THE SYSTEMATICS AND EVOLUTION OF THE NIGHTJARS AND THEIR ALLIES (AVES: CAPRIMULGIFORMES)

By

SNORRI SIGURDSSON

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Date	**Chair of Examining Committee** Dr. Joel L. Cracraft, American Museum of Natural History
_____	_____
Date	**Executive Officer** Dr. Laurel A. Eckhardt
	_____
	Dr. Frank T. Burbrink, College of Staten Island
	_____
	Dr. Robert F. Rockwell, The City College of New York
	_____
	Dr. Nancy B. Simmons, American Museum of Natural History
	_____
	Dr. Dustin R. Rubenstein, Columbia University

Supervising Committee

The City University of New York

ABSTRACT

THE SYSTEMATICS AND EVOLUTION OF THE NIGHTJARS AND THEIR ALLIES (AVES: CAPRIMULGIFORMES)

By Snorri Sigurdsson

Advisor: Dr. Joel L. Cracraft

Recent studies have shown that the avian order Caprimulgiformes includes eight families: the owlet-nightjars (Aegothelidae), the nightjars (Caprimulgidae), the potoos (Nyctibiidae), the frogmouths (Podargidae), the monotypic oilbird (Steatornithidae) and the three families traditionally placed in the order Apodiformes: the swifts (Apodidae), the tree-swifts (Hemiprocnidae) and the hummingbirds (Trochilidae). In this study, a total-evidence approach was utilized to address the relationships of these families. A phylogenetic analysis of a combined dataset of 134 skeletal morphological characters, 14 nuclear loci (exons and introns) and a presence/absence indel matrix, with a taxon sampling of all eight families as well as 16 outgroup taxa provided a better resolved phylogeny for the group than obtained by previous studies. New relationships include the placement of the frogmouths (Podargidae) as the sistergroup to a clade containing the owlet-nightjars (Aegothelidae) and the three "apodiform" families. Both morphological and molecular data supported the sister-relationship of the nightjars (Caprimulgidae) and the potoos (Nyctibiidae).

A phylogeny for the three New World radiations of nightjars (Caprimulgidae) was produced from a four-loci molecular dataset. The taxon sampling was the densest of any

phylogenetic study of the group, not were all but three New World nightjar species sampled, but also 78 of 101 recognized subspecies. This provided an opportunity to address species- and intraspecific-level relationships. The taxonomic modifications resulting from the phylogeny included a reduction in the number of genera for the three radiations, from 14 to 10, and nine subspecies were elevated to full phylogenetic species status resulting in an increase in total species numbers from 89 to 98 for the family.

The modified phylogeny of the New World nightjars was utilized to investigate temporal patterns of diversification, historical biogeography and evolution of habitat choice and migratory behavior. The three New World radiations are for the most part temporally congruent but they show highly independent histories of spatial and ecological diversification that have resulted in divergent patterns of extant species distributions as well as ecology, impacted by multiple independent vicariant events, long-distance dispersal and habitat shifts.

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CHAPTER 1

INTRODUCTION

THESIS BACKGROUND

Avian systematics have undergone a renaissance in the last few decades with the inclusion of molecular information, in particular DNA sequence data, in the studies of evolutionary relationships for all major avian groups (Sibley *et al.*, 1988; Mindell, 1997; Björklund, 1999; Groth & Barrowclough, 1999; Johansson *et al.,* 2001; García-Moreno *et al.,* 2003; Poe & Chubb, 2004; Hackett *et al.,* 2008; McCormack *et al.,* 2012). The result has been a considerable upheaval in avian taxonomy with the status of multiple classically recognized taxa being challenged and new ones introduced. This occurs at all taxonomic levels, from the recognition of new species by the discovery of intraspecific genetic diversity, movement of species between genera or even families and the phylogenetic relationships of the higher-level taxa, the families and orders of modern birds.

