data (Han *et al.*, 2010; Sigurðsson & Cracraft, 2014) have shown, however, that these two species are not closely related (see *Setopagis* account below about *whitelyi*), and that *N. nigrescens* is instead strongly supported as sister to *N. hirundinaceus* (von Spix, 1825). Indeed, several phenotypic characters common to these two species have been largely overlooked. They share similar general plumage patterns, presenting relatively homogeneous upperparts, with no distinction between crown and back, no distinctive markings in the scapulars, face or auriculars, absent or poorly marked nuchal collar (Figure 4),



**Figure 4.** Dorsal views of *Nyctipolus nigrescens* (top, MZUSP 107386) and *Nyctipolus hirundinaceus* (bottom, MZUSP 39591).

white markings in three or four primaries, and reduced white markings in the tail restricted to tips of two or three outermost rectrices.

Their ecologies are also quite similar in many respects despite their occurrence in quite distinct biogeographic domains of South America. Both species prefer rupicolous habitats, roosting and nesting in open and rocky enclaves inside Amazonian *terra firme* forests (*N. nigrescens*), and in the dry, similarly rocky *caatinga* of northeastern Brazil and locally south into similar habitat in southern Espírito Santo state (*N. hirundinaceus*). Their vocal repertoires also share some similarities, which include a loudsong consisting of a single, clear note *wheeo* and a relatively modulated *prruop or prrip* call, which is abbreviated in *N. hirundinaceus*.

The inclusion of these two species in *Nyctipolus* makes sense from the perspective of monophyly and diagnosability, and alternative arrangements, such as their inclusion in *Nyctidromus* (e.g., Sigurðsson & Cracraft, 2014; Pacheco *et al.*, 2021), or even in a broad *Hydropsalis*, would produce a morphologically diverse and undiagnosable genus. Therefore, we recommend the use of the genus *Nyctipolus* for the two above-mentioned species.

**Included species:** *Nyctipolus nigrescens* (Cabanis, 1849) and *N. hirundinaceus* (von Spix, 1825). **Diagnosis:** small-sized (160–200 mm), sexually dimorphic species, diagnosable by the combination of the following characters: homogeneous mottled grey or dark plumage on the upperparts, with no distinction between crown and back, and no contrastingly distinct markings on scapulars, face or auriculars. Collar on hind neck absent (*nigrescens*) or indistinct buff (*hirundinaceus*), and a large white patch on throat. Wings with white band formed by small spots, on second, third and fourth outermost primaries (*nigrescens*) or on the four outermost primaries (*hirundinaceus*). White in tail restricted to the tips of the two outermost rectrices (*hirundinaceus*) or on second and third outermost feathers (*nigrescens* male). Females lack white in tail (*hirundinaceus*) or in both tail and wings (*nigrescens*).

#### Nyctidromus Gould, 1838

Icon. Av., Pt. 2, pl. [12], text.

Type species, by monotypy, *Nyctidromus derbyanus* Gould, 1838, currently *Nyctidromus albicollis derbyanus* Gould, 1838.

The genus *Nyctidromus* and its type species were introduced by J. Gould in 1838 in *Icones Avium*, Pt. 2, pl. [12] and text – see Figure 5 below (Gould, 1838). As diagnostic characters of the genus, Gould cited only general characteristics that are now known to be common to other species, but also referring to specific traits such as the bare tarsi and long tail, as follows: "Rostrum mediocre, ad basin latissimum, hiatu amplissimo, rictu setis elongatis instructo. Nares subhasales, elevata, transversim subovales, aperta. Alse mediocres, remige tertio cateris prastante. Cauda elongata, ampla, subrofundata. Tarsi nudi, elongati, antice scutellati. Digitorum externus et internus breves, intermedius elongatus, ungue pectinato; digitus posticus liber, parvus, et ungue parvulo instructus."

Due to its morphological distinctiveness in comparison to other caprimulgids, the genus *Nyctidromus* has remained in use and monotypic ever since. Nevertheless, its phylogenetic affinities were never well understood, and it was only after the findings of Han *et al.* (2010), confirmed by Sigurðsson and Cracraft (2014), that it became clear that *Nyctidromus albicollis*, a species that occurs from southern USA to southern South America, belongs to the NW3 clade and is, unexpectedly, sister to the Scrub Nightjar, now *N. anthonyi*, a small, greyish-brown species confined to western Ecuador and extreme northwestern Peru.

Nyctidromus anthonyi was originally described as a species in the genus Setopagis by F. Chapman (1923). It was subsequently treated as a subspecies of S. parvula (Gould, 1837), to



**Figure 5.** Illustration of of *Nyctidromus derbyanus*, the type species of *Nyctidromus* Gould, 1838, from the original description.

which it shares a general resemblance, by Peters (1940) and Meyer de Schauensee (1966) without further explanations. However, the distinctiveness of the plumage and, more importantly, the distinct vocalization were re-emphasized to show that it should be better regarded as a separate species (Schwartz, 1968; Robbins *et al.*, 1994), yet its phylogenetic affinities remained rather poorly understood. After being originally included in *Setopagis* and also considered possibly related to *H. cayennensis* (J.F. Gmelin, 1789) due to general appearance and the extensive white in the tail (Schwartz, 1968; see Robbins *et al.*; 1994), the systematics of *anthonyi* remained unresolved; before the publication of Han *et al.* (2010) it remained in the genus *Caprimulgus* Linnaeus, 1758 (e.g., Peters, 1940) and also provisionally in *Antrostomus* (see Cleere, 2010).

As discussed for the genus *Nyctipolus* above, *a posteriori* investigation of some specific phenotypic characters overlooked in traditional classifications highlighted some similarities in the plumage of the sister species now included in *Nyctidromus*. Notwithstanding considerable intraspecific variation, especially observed in the plumage of *N. albicollis*, the two species share the pattern of the upperparts, the rufous auriculars and lores (mottled with dark in *anthonyi*), and extensive white in the tail (Figure 6). They also share some osteological similarities, such as smooth curvature of the lateral margin of the maxillary bone (Costa, 2014). Furthermore, vocalizations of the two *Nyctidromus*, while each showing notable intraspecific variation, approach each other closely in general pattern and quality of the usually bisyllabic, whistled element of the song.

**Included species:** *Nyctidromus albicollis* (J.F. Gmelin, 1789) and *N. anthonyi* (Chapman, 1923).

**Diagnosis:** Medium to large-sized (180–280 mm), presenting a variegated greyish-brown plumage overall, with white throat patch, rufous in the sides of the head, auriculars and lores,



**Figure 6.** Ventral views of *Nyctidromus albicollis* (top, MZUSP 49541) and *Nyctidromus anthonyi* (bottom, ANSP 185147).



**Figure 7.** Lateral views of *Nyctidromus albicollis* (left, MZUSP 49541) and *Nyctidromus anthonyi* (right, ANSP 185147).

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and dark brown or blackish contrasting markings on scapulars. White band towards the wing tip on five outermost primaries, and extensive white in the tail, which broadly covers rectrices 2, 3 and 4 in *albicollis* and the innerwebs of the two outermost rectrices (4 and 5) in *anthonyi*.

## Setopagis Ridgway, 1912

Proc. Biol. Soc. Wash., 25, p. 98.

Type species, by original designation and monotypy, *Caprimulgus parvulus* Gould, 1837, currently *Setopagis parvula* (Gould, 1837).

The genus *Setopagis* was introduced by Ridgway (1912), in the same work as *Nyctipolus*, *Systellura* and *Antiurus* (see below), as a monotypic genus for *Caprimulgus parvulus*. In the diagnosis of the genus, Ridgway mentioned it as being "nearest *Antrostomus*, but differing in the relatively very small bill, and the adult male having a white patch on middle portion of primaries". *Setopagis parvula* is a common, widely distributed species, occurring in most of central and southern parts of South America.

Presenting a great resemblance, and being clearly allied to *S. parvula*, *S. heterura* Todd, 1915, is an uncommon, rather poorly known species that occurs in grasslands and forest edges of northern South America (Costa *et al.*, 2016). It was described by Todd (1915) based mainly on the more extensive white areas in wings and tail, covering both webs of the terminal portion of the three outer pairs of rectrices (Figure 8). The close relationship between these two species



Figure 8. Ventral views of Setopagis parvula (top, MZUSP 74411), and Setopagis heterura (bottom, MZUSP 77954).

was always evident, to the point that Peters (1940) subsumed *S. heterura* as a subspecies of *S. parvula*. Their loudsongs are also quite similar, both starting with a first, long note and ending with a series of descending notes, which are usually described as 'dop dro-dro-dro-dro' (parvula) and 'pik, goble-goble-goble-goble' (heterura) (Cleere, 2010).

Also included in *Setopagis*, the enigmatic Cayenne Nightjar, *S. maculosa* (Todd, 1920), is known only by the century old type specimen (Todd, 1920; Costa *et al.*, 2015; Figure 9). Originally described in *Nyctipolus*, it had also been included in *Caprimulgus* (Peters, 1940; Cleere, 1998, 1999; Holyoak, 2001), provisionally in *Antrostomus* (Cleere, 2010), and is currently tentatively included in *Setopagis* (Dickinson & Remsen, 2013; Costa *et al.*, 2015; Remsen *et al.*, 2023; Gill *et al.*, 2023). The characters allying it to *Setopagis* are mostly the white terminal portions of the three outermost rectrices and the rufous in the auriculars (Figure 9).

The absence of confirmed records of this species at and nearby the type locality, a region where the original habitats are mostly preserved, is difficult to understand. In this light, it is worth noting that, in spite of being considered a valid taxon (see Cleere & Ingels, 2004; Costa



Figure 9. Ventral, dorsal, and lateral views of the holotype of Setopagis maculosa (CMNH 60854).

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et al., 2015), the type specimen bears a notable resemblance to the Pauraque (*Nyctidromus albicollis*), such that it being an aberrant individual of that species cannot be discounted. Possibly, only future molecular studies based on material extracted from the type specimen will reveal whether this species is indeed valid and, if so, uncover its phylogenetic relationships. For now, we follow the current treatment of including it in *Setopagis*, and the diagnosis presented below is tentative.

**Included species:** *Setopagis parvula* (Gould, 1837), *Setopagis heterura* Todd, 1915, *Setopagis maculosa* (Todd, 1920).