The last part, resolving the higher-level evolutionary relationships of modern birds has perhaps been the most challenging task in modern avian systematics, despite an immense increase in the availability of material for data analysis and advances in the variety and efficiency of analytical methods (Cracraft *et al.,* 2004; Dyke & Tuinen, 2004; Poe & Chubb, 2004; Edwards, Jennings & Shedlock, 2005; Livezey & Zusi, 2006, 2007; Chojnowski *et al.,* 2008; Ericson, 2008; Hackett *et al.,* 2008; Mayr, 2008; Kimball *et al.,* 2009; Pratt *et al.,* 2009; Mayr, 2011; Pacheco *et al.,* 2011; McCormack *et al.,* 2012). One of the more challenging projects has been the resolution of the deeper branches on the avian tree, that potentially separate or even break up the 'classical orders' of birds, with the majority of studies failing to provide well resolved phylogenies and a high degree of incongruence is between them.

The most consistent and congruent results among studies resolve the most basal nodes of the avian tree, including the separation of all extant birds into the Palaeognathae (that includes the ratites and the tinamous) and Neognathae (all other extant birds) and the separation of the Neognathae into the Galloanserae (Galliformes and Anseriformes) and the Neoaves. (Sibley & Ahlquist, 1990; Cracraft & Clarke, 2001; Mayr & Clarke, 2003; Cracraft *et al.,* 2004; Chubb, 2004; Fain & Houde, 2004; Ericson *et al.,* 2006; Livezey & Zusi, 2007; Hackett *et al.,* 2008; Pratt *et al.,* 2009; Pacheco *et al.,* 2011; McCormack *et al.,* 2012). The relationships among the families within these three basal clades range from relatively well-supported and mostly congruent within the Anseriformes and Galliformes (Donne-Goussé *et al.,* 2002; Kan *et al.,* 2010; Kriegs *et al.,* 2007; Bonilla *et al.,* 2010) to highly contentious within the paleognaths (Livezey and Zusi, 2007; Hackett *et al.,* 2008; Harshman *et al.,* 2008; Bourdon *et al.,* 2009; Phillips *et al.,* 2010; Smith *et al.,* 2012).

Within avian higher taxa, the most difficult systematic problem has been the resolution of the Neoaves. In numerous studies, the Neoaves are characterized by extremely short basal internodes separating lineages without providing support for most nodes, leading to a large basal polytomy. This has been thought to be an indicator of a rapid diversification event, early in the history of the group (Cracraft *et al.,* 2004; Ericsson *et al.,* 2006; Livezey & Zusi, 2007; Hackett *et al.,* 2008; Pratt *et al.,* 2009; Matzke *et al.,* 2012). Hypotheses about inter-neoavian relationships have been presented in numerous studies using a variety of character data, the majority being from molecular sources (Fain & Houde, 2004; Ericson *et al.,* 2006; Hackett *et al.,* 2008; Pratt *et al.,* 2009; Pacheco *et al.,* 2011; McCormack *et al.,* 2012) but also studies using morphological data

(Mayr & Clarke, 2003; Livezey & Zusi, 2006, 2007). Topological patterns within Neoaves vary considerably between the studies, with lack of resolution a common theme. The studies with the largest datasets, have been most successful in resolving the basal neoavian nodes (Hackett *et al.,* 2008; McCormack *et al.,* 2012) and congruence among studies is increasing, with most Neoavian orders being grouped into taxon-assemblages, such as the 'water-bird assemblage' which includes groups such as penguins, herons, sulids, loons and procalleriforms or the 'higher-landbird assemblage' which includes diverse groups such as parrots, falcons, owls, trogons, piciforms, coraciiforms and by far the largest modern avian order, the passerines (Hackett *et al.,* 2008; Pratt *et al.,* 2009; McCormack *et al.,* 2012).

One of these taxon-assemblages that are consistently found in large-scale phylogenetic studies of modern birds is the caprimulgiform-group (Ericson *et al.,* 2006; Livezey & Zusi, 2006, 2007; Hackett *et al.,* 2008; Pratt *et al.,* 2009; McCormack *et al.,* 2012), which includes families traditionally placed in two orders, Caprimulgiformes and Apodiformes. Resolving the relationships within this group has proven to be extremely challenging, and remains an incomplete task. Evidence suggests that the two orders belonging to this group are not reciprocally monophyletic (Ericson *et al.,* 2006; Hackett *et al.,* 2008; Braun & Huddleston, 2009: Mayr, 2010), and that the lineages leading to most modern groups date back to the origin of the Neoaves, and diverged very rapidly (Ericson *et al.,* 2006; Hackett *et al.,* 2008). Thus, finding characters that prove informative for the inferral of their evolutionary relationships is difficult.

Additionally, the systematics of many of the families belonging to this group are poorly studied. Partial phylogenies, sampling at the genus-level or at the species-level

for chosen genera are available for most groups including the trochilids (i.e. Bleiweiss *et al.,* 1997; Gerwin & Zink, 1998; McGuire *et al.,* 2007), apodids (Thomassen *et al.,* 2003, 2005), aegothelids (Dumbacher *et al.,* 2003), nyctibiids (Mariaux & Braun, 1996), and caprimulgids (Barrowclough *et al.,* 2006; Larsen *et al.,* 2007; Han *et al.,* 2010) but better-sampled phylogenies are needed to fully understand the diversity within these families. This is pivotal to fully understand the evolutionary and historical processes that have shaped the diversification of these groups which is important because the group presents interesting examples of trait evolution, including morphologies and ecologies that are unique in the avian world (such as nocturnal lifestyles, nectarivory, highly modified flight, echolocation and hibernation to name a few) (summarized in delHoyo *et al.,* 1999), variable levels of species diversity (ranging from monotypic families such as Steatornithidae to highly species-rich families such as the trochilids), and complex biogeography (Cracraft, 2001; McGuire *et al.,* 2007; Mayr, 2011; Nesbitt *et al.,* 2011).

The nightjars (Caprimulgidae) are an important family within this group. They are the third-most diverse family, behind the trochilids and apodids (only trailing the latter by three species according to delHoyo *et al.,* 1999), and have a cosmopolitan distribution, with the Neotropics and tropical Africa particularly important areas of high diversity (Holyoak 2001, Dickinson *et al.,* 2003). Of the five families within the group, that are mostly nocturnal and crepuscular, they are by far the most diverse. Hence, with the exception of owls, they are the most important group of nocturnal birds. As with many other bird families, intraspecific diversity is high among caprimulgids, with multiple species further split into subspecies (Holyoak 2001, Dickinson *et al.,* 2003). No study has attempted to investigate whether these subspecies represent true taxonomic

units by using molecular resources. The species diversity of the family may be hugely underestimated.

THESIS LAYOUT

The systematics and evolution of the caprimulgiform families and specifically the nightjars (Caprimulgidae) is the focus of this doctoral thesis. In addition to this introductory chapter there are three main chapters. The main research question, goals and approaches will be summarized in the following sections:

The second chapter of the thesis is a systematic review of the well established taxonomic group that includes the eight families of caprimulgiform and apodiform birds with the goal to resolve the contentious relationships among the major lineages. This is a complex problem as was described above. A total-evidence approach was administered, with representatives of all families sampled, that incorporated a new morphological character set, and a large molecular dataset, assembled from both available published sources and original sequences. The morphological and molecular data sets were examined separately, and the utility of the morphological characters as well as the different molecular markers evaluated. Informative insertion and deletion events in the multi-locus dataset were also included as characters. Finally, the different datasets were combined into a single matrix and analyzed. Such a combined analysis with this degree of character sampling had not been performed before and resulted in a more robustly resolved phylogeny for the group. Fossil taxa were also included in this study, and the morphological characters utilized to address their placement among the extant caprimulgiform taxa.