**Diagnosis**: Medium-sized (190–230 mm), variegated greyish-brown, with a white throat patch (*S. parvula* and *S. heterura*) or two lateral patches (*S. maculosa*) and rufous on the sides of the head and auriculars; white spots towards wing tip on four outermost primaries; white tips on five (*S. parvula* and *S. heterura*) or four outermost rectrices (*S. maculosa*) (Cleere, 2010).

## Roraiman Nightjar (Setopagis whitelyi)

The fourth species currently included in *Setopagis* is the Roraiman Nightjar *Setopagis whitelyi*, an endemic species of the Pantepui mountains of northern South America. It is a medium-sized (~210 mm), blackish nightjar, resembling *N. nigrescens*, with white throat patches that extend laterally on the neck and presenting scattered, conspicuous white tips in some wing coverts of the male (Figures 10 and 11).

*Setopagis whitelyi* was originally described in *Antrostomus* by Salvin (1885), then was included in *Caprimulgus* by Peters (1940), and is currently in *Setopagis* (Remsen *et al.*, 2023; Dickinson & Remsen, 2013). In spite of the superficial resemblance to the other members of this genus, the studies of Han *et al.* (2010) and Sigurðsson and Cracraft (2014) revealed that



**Figure 10.** Ventral views of syntype specimens of *Setopagis whitelyi*, housed at the Natural History Museum, Tring, UK. (NHMUK 1888.8.1.96) at the top, and (NHMUK 1888.8.1.97) at the bottom.



**Figure 11.** Ventral views of specimens of *Setopagis whitelyi*, housed at the National Museum of Natural History, Washington DC, USA. From top to bottom, adult male (USNM 639325), adult male (USNM 639200), and adult female (USNM 639107).

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S. whitelyi is distantly related to the other species of Setopagis, representing a lineage with a long branch-length and no close relatives (see Figure 1). The studies, however, do not agree on where S. whitelyi is positioned in the tree. Han et al. (2010) have found it to be sister to the group including the species currently in the genera Systellura Ridgway, 1912, Eleothreptus G.R. Gray, 1840, Uropsalis W. deW. Miller, 1915 and Hydropsalis, as successive branching lineages. On the other hand, in Sigurðsson and Cracraft (2014) it is sister to that same clade plus *Setopagis* and *Macropsalis* P.L. Sclater, 1866 (this latter not sampled in the Han *et al.* study). Irrespective of these divergences, S. whitelyi is separated by at least one strongly supported node from all other nightjars in Sigurðsson and Cracraft (2014), so molecular studies seem robust in indicating the paraphyly of the genus Setopagis, as currently considered. Two resolutions exist for this matter. First, the use of a broadly-defined Hydropsalis, including the species currently in Systellura, Eleothreptus, Uropsalis, Macropsalis and Hydropsalis (and Setopagis itself, according to Sigurðsson and Cracraft, 2014); and second, to place S. whitelyi in a monotypic genus. While the two alternatives resolve the paraphyly of the genus, from the perspective of diagnosability, the use of an expanded *Hydropsalis*, as mentioned above, would create a highly heterogeneous group in terms of morphology, ecology and behaviour, with no clear diagnosis possible. In the interest of preserving the monophyly of the genera (clades) and also providing a more objective level of diagnosability, and considering that S. whitelyi represents a long-branch lineage, we propose the erection of a monotypic genus. As we have not found any valid generic name available specifically for whitelyi, under Article 13.1.1 (ICZN, 1999: 17) and Article 16.1 (ICZN, 1999: 19), we propose the new generic name:

Tepuiornis Costa, van Els, Braun, Whitney, Cleere, Sigurðsson & Silveira gen. nov.

Etymology: The new generic name is a combination of *Tepui* (a reference to the tabletop mountains where the species is known to occur) and *ornis* (ὄονις, from classical Greek, meaning "bird").

Gender: masculine.

Diagnosis: A medium-sized (*ca.* 210 mm), blackish nightjar, lacking hind neck collar, with white throat patches extending laterally to the neck. Narrow white bar towards wing tip, on three outermost primaries. Tail blackish with white tips to inner webs of second and third outermost rectrices in males. Conspicuous, scattered white markings in the tips of some wing coverts. Males have a large white throat patch, a thin white bar across the three outer primaries and a large white spot on the tips of the second and third outer rectrices. Females are often browner and slightly paler than males, have a thin tawny bar across the three outer primaries and a smaller white spot on the tips of the second and third outer rectrices. Wing chord: male 156–165 mm, female 155–164 mm; tail length: male 96–110 mm, female 92–108; culmen: male 13.5–15 mm, female 13.5–16 mm; tarsus: male 14.0–16.2 mm, female 12.2–16.0 mm; weight: male 30–40 g, female 45–48 g. Measurements from Cleere (1998), supplemented with additional specimens USNM 639200, USNM 639107, USNM 639325.

Molecular diagnosis: We recovered the following synapomorphies for NADH2 (n = 3): C150T, A156G, A162G, A276G, A291G, A774G, A1012G, C1034T; for CYTB (n = 2, *Macropsalis* and *Thermochalcis* missing): C60T, C90T, C112T, A117G, C124T, A129G, A180C, C184T, C330T, T381A, C468T, C522T, A565T, C607T, C637T, C670T, T700C, A773T, A787G, A796G, C827T, T832C, A835C, A883C, A914G, C928T, C1003T, A1015G, A1027G, C1039T, C1108G, C1138T; for RAG-1 (n = 1, *Macropsalis* missing): A153G, G186A, C425T, A674C, C1407T, T1424C, T1676G, C1739A, G1809A, G2072A, T2102C, G2126A, T2213C, C2294T, G2090A, G2594A, T2660C; for ACO1-199 (n = 2, *Macropsalis* missing): G167A, C171A, G224A, C291T, T289G, A507G, G594A, A661G, T745A.

Type species, by original designation and monotypy: *Antrostomus whitelyi* Salvin, 1885. New combination: *Tepuiornis whitelyi* (Salvin, 1885).

ZooBank LSID for new genus: 36D9957A-8645-4B5A-98C5-53104FD9DFD1

Distribution: Endemic to the Pantepui mountains of northern South America, known from Cerros Duida, Ptari-Tepui, Jaua, Urutaní, and Roraima (in southern Venezuela, *ca.* 850–1,800 m; Hilty, 2003; Crease, 2009; Cleere, 2010), in adjacent areas in Brazil (Naka *et al.*, 2006), and in the Pacaraima mountains of western Guyana (*ca.* 850 m, O'Shea *et al.*, 2007).

Habitat: Shrubby edges, bush islands, open areas, and savanna with scattered vegetation, including *Curatella americana* and *Bonnetia sessilis* trees, on the slopes and summits of tabletop Tepui mountains (O'Shea *et al.*, 2007; Crease, 2009).

Comments: *Tepuiornis* gen. nov. differs from the other genera in several respects. From *Uropsalis*, which appears as the first branching lineage within its sister clade, it differs by lacking extended rectrices in males, is smaller in overall size (210–224 mm versus 230–280 mm) and has a distinctive repeated single-note song, distinct from the complex and long songs of *Uropsalis*. Morphologically perhaps most similar to elevationally parapatric *Nyctipolus*, but is larger (210–224 mm versus 195–215 mm), overall darker in coloration, and has larger white bands and spots on wings and larger white spots on tail. Compared to *Systellura*, with which it is locally syntopic, *Tepuiornis* gen. nov. lacks conspicuous buffy collar and averages smaller.

The vocalizations of *Tepuiornis whitelyi* comb. nov. are poorly known. One song-like vocalization was recorded and described from the Pacaraima region of Guyana (O'Shea *et al.*, 2007). It consists of short (*ca.* 0.5 seconds), harsh *hreeer* calls, slightly rising and falling in pitch and amplitude repeated at intervals of 1–4 seconds (O'Shea *et al.*, 2007; ML134205, ML134213). No other vocal types are known to date. In recognizing the relatively high degree of avian differentiation that has been documented in the Tepuis region, it is desirable to obtain recordings from Cerro Roraima (the type locality) and other localities for comparison with the small available sample from the Pacaraimas of Guyana.

#### Systellura Ridgway, 1912

Proc. Biol. Soc. Wash., 25, p. 97.

Type species, by original designation and monotypy, *Stenopsis ruficervix* P.L. Sclater, 1866, currently *Systellura longirostris ruficervix* (P.L. Sclater, 1866).

The monotypic genus *Systellura* was introduced by Ridgway (1912, p. 97) to include *Stenopsis ruficervix* P.L. Sclater, 1866 (now *S. longirostris ruficervix*). At the time of the description, Ridgway presented as diagnostic characters in comparison to *Stenopsis maculicaudus* and *S. cayennensis* "the relatively much shorter and less distinctly emarginated tail and very different style of coloration, the sexes not conspicuously different in colour and the adult male with lateral rectrices not mostly white". Peters (1940) subsumed *Systellura* in *Caprimulgus*, a treatment that persisted until recently; following the recent molecular studies, the name was reinstated by some authorities (e.g., Dickinson & Remsen, 2013; Remsen *et al.*, 2023; Gill *et al.*, 2023).

The species-level taxonomy of the genus *Systellura* presents a complex scenario, with several morphologically and vocally distinct, named populations occurring in a mostly circum-Amazonian distribution, notably in montane areas. Nine subspecies were traditionally considered: *S. l. ruficervix* P.L. Sclater, 1866, *S. l. roraimae* Chapman, 1929, *S. l. atripunctata* Chapman, 1923, *S. l. decussata* (von Tschudi, 1884), *S. l. bifasciata* (Gould, 1837), *S. l. mochaensis* (Cleere, 2006), *S. l. pedrolimai* (Grantsau, 2008), *S. l. longirostris* (Bonaparte, 1825), and *S. l. patagonica* (Olrog, 1962), (Cleere, 2010). In some cases, the morphological and vocal variation

among subspecies is remarkable, to the point of being considered species by some authors (see Cleere, 2010; Sigurðsson & Cracraft, 2014; Pacheco *et al.*, 2021). The study of Sigurðsson and Cracraft (2014) made an important contribution to the knowledge of the relationships among these taxa, revealing the existence of considerable phylogenetic structure and high genetic diversity among some taxa known to be vocally distinct. For instance, specimens of the northern subspecies *S. l. roraimae* and *S. l. ruficervix* form separate clades, with substantial divergence between them (e.g., 3,7% in the mitochondrial gene ND2) and from the other ssp. (5% in ND2). More notably, it was revealed that the traditional polytypic *S. longirostris* is actually paraphyletic; the subspecies *S. l. decussata* is a distinct species, representing a distantly related lineage (see below). Based on this genetic variation, and the noteworthy morphological and vocal variation among the populations (Cleere, 2010), we follow Sigurðsson and Cracraft's (2014) proposal of considering *S. roraimae* and *S. ruficervix* distinct species. Nevertheless, a comprehensive taxonomic revision with a thorough morphological and vocal analysis of this complex is warranted, as some taxonomic issues remain unresolved. Therefore, the species-level taxonomy considered here is tentative.

**Included species:** *Systellura longirostris* (Bonaparte, 1825), *S. ruficervix* (P.L. Sclater, 1866), and *S. roraimae* Chapman, 1929.

**Diagnosis:** medium to large size (230–270 mm), blackish, greyish-brown or brownish overall, with a broad buff, rufous hind-neck collar and white throat patch. White (male) or buff (female) on four outermost primaries, alula, and adjacent wing coverts. Broad terminal white band and white spots on inner webs of three or four outermost rectrices (male) (Figure 12) (Cleere, 2010).



**Figure 12.** Dorsal view of the tail of a male *Systellura longirostris* (MZUSP 79538), showing the typical white tail markings of the genus.

## Tschudi's Nightjar (Systellura decussata)

Systellura decussata was described by von Tschudi (1844, p. 268) as a species in the genus Caprimulgus based on specimens from Peru (Figure 13). It was subsequently included in the genus Stenopsis Cassin, 1851 (Hartert, 1892), until Peters (1940) transferred it back to Caprimulgus but as a subspecies of Caprimulgus longirostris, a treatment that persisted until recently, when it was reinstated as a species based on its vocal distinctiveness, and provisionally allocated in Antrostomus (Cleere, 2010).

The study of Sigurðsson and Cracraft (2014) revealed that *Systellura decussata* represents a distinct species, with no close relatives, separated by three strongly supported nodes in their four-gene molecular phylogeny from the remaining species of *Systellura* as conceived here. Therefore, following our rationale for reestablishing the monophyly of genera, and in recognition of the distant relationship of *S. decussata* to the rest of *Systellura*, we propose its placement in a monotypic genus. As we have not found any valid generic name available specifically for this species, under Article 13.1.1 (ICZN, 1999: 17) and Article 16.1 (ICZN, 1999: 19), we propose the new generic name:

Quechuavis van Els, Costa, Braun, Whitney, Cleere, Sigurðsson & Silveira gen. nov.

Etymology: The new generic name is combination of *Quechua* (the South American Quechua people) + *avis* (bird in Latin). It is a reference to the Quechua aboriginal people of the Inca Empire in South America, especially Peru, where the species' ranges are centred.

Gender: feminine.



**Figure 13.** Ventral (top) and dorsal (bottom) views of the lectotype of *Systellura decussata* (von Tschudi, 1844), housed at the Muséum d'Histoire Naturelle de Neuchâtel, Switzerland (MHNN 92.5425).

Diagnosis: A medium-sized (ca. 200–220 mm), greyish-brown nightjar, with a tawny or buff hind neck collar and white (male) or buff (female) throat patch. A white (male) or buff (female) bar towards wing tip, on four outermost primaries, in the alula and adjacent wing coverts. Males with broad white tips in the three or four outermost tail feathers, absent in the female (Cleere, 2010) (Figure 13). Wing chord: male 136-139 mm, female (n=1) 142 mm; tail length: male 98-106 mm, female – no data; culmen: male 20-22 mm, female – no data; tarsus: male 18 mm, female – no data; weight: male 28.5-35.0 g, female (n=1) 32 g. Measurements from Cleere (1998), supplemented with additional specimen AMNH 229090.

Molecular diagnosis: We recovered the following synapomorphies for NADH2 (n = 3): A52G, G154A, C278T, A318G, A444C, C603T, C606T, A609G, A659G, C666A, C780T, A942G, C969A; for CYTB (n = 1, Macropsalis and Thermochalcis missing): C109T, C159T, C168T, C204T, T354A, A450G, A492G, A513G, A613C, A634C, C704T, C712A, C920T, C964T, T985A, C986T, C1090T; for RAG-1 (n = 1, Macropsalis missing): T405C, T587A, C722T, T1183C, A1227C, T1530C, A1535G, A1694G, C1923T; for ACO1-I99 (n = 1, Macropsalis missing): no synapomorphies found.

Type species, by original designation and monotypy: *Caprimulgus decussatus* von Tschudi, 1844.

New combination: *Quechuavis decussata* (von Tschudi, 1844). ZooBank LSID for new genus: C324BC8C-0BA2-4B8D-9816-33C06AC0C6F1

Distribution: Endemic to the arid littoral and low foothills of western Peru and extreme northern Chile (Arica and Iquique south to Quillagua). In Peru, from sea-level up to 1,300 m, and in Chile reported up to 3,350 m (Cleere, 1999).

Habitat: Wooded edges, clearings, open areas, and desert oases.

Comments: *Quechuavis* gen. nov. differs from the close related genera in several morphological characters. From *Uropsalis* in the lack of extended rectrices in males and the lack of wing bands [although *U. segmentata* (Cassin, 1849) males may have pale outer primaries], overall larger size, and very different song (short and simple, screechy whistles, separate notes, compared to the longer, complex songs composed of multiple syllables of *Uropsalis*). The presumed song of *Quechuavis* consists of short (ca. 0.5 seconds), loud, harsh *cueeo* syllables, which abruptly rise and harshly fall in pitch (see e.g., ML390105111).

Morphological differences between *Setopagis* and *Quechuavis* are more subtle, but *Quechuavis* lacks a white submoustachial stripe. Both have a buffy neck collar, white wing bands and some amount of white on rectrices and overlap in size. *Setopagis* is characterized by a complex song composed of chirping or popping sounds, contrasting with the simpler singlenote songs of *Quechuavis*, which are more reminiscent of that of *Nyctidromus albicollis* or *N. anthonyi* (see Schulenberg *et al.*, 2007).

Morphologically most similar to the phylogenetically more distant *Systellura*, but paler, slightly smaller overall and in terms of wing length, and with less extensive white in both wing and tail. Taxa in *Systellura* are characterized by drawn-out up- or down-slurred highpitched whistles, although the voice of *S. longirostris atripunctata* (with a range abutting that of *Quechuavis*) may somewhat resemble that of *Quechuavis* by being relatively short and more trilled.

Nodal support for separate *Setopagis* and *Quechuavis* lineages is low, likely in part because divergence time estimates between these genera and the aforementioned younger genera in the clade broadly overlap (polytomy). This may be the case, in part, because the ACO1-I9 gene offered no resolution for this genus. We believe that even taking into account a possible polytomy, the evolutionary distinctiveness of *Quechuavis* is evident and that biogeography, vocalizations, and to a lesser extent, morphology, also support recognition of a monotypic *Quechuavis*.

# Eleothreptus G.R. Gray, 1840

List Gen. Birds, p. 7.

Type species, by original designation and monotypy, *Amblypterus anomalus* Gould, 1838, currently *Eleothreptus anomalus* (Gould, 1838). *Eleothreptus* G.R. Gray, 1840 was published as a *nomen novum* for *Amblypterus* Gould, 1838, a junior homonym of *Amblypterus* Agassiz, 1833.



**Figure 14.** Ventral views of males *Eleothreptus candicans* (top, MZUSP 76174) and *Eleothreptus anomalus* (bottom, MZUSP 81226).

The genus Eleothreptus comprises two small, enigmatic nightjar species confined to central and southeastern parts of South America, occurring in open wooded country, grasslands and marshlands (Cleere, 1999, 2010). They are characterized by greyish-brown plumage with scattered dark markings, and lack of white in the throat and the mid-wing (Figure 14). More remarkably, males have highly modified, curved primaries that produce a slapping sound during territorial and courtship display flights (Cleere, 2002). Male wings present unique morphology [E. anomalus (Gould, 1838)] or coloration [E. candicans (von Pelzeln, 1867)]: the former with the most distinct outer-wing or "hand" morphology of all caprimulgids (Figure 15), possibly related to audio-mechanical display flights, whereas E. candicans has remarkably extensive white in the outer primaries (Figure 14), with more visually oriented displays. Eleothreptus anomalus presents a courtship flight, flying and gliding low over the ground (Cleere, 1998), and E. candicans defends territories with one or more 'display arenas' at which males perform nuptial flights (Pople, 2014). In display flights, males of both species give similar, soft calls. Territorial songs of both species are sharp, insect-like tick notes delivered from a stationary perch every few seconds, either singly (anomalus) or sometimes as a doublet (candicans), very much like some species of Hydropsalis.

The genus *Eleothreptus* was introduced by Gray (1840) as a substitute name for *Amblypterus* Gould, 1838, which was preoccupied, to include *A. anomalus*. The similarities in morphology and behaviour with *E. candicans* have traditionally indicated that the two species are closely related and warranted the inclusion of *E. candicans* in that genus (Cleere, 2002), a treatment strongly supported by molecular studies (Larsen *et al.*, 2007; Han *et al.*, 2010; Sigurðsson & Cracraft, 2014). In addition, the studies have also converged in finding this genus as sister to *Systellura*. The uniqueness of the morphological traits of these species, together with peculiar behaviour in comparison to other genera, makes clear that they merit their own



**Figure 15.** Ventral view of the right wing of a male *Eleothreptus anomalus*. Banhado dos Pachecos Wildlife Refuge, RS, Brazil (Photo by Ismael Franz).

genus. For this reason, we support the reinstatement of *Eleothreptus* for the two abovementioned species.

**Included species:** *Eleothreptus candicans* (von Pelzeln, 1867), and *Eleothreptus anomalus* (Gould, 1838).

**Diagnosis:** small-sized (180–210 mm), greyish/brownish nightjars, with dark thin markings on scapulars, and pale thin markings on breast and wing coverts; indistinct hind neck collar, lack of white in the throat and in the mid-wing. Males with elongated and conspicuously curved primaries.

## Uropsalis W. deW. Miller, 1915

Bull. Am. Mus. Nat. Hist., 34, p. 516.

Type species, by original designation, *Hydropsalis lyra* Bonaparte, 1850, currently *Uropsalis lyra* (Bonaparte, 1850).