The third chapter addresses the systematics of the nightjars (Caprimulgidae) with emphasis on the three New World radiations which systematic studies have demonstrated are monophyletic units. A new molecular phylogeny was generated from DNA sequences of both mitochondrial and nuclear loci utilizing both fresh tissue and ancient DNA extracted from museum skin specimens. Nearly all recognized species in these three radiations were sampled. Additionally, to investigate the genetic aspects of the recognized intraspecific diversity, subspecies were sampled extensively. This is by far the largest phylogenetic study of New World nightjars and nearly completely sampled phylospecies-level phylogenies are still rare in avian systematics. The phylogenetic results, along with identification of morphological and molecular traits, were employed as evidence to support taxonomic modification of numerous nightjar taxa. Some subspecies were elevated to full phylospecies status and many species were transferred to different genera. Some of these taxonomic modifications have been anticipated by other researchers of caprimulgid taxonomy, both old and recent, (i.e. Friedmann, 1945 and Cleere, 2010), of which the results here are the first molecular evidence to support those suggestions. But, there are also numerous new insights which not only alter the taxonomy of the group but provide information about diversification patterns that were previously unknown.

In the fourth and final chapter, the phylo-species phylogeny generated in chapter 3, is employed to investigate the spatial and temporal patterns of diversification of the three New World nightjar radiations in the latter half of the Cenozoic. Having a phylogeny that includes nearly all phylospecies of New World nightjars allows for a thorough investigation of their biogeographic history. Dated cladograms for both the

caprimulgids and other caprimulgiform taxa were generated using molecular clock analyses that incorporated fossil calibrations. The dated phylogeny of the New World nightjars along with biogeographic analyses that reconstruct ancestral areas using statistical methods, as implemented in recent software tools, allowed for a detailed investigation of the history of spatial diversification and the evolution of distributional ranges across the New World. The role of processes that may have induced or prevented speciation or dispersion of taxa was evaluated (such as presence of geographic barriers, opportunities for dispersion from source areas and long-distance dispersal events). Important areas for nightjar diversification were also identified. Finally, to investigate aspect of niche evolution, ancestral trait analyses, that reconstruct the evolution of ecological traits such as habitat choice and migratory behavior on the phylogenies, were performed. The histories of the three radiations are thought to be independent yet temporally congruent for the most part. This allowed for comparisons of the generality of patterns, both of spatial diversification and trait evolution across continents. Such large-scale biogeographic studies are not common, particularly not with this dense level of taxon sampling. Thus, the patterns seen in the study should provide insight into general patterns and processes that characterize the diversification histories of avian radiations in North, Central and South America.

Combined, the three chapters in this dissertation are an important contribution for addressing the complex systematics of the caprimulgiforms, and the caprimulgids in particular. Studies on these taxa are few and far between in any field of biology and although recent studies have improved the knowledge about the evolution and systematics of these groups, this dissertation provides a significant addition of data

(morphology and molecular data), analytical approaches (phylogenetic analyses, molecular dating analyses, biogeographic analyses and ancestral trait reconstructions), evaluations of taxonomy with suggested modifications, and insight into the evolutionary relationships, biogeography and diversification history of a truly intriguing group of birds.