The genus *Uropsalis* was introduced by Miller (1915) and includes *U. lyra* (Bonaparte, 1850) and *U. segmentata* (Cassin, 1849), two sexually dimorphic nightjar species endemic to Andean humid montane forests. They are characterized by the variegated (*U. segmentata*) or spotted (*U. lyra*) brownish or blackish plumage overall, absence of white in throat and wings, and, mainly, by the remarkably elongated outermost rectrices of the males (Figure 16). They inhabit forest clearings, glades, and open wooded habitats, from 800 m (*U. segmentata*) and 1,950 m (*U. lyra*), up to 3,500 m (Cleere, 2010). They are apparently polygynous species, with males displaying in communal leks, calling, circling or chasing females in flight (Gertler & McKay, in Hilty & Brown, 1986; Fjeldså & Krabbe, 1990).

In describing this genus, Miller (1915) stated that it differs from *Hydropsalis* mainly by the shorter length of the central pair of rectrices, and from *Macropsalis* by several plumage traits, such as the shorter wings and colour, size, and shape of rectrices and remiges. The close relationship between these two species was recovered by the studies of Han *et al.* (2010) and Sigurðsson and Cracraft (2014), albeit the clade is in different positions in the trees. In the former, it is sister to the clade comprising *Hydropsalis maculicaudus*, *H. cayennensis*, *H. torquata* 



**Figure 16.** Ventral views of males *Uropsalis lyra* (top, NHMUK 1890.2.18.176) and *Uropsalis segmentata* (bottom, NHMUK 1897.11.12.9).

(J.F. Gmelin, 1789) and *H. climacocerca* (von Tschudi, 1844); in the latter it is sister to the clade comprising those species plus *Q. decussata* comb. nov., *Setopagis* spp, and *Macropsalis forcipata*. The distinctiveness of the *Uropsalis* species in comparison to closely related taxa, regarding morphology, behaviour, and in accordance with the genetic data, indicates that they are best treated in their own genus. Apart from the plumage features and lekking behaviour that characterize these species, several osteological traits support the cohesiveness of *Uropsalis*, such as a prominent occipital skull region, a narrow rostral end of the parasphenoid bone, a long basipterygoid process, and the presence of a foramen in the olfactory nerve depression (Costa, 2014).

Included species: *Uropsalis lyra* (Bonaparte, 1850), *U. segmentata* (Cassin, 1849).

**Diagnosis:** Medium to large-sized (200–280 mm), spotted or variegated brownish nightjars, lacking white in the throat and in the wings. The outermost pair of rectrices highly elongated in the male, the tips with narrow white margins.

## Hydropsalis Wagler, 1832 and Macropsalis P.L. Sclater, 1866

The terminal clade of the NW3 lineage is a well-supported group that comprises the following species: *Macropsalis forcipata, Hydropsalis cayennensis, H. maculicaudus, H. torquata* and *H. climacocerca*. The molecular studies converged concerning the position of these species in the tree, however *M. forcipata* was not sampled in the study of Han *et al.* (2010). In Sigurðsson and Cracraft (2014), that species is embedded within *Hydropsalis*, being the second branching lineage in the group, after *H. maculicaudus* which is the sister taxon to all the other species. This result renders the genus *Hydropsalis* paraphyletic, and for the sake of monophyly, two resolutions exist: 1) to transfer *M. forcipata* to the genus *Hydropsalis*; or 2) to maintain *Macropsalis*, to include *H. maculicaudus* in a monotypic genus, and to keep the four remaining species in *Hydropsalis*. Both treatments have pros and cons, and the decision is not straightforward. From the perspective of diagnosability, either decision will make the genus *Hydropsalis* rather heterogeneous, obviously to a greater extent by including *maculicaudus* and *forcipata*.

The genus *Hydropsalis* is the oldest generic name for the NW3 clade and has *H. torquata* as the type species. It was introduced by Wagler (1832, p. 1222), who stated in the original description that it presents "character universalis Caprimulgi; cauda profunde furcate, rectrice extima elongatissima". In his detailed monograph on the genera Hydropsalis and Antrostomus, Cassin (1852) mentioned that the genus as then considered (including Uropsalis, Macropsalis and the long-tailed Hydropsalis spp.) could be arranged in two groups: one with a simply graduated tail (such as M. forcipata), and the other with the central pair of rectrices equalizing in length with the external ones (such as *H. climacocerca*), for which he considered, respectively, the subgenera Hydropsales and Psaluri, described by Bonaparte in the Conspectus Avium. The genus Macropsalis was later introduced by Sclater (1866) to embrace the species of the former group mentioned by Cassin, i.e., M. forcipata Nitzsch, 1840, U. lyra (Bonaparte, 1850) and U. segmentata (Cassin, 1849), stating as the main characters the absence of white in the primaries and the singly forked tail with the outermost pair of rectrices more than double the length of the median pair (Sclater, 1866, p.141). The recent molecular studies show, however, that Macropsalis is distantly related to Uropsalis and is, indeed, closer to Hydropsalis species, including *H. cayennensis* and *H. maculicaudus*.

Morphologically, the five species in this clade present remarkable interspecific variation in plumage, including wing and tail morphology and markings. Contour plumage may be variably spotted, brownish (torquata and climacocerca), blackish (maculicaudus and forcipata) or

greyish or buff (*cayennensis*), with conspicuous buff or tawny hind neck collar and buffier or whitish markings on wing coverts. *Macropsalis forcipata, H. maculicaudus* and *H. torquata* lack white throat patches and bands in the wings, both of which are present in the four outermost primaries of *H. cayennensis* and *H. climacocerca*. As mentioned above, the most striking difference between these species is the tail morphology, with the outermost pair of rectrices elongated in *M. forcipata* and *H. torquata*, and to a much lesser degree in *H. climacocerca* (Figures 18 and 20, see below). A detailed description of the morphological variation in this group is presented in Table I.

Regarding the behaviour of these species, they are known to perform aerial displays, with males flying, chasing and/or circling females, and presenting remarkably simple vocalizations,

**Table I.** Plumage characters in the species of the genera *Macropsalis* and *Hydropsalis*, based on museum specimens and from Cleere (2010).

Plumage traits	M. forcipata	H. maculicaudus	H. cayennensis	H. torquata	H. climacocerca
Crown	Mottled dark	Dark	Greyish/buffish streaked in black	Greyish streaked in black	Greyish, brownish streaked dark
Supercilium	Subtle, pale	Conspicuous, buff	Conspicuous, buff whitish	Conspicuous, whitish	Variable; absent, buff or white
Moustachial stripe	Subtle, buff	Subtle, buff	Subtle, buff	Conspicuous, whitish	Inconspicuous
Hind neck	Tawny/buff	Tawny/buff	Tawny/buff/rufous	Rufous	Buff
Throat	No white patch	No white patch	White patch	Inconspicuous, pale	White
Face and auriculars	Mottled buff and blackish	Mottled brownish	Mottled brown, buff	Mottled dark brown	Variable; from dark brown to pale buff
Upperparts	Blackish	Grayish, blackish	Greyish, pale brownish	Greyish, brownish	Variable; from dark brown, to greyish, to light brown
Underparts	Barred, blackish and whitish	Breast mottled with large pale/white spots	Breast mostly buff finely barred; belly buff whitish, barred in brown	Breast mottled brownish, buff and white; belly buff whitish, barred in brown	Variable; breast mottled dark brown to buff; belly buff whitish barred in brown
Scapulars	Buff markings	Dark with large buff markings	Variable; usually with large dark and pale buff markings	Variable; usually large black and buff markings	Variable; usually large black and pale buff markings
Wing coverts	Series of buff spots	Series of large buff spots	Series of large buff spots	Series of large buff spots	Usually large buff spots
Remiges (male)	No marks	No marks	White band on four outermost feathers	No marks	White band on four outermost feathers
Remiges (fem)	No marks	No marks	No marks	No marks	No marks
Rectrices (male)	White edges on inner webs of all feathers. Outermost 410- 680 mm	White terminal band and single medial white spots on inner webs of all but the central feathers	All but central feathers mostly white	Tips and innerwebs of outermost feathers white (Figure 20) Outermost 240- 380 mm	All but central pair of feathers mostly white (Figure 20)
Rectrices (fem)	Lacking markings. No long rectrices.	Lacking markings	Lacking markings	Lacking markings. No long rectrices	Lacking markings

which are single, high-frequency 'tip', 'chip' or 'tsip' notes repeated at intervals of roughly 1–3 seconds. Especially in H. climacocerca, song bouts may be punctuated by flights 3-6 m above water in which dramatic, diving twists are accompanied by loud, strident, mechanical bursts of sound apparently produced by air being forced through the spread rectrices by a rapid burst of wingbeats, or perhaps by the violent wingbeats themselves, with the spread, largely white tail acting more as a visual marker (BMW pers. obs.). These birds also perform terrestrial displays wherein males stand near females and produce a mechanical thumping or popping sound with occasional very low, jumping motions but only slight physical movement of wings or tail (BMW pers. obs). Hydropsalis maculicaudus and H. cayennensis, on the other hand, have louder, conspicuous loudsongs consisting of 'pt sweet', varying in the frequency of the second note between the species. For this reason, Davis (1962) included these two species in the genus Antiurus Ridgway, 1912, for which H. maculicaudus is the type species and where it was included (see e.g., Cory, 1918; Pinto, 1938) until merged in Caprimulgus by Peters (1940). In the original description of Antiurus, Ridgway mentioned that the species presents a peculiar pattern of coloration, as well as the outermost primary equal or longer than ninth, and rectrices relatively broader and wider terminally.

Considering the above-mentioned morphological variation, and seeking for more finetuned diagnoses of the genera, we propose here the maintenance of *Macropsalis Sclater*, 1866; the reinstatement of the genus *Antiurus Ridgway*, 1912 for *Hydropsalis maculicaudus*; the



Figure 17. Ventral and dorsal views of male Antiurus maculicaudus (MZUSP 85385).

reinstatement of the genus *Thermochalcis* Richmond, 1915 for *H. cayennensis*; and the use of *Hydropsalis* for *H. climacocerca* and *H. torquata*, as follows.

# Antiurus Ridgway, 1912

Proc. Biol. Soc. Wash., 25, p. 98.

Type species, by original designation and monotypy, *Stenopsis maculicaudus* Lawrence, 1862, currently *Hydropsalis maculicaudus* (Lawrence, 1862).

Included species: Antiurus maculicaudus (Lawrence, 1862).

**Diagnosis**: medium size (190–210 mm), dark crown, contrasting with a conspicuous pale/whitish supercilium and conspicuous rufous nuchal collar; mottled breast with large pale whitish spots; rectrices relatively wider terminally with large white terminal patches (Figure 17).

## Macropsalis P.L. Sclater, 1866

Proc. Zool. Soc. London, 34, p. 143.

Type species, by subsequent designation (E. Hartert, 1892, p. 601.), *Caprimulgus forcipatus* Nitzsch, 1840, currently *Macropsalis forcipata* (Nitzsch, 1840).

**Included species:** Macropsalis forcipata (Nitzsch, 1840)

**Diagnosis:** Large size (280–310 mm), variegated brownish or blackish overall, with no white patch in the throat and a broad tawny or rufous hind neck collar. Wing coverts with large buff spots. Primaries black with no white markings, the three outermost remiges notably longer and broader. Rectrices presenting a white edge on inner webs, the outermost pair of feathers greatly lengthened (480–680 mm) (Figure 18).



Figure 18. Dorsal (top and bottom right) and ventral (bottom left) views of Macropsalis forcipata (MZUSP 104233).

## Thermochalcis Richmond, 1915

Proc. Biol. Soc. Wash., 28, p. 98.

Type species, by original designation and monotypy, *Stenopsis cayennensis* J.F. Gmelin, 1789, currently *Hydropsalis cayennensis* (J.F. Gmelin, 1789).

## **Included species:** *Thermochalcis cayennensis* (J.F. Gmelin, 1789)

**Diagnosis:** Medium size (200–225 mm), variegated greyish-brown, with a white or buff supercilium and malar stripe, white patch in the throat and a broad tawny or buff hind neck collar. Males are largely white on underparts, with primaries black with white markings on four outermost remiges, and a squared tail with all but central feathers showing extensive white (Figure 19). Female with light brown wing markings, and brown and black banded rectrices.



Figure 19. Ventral and dorsal views of male Thermochalcis cayennensis (MZUSP 73301).

# Hydropsalis Wagler, 1832

Isis von Oken, 25, col. 1222.

Type species, by subsequent designation (G.R. Gray, 1855, p. 11.), *Caprimulgus furcifer* Vieillot, 1817, currently *Hydropsalis torquata furcifer* (Vieillot, 1817).

**Included species:** *Hydropsalis torquata* (J.F. Gmelin, 1789), and *H. climacocerca* (von Tschudi, 1844).

**Diagnosis:** medium to large size (200–300 mm), variegated brownish or greyish overall, with white throat patch and a tawny/buff/rufous hind neck collar. Wing coverts boldly spotted buff. Tail conspicuously forked in the male with longer outermost pair of rectrices, equalling (climacocerca) or nearly doubling (torquata) in length with the central pair of rectrices (Figure 20). Outermost pair of rectrices showing a diagonal black and white pattern. Narrow anterior end of the rostrum parasphenoid, in the basis of the skull.



**Figure 20.** Ventral views of males *Hydropsalis torquata* (top, MZUSP 34038) and *Hydropsalis climacocerca* (bottom, MZUSP 76389).

## CLASSIFICATION

In summary, the reclassification of the NW3 clade (*sensu* Han *et al.*, 2010) of Neotropical nightjars yields the following linear sequence, using the conventions of starting at the deepest node and listing first the least-diverse taxon (in terms of next-lowest taxonomic rank):

## Nyctiprogne Bonaparte, 1857

*Nyctiprogne leucopyga* (von Spix, 1825) *Nyctiprogne vielliardi* (Lencioni-Neto, 1994)

## Lurocalis G.R. Gray, 1855

Lurocalis rufiventris Taczanowski, 1884 Lurocalis semitorquatus (J.F. Gmelin, 1789)

## Nyctipolus Ridgway, 1912

*Nyctipolus nigrescens* (Cabanis, 1849) *Nyctipolus hirundinaceus* (von Spix, 1825)

## Nyctidromus Gould, 1838

Nyctidromus anthonyi (Chapman, 1923) Nyctidromus albicollis (J.F. Gmelin, 1789)

*Tepuiornis* Costa, van Els, Braun, Whitney, Cleere, Sigurðsson & Silveira, **gen. nov.** *Tepuiornis whitelyi* (Salvin, 1885), **comb. nov.** 

## Uropsalis, W. deW. Miller, 1915

Uropsalis segmentata (Cassin, 1849) Uropsalis lyra (Bonaparte, 1850)

*Quechuavis* van Els, Costa, Braun, Whitney, Cleere, Sigurðsson & Silveira, **gen. nov.** *Quechuavis decussata* (von Tschudi, 1844), **comb. nov.** 

## Setopagis Ridgway, 1912

Setopagis heterura Todd, 1915 Setopagis maculosa Todd, 1920 Setopagis parvula (Gould, 1837)

#### Antiurus Ridgway, 1912

Antiurus maculicaudus (Lawrence, 1862)

#### Macropsalis P.L. Sclater, 1866

Macropsalis forcipata (Nitzsch, 1840)

## Thermochalcis Richmond, 1915

Thermochalcis cayennensis (J.F. Gmelin, 1789)

## Hydropsalis Wagler, 1832

Hydropsalis climacocerca (von Tschudi, 1844) Hydropsalis torquata (J.F. Gmelin, 1789)

# Systellura Ridgway, 1912

Systellura longirostris (Bonaparte, 1825)

#### Eleothreptus, G.R. Gray, 1840

*Eleothreptus candicans* (von Pelzeln, 1867) *Eleothreptus anomalus* (Gould, 1838)

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APPENDIX 1. List of skeleton specimens of Caprimulgidae analysed, with details of institution, specimen number and locality. Legend: AMNH – American Museum of Natural History, New York, USA; NHMUK – Natural History Museum, Tring, UK; CMNH – Carnegie Museum of Natural History, Pittsburgh, USA; CUOC – Cornell University Ornithological Collection, Ithaca, USA; FLMNH – Florida Museum of Natural History, Gainesville, USA; FMNH – Field Museum of Natural History, Chicago, USA; KUNHM – Kansas University Natural History Museum, Lawrence, USA; LSUMNS – Louisiana State University Museum of Natural Science, Baton Rouge, USA; MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, USA; MNHN – Muséum National d'Histoire Naturelle, Paris, France; Museu Paraense Emílio Goeldi (MPEG), Belem, Brazil; MVZ – Museum of Vertebrate Zoology, Berkeley, USA; MZUSP – Museu de Zoologia da Universidade de São Paulo, Brazil; UMMZ – University of Michigan Museum of Zoology, Ann Arbor, USA; USNM – National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

Species	Institution	#	Locality
Eurostopodus mystacalis	KUNHM	98274	Australia, New South Wales
Eurostopodus nigripennis	NHMUK	1894.12.22.1	Ilhas Solomon
Eurostopodus argus	KUNHM	98486	Australia, New South Wales, 14 km before Paluma
Eurostopodus guttatus	UMMZ	214242	Australia, Western Australia
Eurostopodus guttatus	MVZ	143442	Australia, Muloorina, South Australia
Eurostopodus guttatus	NHMUK	1981.95.6	Australia, L. Alexandrina, Mulgundawa
Lyncornis macrotis	USNM	431310	Vietnã, Caryu Danar
Lyncornis macrotis	USNM	431311	Vietnã, Caryu Danar
Lyncornis macrotis	USNM	607328	Filipinas, Luzon, Cagayan, Baggao Mun.
Chordeiles nacunda	MZUSP	90513	Brasil, Estado de São Paulo
Chordeiles nacunda	MZUSP	98499	Brasil, Estado de São Paulo, São Vicente
Chordeiles nacunda	CMNH	1866	Argentina, Entre Rios, Estancia La Calera Gualeguay
Chordeiles nacunda	LSUMNS	151635	Bolívia, Santa Cruz Dept.
Chordeiles nacunda	LSUMNS	169279	Bolívia, Santa Cruz Dept.
Chordeiles nacunda	USNM	635857	Uruguai, Artigas, Mosolle, 30 km at Estancia Artigas
Chordeiles nacunda	USNM	614647	Argentina, Entre Rios, Estancia El Tala
Chordeiles nacunda	USNM	635858	Uruguai, Artigas, Mosolle, 30 km at Estancia Artigas
Chordeiles nacunda	USNM	614646	Argentina, Entre Rios, Estancia El Tala
Chordeiles nacunda	USNM	630313	Uruguai, Maldonado, Rocha, ca. 74 km
Chordeiles nacunda	FMNH	297444	Colômbia, Meta, Carimagua
Chordeiles nacunda	FMNH	297445	Colômbia, Meta, Carimagua
Chordeiles nacunda	FMNH	298016	Colômbia, Meta, Carimagua
Chordeiles nacunda	MVZ	120731	Colômbia
Chordeiles nacunda	NMHN	1880.115	-
Chordeiles minor	FMNH	452018	EUA, Minnesota, Washington Co.
Chordeiles minor	FMNH	428815	EUA, Wisconsin
Chordeiles minor	FMNH	467660	EUA, Wisconsin
Chordeiles minor	FMNH	468734	EUA, Illinois, DuPage Co., Lisle, 53 and Maple
Chordeiles minor	FMNH	443609	EUA, Wisconsin