CHAPTER 2

THE SYSTEMATICS OF THE CAPRIMULGIFORMES

1. INTRODUCTION

The Caprimulgiformes are an intriguing order of birds that have proven to be one of the most problematic avian groups for systematic studies at the familylevel. Traditionally, the order includes five families: the oilbird (Steatornithidae) with a single species, *Steatornis caripensis*; the potoos (Nyctibiidae), with 7 species in the genus *Nyctibius*; the frogmouths (Podargidae) with 12 species in two genera, *Podargus* (3 species) and *Batrachostomus* (9 species); the nightjars (Caprimulgidae), the largest family, with 89 species in 15 genera; and, finally, the owlet-nightjars (Aegothelidae) with 9 species in the genus *Aegotheles* (del Hoyo *et al*., 1999, Holyoak, 2001). These five families were grouped together because they share a variety of characters in their external morphology and behavior including cryptically colored plumage, and nocturnal or crepuscular activity associated with a lifestyle that is not particularly common in other avian orders (Strigiformes being the main exception). Due to their cryptic lifestyles, many species in these families are uncommonly encountered and thus relatively little is known about their biology (Cleere & Nurney, 1998; del Hoyo *et al*., 1999; Holyoak, 2001).

Recent systematic studies that either focus on the caprimulgiforms or include them have demonstrated that the order is not monophyletic as the Apodiformes is embedded among the caprimulgiform families (Ericson *et al.*, 2006; Hackett *et al.*, 2008; Mayr, 2010; Nesbitt *et al.*, 2011). The Apodiformes traditionally include three families: the swifts (Apodidae), with over 90 species in 19 genera; their close relatives the tree-swifts (Hemiprocnidae), with 4 species in a single genus *Hemiprocne*; and the hummingbirds (Trochilidae), an extremely diverse family with well over 300 species in

over 100 genera (del Hoyo *et al*, 1999). Interestingly, the majority of species in the apodiform families are diurnal, in particular the trochilids. Thus, placing these three families within the Caprimulgiformes does not only drastically change the taxonomic status of the two orders, but ideas about character evolution and ecology, in particular those that related to nocturnal vs. diurnal lifestyles (Braun & Huddleston, 2009). Hereafter, the name Caprimulgiformes will be used for the whole clade, including the families previously placed in Apodiformes (collectively termed here the Apodi).

Although the monophyly of this expanded Caprimulgiformes is well supported by molecular sequence data (Ericson *et al.*, 2006; Hackett *et al.*, 2008), the relationships among the caprimulgiform families are still a matter of significant debate, with molecular analyses disagreeing with one another as well as with morphological studies (Johansson *et al.*, 2001; Mayr, 2002, 2008, 2010; Mayr *et al.*, 2003; Cracraft *et al.*, 2004; Ericson *et al*, 2006; Livezey & Zusi, 2006, 2007; Hackett *et al.*, 2008; Braun & Huddleston, 2009) (**Figure 1**). A high diversity of data sources and analytical approaches may explain some of these conflicts, but all evidence points to the well-recognized lack of resolution at the base of the neoavian radiation, which is hypothesized to have evolved very rapidly. The majority of caprimulgiform families belong to these basal lineages, in which very short internodes create problems for phylogenetic analyses in many neoavian groups (Cracraft *et al.*, 2004; Fain & Houde, 2004; Ericsson *et al.*, 2006; Hackett *et al.*, 2008; Pratt *et al.*, 2009; Pacheco *et al.*, 2011; Matzke *et al.*, 2012).

Because of these problems some studies have even cast doubt on the monophyly of the expanded Caprimulgiformes (Mayr & Clarke, 2003; Mayr *et al.*, 2003; Cracraft *et al.*, 2004; Fain & Houde, 2004; Braun & Huddleston, 2009; Pacheco *et al.*, 2011). Even