Species	Institution	#	Locality
Chordeiles minor	USNM	614373	EUA, New Mexico, Ramah
Chordeiles minor	USNM	491871	EUA, Virginia, Annandale
Chordeiles minor	USNM	634891	EUA, California, Lassen Co., Ravendale
Chordeiles minor	CUOC	42346	EUA, New York, Tompkins Co., Ithaca, Cornell Campus
Chordeiles minor	CUOC	42347	EUA, New York, Tompkins Co., Ithaca, Cornell Campus
Chordeiles minor	CUOC	53019	EUA, Colorado, Fremont Canon
Chordeiles minor	AMNH	29691	EUA, New Jersey, Ocean Co.
Chordeiles minor	AMNH	15670	EUA, South Dakota, Jackson Co., Jackson Flat
Chordeiles minor	AMNH	26579	EUA, New Jersey, Essex Co., Franklin Township
Chordeiles minor	AMNH	8979	EUA, New York, Far Rockaway
Chordeiles gundlachii	FMNH	376624	Cuba, Prov. Pinar del Rio, 1,7 mi. S of Herradura
Chordeiles gundlachii	USNM	555519	Bahamas, Nassau
Chordeiles gundlachii	USNM	562472	Cuba, Guantanamo Bay, U.S. Naval Base
Chordeiles gundlachii	USNM	555516	Bahamas, Nassau
Chordeiles gundlachii	USNM	555517	Bahamas, Nassau
Chordeiles gundlachii	CMNH	14290	EUA, Florida, Monroe Co., Florida Keys
Chordeiles acutipennis	AMNH	18303	EUA, Arizona, Maricopa Co., Cave Creek
Chordeiles acutipennis	AMNH	7028	Peru, NW Nazca
Chordeiles acutipennis	AMNH	13245	EUA, Arizona, Cochise Co.
Chordeiles acutipennis	AMNH	18720	EUA, New Mexico, Hidalgo Co., San Simon Creek
Chordeiles acutipennis	AMNH	16638	EUA, Arizona, Cochise Co.
Chordeiles acutipennis	AMNH	16637	EUA, Arizona, Cochise Co.
Chordeiles acutipennis	FMNH	105400	EUA, Texas, Brewster Co., Chisos Mts.
Chordeiles acutipennis	USNM	344128	Venezuela, Carapito
Chordeiles acutipennis	USNM	226726	EUA, Arizona, Arlington
Chordeiles acutipennis	CMNH	13083	EUA, Novo Mexico, Curry Co., S. of Clovis
Chordeiles acutipennis	CMNH	8005	EUA, Arizona, Cochise Co., Portal
Chordeiles acutipennis	LSUMNS	17830	México, San Luís Potosí
Chordeiles acutipennis	LSUMNS	31860	Honduras, Choluteca Dept.
Chordeiles acutipennis	LSUMNS	48734	México, Quintana Roo
Chordeiles rupestris	MZUSP	90625	Brasil, Rondônia, Abunã, ilha fluvial no alto rio Madeira
Chordeiles rupestris	MZUSP	90626	Brasil, Rondônia, Abunã, ilha fluvial no alto rio Madeira
Chordeiles rupestris	MZUSP	90627	Brasil, Rondônia, Abunã, ilha fluvial no alto rio Madeira
Chordeiles rupestris	LSUMNS	48732	Peru, Ucayali Dept.
Chordeiles rupestris	LSUMNS	48733	Peru, Ucayali Dept.

Species	Institution	#	Locality
Chordeiles rupestris	LSUMNS	50736	Peru, Ucayali Dept.
Chordeiles rupestris	LSUMNS	118557	Peru, Loreto Dept.
Chordeiles pusillus	USNM	622336	Guiana, Karaudanawa, ca. 4 km S
Chordeiles pusillus	USNM	622323	Guiana, Karaudanawa, ca. 4 km S
Chordeiles pusillus	USNM	622249	Guiana, Karaudanawa, ca. 4 km S
Chordeiles pusillus	KUNHM	91072	Guiana, Karaudanawa, 4 km S
Chordeiles pusillus	KUNHM	91107	Guiana, savanna Parabara
Lurocalis semitorquatus	MZUSP	90494	Brasil, São Paulo, cidade de São Paulo
Lurocalis semitorquatus	MZUSP	85902	Brasil, São Paulo, cidade de São Paulo
Lurocalis semitorquatus	LSUMNS	105663	Peru, Dept. Pasco, Cumbre de Ollón, 12km E Oxapampa
Lurocalis semitorquatus	AMNH	18303	-
Lurocalis semitorquatus	CUOC	42345	_
Lurocalis semitorquatus	USNM	488522	Panamá, Ceraguas, Isla Cebaco, Platanal
Lurocalis semitorquatus	USNM	488523	Panamá, Ceraguas, Isla Cebaco, Platanal
Lurocalis semitorquatus	USNM	622777	Guiana, Linden, East of
Lurocalis semitorquatus	CUOC	42245	-
Nyctiprogne leucopyga	USNM	632514	Guiana, Upper Takutu-Upper Essequibo
Nyctiprogne leucopyga	USNM	562195	Brasil, Pará, Rio Xingu, Margem leste, Altamira
Nyctiprogne leucopyga	USNM	562194	Brasil, Pará, Rio Xingu, Margem leste, Altamira
Nyctiprogne leucopyga	USNM	429363	Venezuela, Amazonas, Laja Arapacua, Rio Pacimoni
Nyctiprogne leucopyga	USNM	429368	Venezuela, Amazonas, Laja Arapacua, Rio Pacimoni
Phalaenoptillus nuttallii	AMNH	18722	EUA, New Mexico, Otero Co.
Phalaenoptillus nuttallii	AMNH	18302	EUA, Arizona, Maricopalo Co., Phoenix
Phalaenoptillus nuttallii	AMNH	20632	EUA, New Mexico, Bernalillo Co., Albuquerque
Phalaenoptillus nuttallii	AMNH	23647	EUA, California, Shasta Co., Happy Valley
Phalaenoptillus nuttallii	AMNH	26230	EUA, California, Shasta Co., Burney
Phalaenoptillus nuttallii	FMNH	342824	EUA, Texas, Brewster Co., Panther Junction
Phalaenoptillus nuttallii	FMNH	291368	EUA, Arizona, Cochise Co., Portal
Phalaenoptillus nuttallii	FMNH	337176	EUA, New Mexico, Bernalillo Co., Cedar Crest
Phalaenoptillus nuttallii	USNM	554124	EUA, Arizona, Pima Co.
Phalaenoptillus nuttallii	USNM	634988	EUA, California, Lassen County, County Road 506
Phalaenoptillus nuttallii	CMNH	13201	EUA, Arizona
Phalaenoptillus nuttallii	CMNH	13272	EUA, Arizona, Maricopa Co., Phoenix
Siphonorhis brewsteri	USNM	354527	Haiti, Ilha Gonave
Siphonorhis brewsteri	KUNHM	95182	República Dominicana, Puerto Escondido

Species	Institution	#	Locality
Nyctiphrynus ocellatus	MZUSP	98497	Brasil, Bahia, Pacangê, Reserva da Michelin
Nyctiphrynus ocellatus	NMNH	345891	Brasil, Mato Grosso, Três Barras, Rio Paraguai
Nyctiphrynus ocellatus	NMNH	562200	Brasil, Pará, Rio Xingu, Margem Leste, Altamira
Nyctiphrynus ocellatus	NMNH	562201	Brasil, Pará, Rio Xingu, Margem Leste, Altamira
Nyctiphrynus ocellatus	FMNH	433075	Peru, Madre de Dios, Moskitania,
Nyctiphrynus ocellatus	FMNH	315175	Peru, Madre de Dios, ridge above Hda. Amazonía
Nyctiphrynus ocellatus	FMNH	320460	Peru, Madre de Dios, Hacienda Amazonía
Antrostomus carolinensis	AMNH	27976	EUA, North Carolina, Lee Co.
Antrostomus carolinensis	FMNH	379200	EUA, Florida, Dade Co., Miami
Antrostomus carolinensis	FMNH	443592	EUA, Florida, Monroe Co., Key West
Antrostomus carolinensis	FMNH	360349	EUA, Florida, Monroe Co., Key Largo, US Highway
Antrostomus carolinensis	USNM	562546	Panamá, Bocas del Toro, Big Zapatilla Key
Antrostomus carolinensis	USNM	622561	EUA, Florida, Okaloosa, Eglin AFB
Antrostomus carolinensis	USNM	622565	EUA, Florida, Okaloosa, Eglin AFB
Antrostomus carolinensis	CUOC	37318	Costa Rica
Antrostomus carolinensis	CUOC	44045	EUA, Florida, Hillsborough Co., Tampa Bay area
Antrostomus vociferus	AMNH	7964	EUA, Southampton, L.I.
Antrostomus vociferus	AMNH	21553	EUA, New Jersey, Essex Co., Newark Airport
Antrostomus vociferus	AMNH	26577	EUA, New York, Manhattan
Antrostomus vociferus	CMNH	11078	EUA, Virginia, Henrico Co., Richmond
Antrostomus vociferus	CMNH	1658	-
Antrostomus vociferus	USNM	499185	EUA, Virginia, Alexandria
Antrostomus vociferus	USNM	502467	EUA, Florida bay
Antrostomus vociferus	LSUMNS	14770	México, S.L.P., Mt. Just SE of Canada Grande
Antrostomus vociferus	LSUMNS	104889	EUA, Louisiana, Jefferson Par., Metairie
Antrostomus ridgwayi	AMNH	14196	México
Antrostomus ridgwayi	MCZ	342974	México, Chiapas, Tuxtlangutz
Antrostomus ridgwayi	FLMNH	33870	Guatemala, Baja Verapaz, San Geronimo
Antrostomus rufus	USNM	347720	Panamá, Pascora, Rio Pascora
Antrostomus rufus	USNM	347730	Panamá, Chepo
Antrostomus saturatus	LSUMNS	138599	Costa Rica, San José, La Georgina, km 95 Pan Am. Highway
Antrostomus saturatus	USNM	429774	Panamá, Chiriqui, Cerro Punta
Antrostomus saturatus	USNM	488517	Panamá, Chiriqui, Volcan Baru
Nyctipolus nigrescens	MZUSP	98498	Brasil, Rondônia, Caiçara

Species	Institution	#	Locality
Nyctipolus nigrescens	USNM	621718	Guiana, Acari mountains
Nyctipolus nigrescens	AMNH	19266	Venezuela, Est. Bolívar, Rio Carapo, Base Camp
Nyctipolus nigrescens	FMNH	318684	Venezuela, Terr. Amazonas, Cerro de La Neblina
Nyctipolus nigrescens	LSUMNS	118174	Peru, Dept. San Martín, ca. 15 km NE Jirillo
Nyctipolus nigrescens	LSUMNS	118175	Peru, Dept. San Martín, ca. 15 km NE Jirillo
Systellura longirostris	USNM	322111	Chile, Los Andes
Systellura longirostris	USNM	322960	Chile, Valparaíso
Systellura longirostris	LSUMNS	93862	Peru, Dept. De La Libertad, 2 km SW Otuaco,
Systellura longirostris	LSUMNS	113657	Peru, Dept. Huánuco, Bosque Zapatagocha above Acomayo,
Systellura longirostris	LSUMNS	169587	Peru, Dept. Cajamarca, Quebrada Lanchal, 8 km ESE Sallique, 3150m
Systellura longirostris	LSUMNS	114249	Peru, Dept. Ica, 0.5 km E km 235 Pan-Am. Hwy, 100m.
Nyctidromus albicollis	MZUSP	90624	Brasil, cidade de São Paulo
Nyctidromus albicollis	MZUSP	85897	Brasil, cidade de São Paulo
Nyctidromus albicollis	MZUSP	85898	Brasil, cidade de São Paulo
Nyctidromus albicollis	MZUSP	85899	Brasil, cidade de São Paulo
Nyctidromus albicollis	AMNH	10318	Guatemala, Camalote
Nyctidromus albicollis	AMNH	10299	Guatemala, Dept. San José, Papaturra
Nyctidromus albicollis	AMNH	12566	México
Nyctidromus albicollis	FMNH	298017	Colômbia, Meta, Carimagua, 150m.
Nyctidromus albicollis	FMNH	376562	Equador, Pichincha, Santo Domingo
Nyctidromus albicollis	FMNH	376559	Guiana, West Demerara-Essequibo Coast, Tapakuma
Nyctidromus albicollis	FMNH	318681	Venezuela, Territorio Amazonas, San Carlos
Nyctidromus albicollis	CUOC	37294	Costa Rica, Guapiles
Nyctidromus albicollis	CUOC	52150	México, Puebla, Hueytamalco, Rancho Las Margaritas
Nyctidromus albicollis	CMNH	8902	Belize, Toledo, Big Fall
Nyctidromus albicollis	NHMUK	1902.2.2.9	EUA, Texas, Brownville
Nyctidromus albicollis	NHMUK	1974.11.20	Panamá, Darien, El Real
Nyctidromus anthonyi	LSUMNS	75600	Peru, Depto. Amazonas, Bagua, Hda Valor
Eleothreptus anomalus	KUMNH	91797	Paraguai, Misiones, 5km NW Yabebyry
Uropsalis segmentata	FMNH	433080	Peru, Cuzco, Paucartambo
Uropsalis segmentata	LSUMNS	89704	Peru, Depto. Amazonas
Uropsalis segmentata	LSUMNS	89705	Peru, Depto. Amazonas
Uropsalis segmentata	LSUMNS	106948	Peru, Depto Pasco
Uropsalis lyra	UMMZ	207243	Peru, Cuzco

Species	Institution	#	Locality
Uropsalis lyra	LSUMNS	170391	Peru, Cajamarca
Setopagis parvula	FMNH	334393	Bolívia, Santa Cruz, Purubi, 30km S San Jose de Chiquitos
Setopagis parvula	USNM	555943	Paraguai, Amambay, Parque Nacional Cerro Cora
Setopagis parvula	USNM	555944	Paraguai, Dept. Itapua
Setopagis parvula	USNM	635996	Uruguai, Artigas, Colonia Palmas, Estancia Mandiyu
Setopagis parvula	USNM	620758	Argentina, Corrientes, Manuel Derqui
Setopagis parvula	LSUMNS	151639	Bolívia, Dept. Santa Cruz, PN Noel Kempff Mercado
Hydropsalis cayennensis	USNM	346330	Colômbia, La Guajira, Maicao
Hydropsalis cayennensis	USNM	555698	Trinidad e Tobago, Tobago, Hillsborough Dam
Hydropsalis cayennensis	USNM	555699	Trinidad e Tobago, Tobago, Hillsborough Dam
Hydropsalis cayennensis	USNM	621954	Guiana, Linden Highway and St. Cuthbert's Road
Hydropsalis cayennensis	USNM	622317	Guiana, Linden
Hydropsalis cayennensis	USNM	622382	Guiana, East Demerara, Timehri International Airport
Hydropsalis cayennensis	USNM	498901	Antilhas, Curaçao
Hydropsalis cayennensis	CUOC	51334	Antilhas, Curaçao, San Nicolaas
Hydropsalis cayennensis	CUOC	50786	Antilhas, Curaçao
Hydropsalis maculicaudus	USNM	344129	Venezuela, Carapito
Hydropsalis maculicaudus	USNM	623217	Guiana, Bara Bara River, near Moruka river
Hydropsalis torquata	FMNH	334973	Bolívia, Santa Cruz, Nuflo de Chavez Concepción
Hydropsalis torquata	FMNH	334974	Bolívia, Santa Cruz, Nuflo de Chavez Concepción
Hydropsalis torquata	LSUMNS	65298	Peru, Dept. Loreto, Rio Curanja, Balta
Hydropsalis torquata	LSUMNS	64992	Peru, Dept. Loreto, Balta
Hydropsalis torquata	USNM	227818	Uruguai, Rio Negro
Hydropsalis torquata	CUOC	50843	Uruguai, Rivera, Cerro Trinidad
Hydropsalis torquata	CUOC	52234	Uruguai, Rivera, Cerro Trinidad
Hydropsalis climacocerca	USNM	562201	Brasil, Pará, Rio Xingu, Margem Leste, Altamira
Hydropsalis climacocerca	USNM	562202	Brasil, Pará, Rio Xingu, Margem Leste, Altamira
Hydropsalis climacocerca	USNM	621955	Guiana, Upper Essequibo River
Hydropsalis climacocerca	USNM	621956	Guiana, Upper Essequibo River
Hydropsalis climacocerca	USNM	637265	Guiana, Upper Takutu – Upper Essequibo
Hydropsalis climacocerca	FMNH	291747	Peru, Madre de Dios, alto rio Madre de Dios

Species	Institution	#	Locality
Hydropsalis climacocerca	FMNH	320463	Peru, Madre de Dios, Rio Palotoa, 12 km from mouth
Hydropsalis climacocerca	LSUMNS	64991	Peru, Dept. Loreto, Rio Curanja, Balta
Hydropsalis climacocerca	LSUMNS	120980	Peru, Dept. Loreto, Isla Pasta, Rio Amazonas
Macropsalis forcipata	MZUSP	85903	Brasil, Estado de São Paulo
Caprimulgus aegyptius	NHMUK	1986.71.5	Arábia
Caprimulgus aegyptius	NHMUK	1888.12.6.145	_
Caprimulgus affinis	USNM	20311	Indonesia, Java, Ratoe
Caprimulgus affinis	USNM	225822	Indonesia, Celebes, Parigi
Caprimulgus affinis	USNM	223983	Filipinas, Cauacao
Caprimulgus affinis	USNM	223984	Filipinas, Cauacao
Caprimulgus affinis	NHMUK	1850.8.15.85	Java
Caprimulgus batesi	USNM	622984	Gabão, Ogooue Maritime Prov., Rabi Oil Field
Caprimulgus batesi	USNM	623010	Gabão, Ogooue Maritime Prov., Rabi Oil Field
Caprimulgus climacurus	USNM	347442	Libéria
Caprimulgus climacurus	USNM	322580	Camarões, Makondo-Matitigi
Caprimulgus climacurus	USNM	431698	Kênia, Lake Victoria, Rusinga Island
Caprimulgus climacurus	USNM	347443	Libéria
Caprimulgus climacurus	LSUMNS	51042	Kênia, 14 mi. N Ijara
Caprimulgus climacurus	NHMUK	1952.2.509.510	Nigéria, Oban District
Gactornis enarratus	FMNH	352811	Madagascar, Fivondronana de Tolagnaro
Gactornis enarratus	MCZ	343119	Madagascar, Forest Sianaka
Gactornis enarratus	NHMUK	1897.5.10.1	Madagascar
Caprimulgus fossii	USNM	430459	Zimbabue, Bulawayo
Caprimulgus fossii	USNM	430801	Zimbabue, Zambezi River, Bingas
Caprimulgus fossii	USNM	430799	Zimbabue, Zambezi River
Caprimulgus fossii	USNM	430660	Zimbabue, Sawmills
Caprimulgus fossii	USNM	430458	Zimbabue
Caprimulgus fossii	USNM	32782	Kênia, Kilifi
Caprimulgus fossii	CUOC	50528	África do Sul, 10km E. Pongola
Caprimulgus inornatus	USNM	319984	Senegal, Casamance, Diabane
Caprimulgus inornatus	USNM	431697	Kênia, Nyanza, Kakamega Forest
Caprimulgus madagascariensis	FMNH	436501	Madagascar, Mahajanga, RNI de Namoroka
Caprimulgus madagascariensis	USNM	432198	Madagascar, Ambalanjanakomby
Caprimulgus madagascariensis	USNM	432227	Madagascar, Tamatave, Perinet
Caprimulgus natalensis	USNM	313071	Gabão
Caprimulgus poliocephalus	FMNH	357952	Burundi, Cibitoke, Ndora
Caprimulgus poliocephalus	LSUMNS	153210	Tanzânia, Ivinga Region, Mufundi District
Caprimulgus fraenatus	FMNH	28022	Kênia, Kakamega forest

Species	Institution	#	Locality
Caprimulgus fraenatus	USNM	499379	Kênia, Nakuru
Caprimulgus fraenatus	FLMNH	38713	Zimbabue
Caprimulgus tristigma	USNM	558539	África do Sul, Transvaal, Naboomspruit
Caprimulgus tristigma	USNM	430800	Zimbabue, Zambezi River
Caprimulgus ruficollis	NMHN	1997.1133	_
Caprimulgus europaeus	USNM	431701	Kênia, Nyanza
Caprimulgus europaeus	USNM	490326	Egito, Matruh, Bahig
Caprimulgus europaeus	USNM	552944	Chipre, Famagusta
Caprimulgus europaeus	USNM	552945	Chipre, Famagusta
Caprimulgus europaeus	NHMUK	1846.4.7.15	Inglaterra
Caprimulgus europaeus	NHMUK	1955.7.1	Inglaterra, Lincoln, Bourne Woods
Macrodipteryx longipennis	FMNH	319987	Guiné, Mali
Macrodipteryx longipennis	NHMUK	1976.43.1	Gana, Tafo-Akim.
Macrodipteryx longipennis	NHMUK	1976.43.2	Gana, Tafo-Akim.
Macrodipteryx vexillarius	FMNH	444039	Malawi, Dedza, Chongoni Forest Reserve, N Gawani
Macrodipteryx vexillarius	USNM	431637	Zimbabue, Gwaai Reserve
Macrodipteryx vexillarius	USNM	430848	Zimbabue, Wankie
Macrodipteryx vexillarius	USNM	430849	Zimbabue, Wankie
Macrodipteryx vexillarius	LSUMNS	96266	Zambia, 30 mi. E Solwezi

APPENDIX 2. List of skin specimens of Caprimulgidae analysed, with details of institution, specimen number and locality. Legend: ANSP – Academy of Natural Sciences of Drexel University, Philadelphia, USA; LSUMNS – Louisiana State University Museum of Natural Science, Baton Rouge, USA; MHNN – Muséum d'Histoire Naturelle de Neuchâtel, Switzerland; MZUSP – Museu de Zoologia da Universidade de São Paulo, Brazil; NHMUK – Natural History Museum, Tring, UK; USNM – National Museum of Natural History, Smithsonian Institution, Washington DC, USA; AMNH – American Museum of Natural History, New York, USA. \* Indicates type specimens.