so, the studies with the most thorough taxon and character sampling do support the monophyly of the group (Ericson *et al.*, 2006; Hackett *et al.*, 2008), but the problem remains of resolving the relationships of the families within the order. Some of these inter-ordinal relationships are well supported in most studies. Relationships within the Apodi are well resolved with Trochilidae being the sister-group of a clade containing Apodidae and Hemiprocnidae. Another well-supported relationship is the placement of the aegothelids as the sister-group of these three families. This Aegothelidae/Apodi clade is named Apodoidea in this study. The Apodoidea and the relationships among its families are supported by both molecular and morphological studies (Mayr, 2002, 2010; Mayr *et al.*, 2003. Cracraft *et al.*, 2004; Barrowclough *et al.*, 2006; Ericson *et al.*, 2006; Hackett *et al.*, 2008; Braun & Huddleston, 2009; Nesbitt *et al.*, 2011; Pacheco *et al.*, 2011) but some morphological studies disagree (Livezey & Zusi, 2007). A diverse array of proposed relationships for the remaining families has been presented in various studies, including sister-relationships between Caprimulgidae and Podargidae (Barrowclough *et al.*, 2006), Caprimulgidae and Nyctibiidae (Mayr, 2002, 2010; Nesbitt *et al.*, 2011), and Nyctibiidae and Steatornithidae (Hackett *et al.*, 2008) although the general consensus is lack of resolution for these families.

Studies that attempted to combine molecular and morphological data are few (Mayr *et al.*, 2003; Nesbitt *et al.*, 2011) and either they failed to sample the order thoroughly resulting in a non-monophyletic Caprimulgiformes (Mayr *et al.*, 2003) or they utilized a relatively small molecular dataset that lacked resolving power (Nesbitt *et al.*, 2011). Total-evidence approaches that incorporate both kinds of character data should be helpful in addressing contentious relationships, as one source of data may provide

phylogenetic resolution when the other does not (e.g. Wiens *et al*, 2010). Incorporating morphological data also allows for the addition of fossil taxa and the Caprimulgiformes have a relatively rich Cenozoic fossil record (summarized in Mayr, 2009), which should be included in a comprehensive analysis of their relationships.

In this study, I provide a total-evidence approach to address the uncertainties in the phylogenetic relationships within the Caprimulgiformes. A new morphological matrix was assembled using characters that specifically capture taxonomically informative variation within the Caprimulgiformes. In addition, molecular sequences from 14 nuclear markers are analyzed, both separately and combined with the morphological data, using a variety of phylogenetic criteria. These data also provide an opportunity to re-evaluate the phylogenetic placement of important fossil taxa previously assigned to this order.

2. METHODS

2.1 MORPHOLOGICAL DATA

Osteological characters were identified, described and scored from skeletons of 16 ingroup taxa, representing all caprimulgiform families as well as 13 outgroup taxa including two representatives of the Galloanserae and 11 of Neoaves. The following taxa were examined: CAPRIMULGIFORMES: Steatornithidae: *Steatornis caripensis*; Podargidae: *Batrachostomus javensis*, *Podargus strigoides*; Nyctibiidae: *Nyctibius grandis*; Caprimulgidae: *Caprimulgus macrurus*, *Caprimulgus longirostris*, *Chordeiles minor*, *Eurostopodus macrotis*, *Phalaenoptilus nuttallii*; Aegothelidae: *Aegotheles cristatus*. APODIFORMES: Hemiprocnidae: *Hemiprocne mystacea*; Apodidae: *Streptoprocne zonaris*; Trochilidae: *Amazilia fimbriata*, *Colibri coruscans*, *Phaethornis superciliosus*. The taxa chosen as outgroup-taxa were: Anseriformes: *Anser erythropus*, Galliformes: *Gallus gallus*, Accipitriformes: *Buteo jamaicensis*, Coliiformes: *Colius colius*, Columbiformes: *Treron vernans*, Cuculiformes: *Coccyzus americanus,* Eurypygiformes: *Eurypyga helias*, Musophagiformes: *Tauraco erythrolophus*, Leptosomatiiformes: *Leptosomus discolor*, Passeriformes: *Tyrannus tyrannus* and *Turdus falcklandii*, Strigiformes: *Strix occidentalis*, Trogoniformes: *Trogon violaceus* (See **Appendix I** for specimen details). *Gallus* was chosen to root the morphological tree. The neoavian taxa were chosen to represent diverse clades across the neoavian tree. Although the sistergroup of the Caprimulgiformes is not known, both columbiform and traditionally defined "gruiform" taxa (including *Eurypyga*) have been placed as close relatives of the caprimulgiforms in analyses of molecular data (Ericson *et al.*, 2006;

Hackett *et al.*, 2008) whereas mousebirds (Coliiformes), trogons (Trogoniformes), owls (Strigiformes), birds of prey (Falconiformes), turacos (Musophagiformes), passerines (Passeriformes) and the cuckoo-roller (*Leptosomus*) (Mayr & Clarke, 2003; Livezey & Zusi, 2007) are among the taxa associated with the Caprimulgiformes in previous morphological analyses.