Species	Institution	#	Locality
Lurocalis semitorquatus	MZUSP	84591	Brazil, MT, São Benedito, Ramal Sauré
Lurocalis semitorquatus	MZUSP	92608	Brazil, AM, RDS Bararati
Lurocalis semitorquatus	MZUSP	89901	Brazil, PA, Faz. Fartura
Lurocalis semitorquatus	MZUSP	73736	Brazil, SP, Santos
Lurocalis semitorquatus	MZUSP	78293	Brazil, SP, E.E. Bananal
Lurocalis rufiventris	LSUMNS	104663	Peru, Depto. Pasco
Nyctiprogne leucopyga	MZUSP	73306	Brazil, RR, Rio Branco, opposite Boa Vista
Nyctiprogne leucopyga	MZUSP	73307	Brazil, RR, Rio Branco, opposite Boa Vista
Nyctiprogne leucopyga	MZUSP	93630	Brazil, RR, Caracaraí, rio Jufari
Nyctiprogne leucopyga	MZUSP	93631	Brazil, RR, Caracaraí, rio Jufari
Nyctiprogne leucopyga	MZUSP	93629	Brazil, RR, Rio Jufari, Ilha do Anário
Nyctiprogne leucopyga	MZUSP	76504	Brazil, AM, Baixo Javari, Atalaia do Norte
Nyctiprogne leucopyga	MZUSP	76505	Brazil, AM, Baixo Javari, Atalaia do Norte
Nyctiprogne leucopyga	MZUSP	92610	Brazil, AM, RDS Bararati
Nyctiprogne leucopyga	MZUSP	93632	Brazil, AM, Barcelos, rio Jufari

Species	Institution	#	Locality
Nyctiprogne leucopyga	MZUSP	95786	Brazil, AM, Rio Sucunduri
Nyctiprogne leucopyga	MZUSP	95787	Brazil, AM, Ilha na boca do rio Acari
Nyctiprogne leucopyga	MZUSP	95788	Brazil, AM, Ilha na boca do rio Acari
Nyctiprogne vielliardi	MZUSP	74687*	Brazil, BA, Manga, Rio São Francisco
Nyctidromus albicollis	MZUSP	73304	Brazil, RR, Rio Branco, opposite Boa Vista
Nyctidromus albicollis	MZUSP	73305	Brazil, RR, Rio Branco, opposite Boa Vista
Nyctidromus albicollis	MZUSP	77959	Brazil, RR, Serra da Lua
Nyctidromus albicollis	MZUSP	76749	Brazil, AM, Rio Abacaxis, Paca
Nyctidromus albicollis	MZUSP	80509	Brazil, AM, Rio Roosevelt, Pousada
Nyctidromus albicollis	MZUSP	32013	Brazil, Capanema
Nyctidromus albicollis	MZUSP	82007	Brazil, PA, Fazenda Fartura
Nyctidromus albicollis	MZUSP	83563	Brazil, PA, Almeirim, Ilha de Ipanema
Nyctidromus albicollis	MZUSP	79538	Brazil, TO, Mateiros
Nyctidromus anthonyi	ANSP	185147	Ecuador, Prov. Guayas
Nyctipolus nigrescens	MZUSP	114530	Brazil, AM, Santa Isabel do Rio Negro
Nyctipolus nigrescens	MZUSP	114531	Brazil, AM, Santa Isabel do Rio Negro
Nyctipolus nigrescens	MZUSP	99060	Brazil, AM, Fazenda Fartura
Nyctipolus nigrescens	MZUSP	70523	Brazil, RO, Porto Velho
Nyctipolus nigrescens	MZUSP	78143	Brazil, MT, Vila Rica, Fazenda Ipê
Nyctipolus nigrescens	MZUSP	78144	Brazil, MT, Vila Rica, Fazenda Ipê
Nyctipolus nigrescens	MZUSP	78145	Brazil, MT, Vila Rica, Fazenda Ipê
Nyctipolus nigrescens	MZUSP	81437	Brazil, MT, Brasnorte
Nyctipolus nigrescens	MZUSP	88366	Brazil, MT, Sinop
Nyctipolus hirundinaceus	MZUSP	39591	Brazil, PB, Coremas
Nyctipolus hirundinaceus	MZUSP	39592	Brazil, PB, Coremas
Nyctipolus hirundinaceus	MZUSP	39593	Brazil, PB, Coremas
Nyctipolus hirundinaceus	MZUSP	39594	Brazil, PB, Coremas
Nyctipolus hirundinaceus	MZUSP	39595	Brazil, PB, Coremas
Nyctipolus hirundinaceus	MZUSP	7623	Brazil, BA, Juazeiro
Setopagis parvula	MZUSP	74411	Brazil, MS, Três Lagoas, Fazenda Floresta
Setopagis parvula	MZUSP	97800	Brazil, São Gabriel do Oeste
Setopagis parvula	MZUSP	81023	Brazil, Trindade
Setopagis parvula	MZUSP	94577	Brazil, Campinaçu
Setopagis parvula	MZUSP	79897	Brazil, DF, BR20, Brasília
Setopagis heterura	MZUSP	77954	Brazil, RR, Serra da Lua
Setopagis heterura	CMNH	41904*	Colombia, Santa Marta, La Tigrera
Setopagis maculosa	CMNH	60854*	French Guiana
Tepuiornis whitelyi	USNM	639107	Guyana
Tepuiornis whitelyi	USNM	639200	Guyana
Tepuiornis whitelyi	USNM	639325	Guyana
Tepuiornis whitelyi	NHMUK	1888.8.1.96*	Guyana, Mt. Roraima
Tepuiornis whitelyi	NHMUK	1888.8.1.97*	Guyana, Mt. Roraima
Antiurus maculicaudus	MZUSP	83560	Brazil, PA, Almeirim, Ilha de Ipanema

Species	Institution	#	Locality
Antiurus maculicaudus	MZUSP	81024	Brazil, Trindade
Antiurus maculicaudus	MZUSP	85385	Brazil, Peixe, 18 km a leste do rio Araguaia
Macropsalis forcipata	MZUSP	90320	Brazil, SP, Paraibuna
Macropsalis forcipata	MZUSP	97795	Brazil, SP, Apiai
Macropsalis forcipata	MZUSP	97796	Brazil, SP, Apiaí
Macropsalis forcipata	MZUSP	101545	Brazil, SP, Jambeiro
Hydropsalis torquata	MZUSP	79892	Brazil, SP, Campo Limpo Paulista
Hydropsalis torquata	MZUSP	94505	Brazil, SP, Santana de Parnaíba
Hydropsalis torquata	MZUSP	95040	Brazil, SP, Região de São Vicente
Hydropsalis torquata	MZUSP	97799	Brazil, SP, Iguape
Hydropsalis torquata	MZUSP	101489	Brazil, SP, Iguape
Hydropsalis torquata	MZUSP	73705	Brazil, SC, Palhoça
Hydropsalis climacocerca	MZUSP	46487	Brazil, PA, Rio Tapajós (Leste), Fordlândia
Hydropsalis climacocerca	MZUSP	46489	Brazil, PA, Rio Tapajós (Leste), Fordlândia
Hydropsalis climacocerca	MZUSP	46490	Brazil, PA, Rio Tapajós (Leste), Fordlândia
Hydropsalis climacocerca	MZUSP	46491	Brazil, PA, Rio Tapajós (Leste), Fordlândia
Hydropsalis climacocerca	MZUSP	58396	Brazil, PA, Rio Tapajós (Leste), Fordlândia
Hydropsalis climacocerca	MZUSP	58398	Brazil, PA, Rio Tapajós (Leste), Fordlândia
Uropsalis lyra	NHMUK	1890.2.18.176	_
Uropsalis segmentata	NHMUK	1897.11.12.9	_
Systellura longirostris	MZUSP	102645	Brazil, Andari
Systellura longirostris	MZUSP	102646	Brazil, Raso da Catarina
Systellura longirostris	MZUSP	102649	Brazil, Raso da Catarina
Systellura longirostris	MZUSP	81227	Brazil, TO, Catalão
Systellura longirostris	MZUSP	102647	Brazil, Serra Itatiaiuçu
Systellura longirostris	MZUSP	102648	Brazil, BA, Diamantina
Systellura longirostris	MZUSP	36299	Brazil, RJ, Parque Nacional do Itatiaia
Systellura longirostris	MZUSP	36300	Brazil, RJ, Parque Nacional do Itatiaia
Quechuavis decussata	MHNN	92.5425*	Peru
Quechuavis decussata	AMNH	229090	Peru
Eleothreptus anomalus	MZUSP	16218	Brazil, SP, Ipiranga
Eleothreptus anomalus	MZUSP	31806	Brazil, SP, Rio das Pedras
Eleothreptus anomalus	MZUSP	53217	Brazil, SP, Avaré, Fazenda Pedras
Eleothreptus anomalus	MZUSP	51053	Brazil, Umbara
Eleothreptus candicans	MZUSP	76174	Brazil, GO, Parque Nacional das Emas
Eleothreptus candicans	MZUSP	76175	Brazil, GO, Parque Nacional das Emas
Thermochalcis cayennensis	MZUSP	77955	Brazil, RR, Serra da Lua
Thermochalcis cayennensis	MZUSP	77957	Brazil, RR, Parque Nacional Viruá
Thermochalcis cayennensis	MZUSP	77958	Brazil, RR, Parque Nacional Viruá
Thermochalcis cayennensis	MZUSP	93626	Brazil, RR, Caracaraí, rio Jufari
Thermochalcis cayennensis	MZUSP	93627	Brazil, RR, Caracaraí, rio Jufari
Thermochalcis cayennensis	MZUSP	93628	Brazil, RR, Rio Jufari, Ilha do Anário