Characters were compared with homologous characters from the 2954 morphological character set of Livezey & Zusi (2006) as well as characters from Mayr (2005, 2009). A character matrix of 134 characters was assembled in Mesquite 2.5 (Maddison & Maddison, 2011). All characters were treated with equal weight. Fifteen of the 134 characters were treated as ordered whereas the remaining characters were unordered (see **Appendix II** for character list and descriptions). Additionally, 10 fossil specimens, representing various caprimulgiform taxa, were included in the morphological character matrix (also in **Appendix II**), using the same morphological characters. Characters were identified and scored using photographs of the fossils as well as descriptions from the literature. The fossils varied in the quality of their preservation, the majority of them having a high number of skeletal parts missing or badly preserved. The bones that were most informative from the fossil specimens were the coracoid and the humerus, whereas characters from the skull, sternum and pelvis were generally hard to identify and score. As a result, the number of missing characters is very high among the fossil specimens (up to 90% in the most extreme case). The fossil taxa included were: *Fluvioviridavis platyrhamphus* Mayr and Daniels 2001 (Nesbitt *et al.*, 2011), *Masillapodargus longipes* Mayr 1999 (Mayr, 1999), *Paraprefica kelleri* Mayr 1999 (Mayr, 2005), *Jungornis tesselatus* Karhu 1988 (Karhu 1999), *Argornis caucasicus* 1999

(Karhu, 1999), *Eocypselus vincenti* Harrison 1984 (Dyke *et al.*, 2004; Mayr, 2010); *Eurotrochilus spp.* (Louchart *et al.*, 2008 and Bochenski & Bochenski, 2008); *Aegialornis spp.* (Collins, 1976), *Parargornis messelensis* Mayr 2003 (Mayr, 2003) and *Protocypselopmorphus manfredkelleri* Mayr 2005 (Mayr, 2005). The morphological matrix was analyzed both with and without the ten fossil taxa included.

As there is strong evidence for a monophyletic Caprimulgiformes based on previous studies (Ericson *et al.*, 2006; Livezey & Zusi, 2007; Hackett *et al.*, 2008) as well as the results from the combined analysis of this study (see below) emphasis here was placed on sampling morphological characters that might be potentially informative of relationships within the order. Thus, the same morphological matrix was analysed with only the 16 caprimulgiform taxa and a single galloanseran outgroup taxon included, to investigate the utility of the characters at resolving the intra-ordinal relationships and how the levels of homoplasy are affected when the 13 neoavian taxa have been removed.

2.2 MOLECULAR DATA

As previous studies of molecular data have demonstrated (Ericson *et al.*, 2006, Hackett *et al.*, 2008), the use of multiple informative markers is the optimal approach for testing monophyly of the Caprimulgiformes as well as relationships within the order. Thus, sequence data from 14 nuclear markers were assembled for the same taxa sampled in the morphological study (with a few exceptions), plus a number of additional taxa (see below). Thirteen loci were chosen from the dataset of Hackett *et al.* (2008) and downloaded from Genbank: exons 3 through 8 from aldolase B fructose-biphosphate gene (*ALDOB*), exons 6 through 8 from clathrin heavy chain gene (*CLTC)*, exons 1 and 2

from crystalline alpha A gene (*CRYAA*), exons 5 through 9 from eukaryotic translation elongation factor 2 gene (*EEF2*), exon 2 from early growth response 1 gene (*EGR1*), exons 6 through 8 from fibrinogen beta chain gene (*FGB*), exons 2 through 4 from growth hormone 1 gene (*GH1*), exons 4 and 5 from muscle skeletal receptor tyrosine kinase gene (*MUSK*), exon 3 from v-myc myelocytomatosis viral oncogene-like protein gene (*MYC*), exons 2 and 3 from pterin-4 alpha-carbinolamine dehydratase gene (*PCBD1*), the recombination activating gene 1 (*RAG-1*), exons 1 through 4 from the rhodopsin gene (*RHO*), and exons 5 and 6 from transforming growth factor beta 2 gene (*TGFB2*). All interspaced introns are included where present and the introns are in fact the bulk of the dataset (over 70%), as the exons are much shorter in length. The full dataset from Hackett *et al*. (2008) was not used as some markers were not available for key taxa, or did not provide any resolution for the caprimulgiform families when analyzed individually.

Many of these markers have been used in avian systematic studies at relatively high taxonomic levels, in particular *FGB, GH1, RAG-1, MUSK* and *MYC* (Ericson & Johansson, 2003; Mayr *et al.*, 2003; Barker *et al.*, 2004; Beresford *et al.*, 2005; Zuccon *et al.*, 2006; Hackett *et al.*, 2008; Harshman *et al.*, 2008; Treplin *et al.*, 2008; Patou *et al.*, 2009; Han *et al.*, 2010; Lovette *et al.*, 2010) which have proven to be useful at these levels, as they are slowly evolving in birds with low levels of saturation. Recombination activating gene 2 (*RAG-2*) was also amplified, sequenced, and added to the nuclear dataset in this study. *RAG-2* is closely linked and functionally related to the recombination activating gene 1 (*RAG-1*), albeit considerably shorter (1153bp), and has been employed to a lesser degree in avian systematics.

Some of the markers in the dataset of Hackett *et al.* (2008) had transposable element insertions, some as long as 660bp. These insertions have been mapped and investigated with regards to their diversity, phylogenetic utility and homoplasy in a recent study (Han *et al*., 2011). In the marker subset used here, a number of these insertions remain. Those that were phylogenetically important (not autapomorphic or homoplasious across the Neornithes sampled) (see list in **Table 1**) were scored in a simple presence/absence matrix (**Appendix III**).

The taxon sampling for the molecular data focused on the same taxa as the morphological dataset with a few differences. The same genera were sampled for all the caprimulgiform families. However *Caprimulgus macrurus, Chordeiles minor* and *Phalaenoptilus nuttallii* of the Caprimulgidae were not included, nor were *Amazilia* of the Trochilidae and *Apus* of Apodidae. Due to lack of specimen availability, a few congeneric species replaced the species used in the morphological dataset. *Aegotheles insignis* replaced *A. cristatus*, *Batrachostomus septimus* replaced *B. javanensis* and *Phaethornis griseogularis* replaced *P. superciliosus*. Two species were added to the matrix, including a potoo (*Nyctibius bracteatus)* and a swift (*Aerodramus vanikorensis*).

All of the same outgroup genera were included, but one different species was used: *Trogon personatus* replaced *Trogon violaceus.* Also the following taxa were added: Struthioniformes (*Struthio camelus)*, Phoenicopteriformes (*Phoenicopterus chilensis*), Charadriiformes *(Charadrius vociferus*), Gaviiformes (*Gavia immer*), Gruiformes (*Grus canadensis*), and Passeriformes (*Acanthisitta chloris*). A total of 32 taxa were therefore included in the molecular dataset (see list of taxa and Genbank reference numbers in

Appendix IV). The dataset is not complete as there are sequences for some markers that are not available for all taxa.

The molecular data matrix was aligned in Geneious (Drummond *et al.*, 2010) using the Muscle Alignment feature (Edgar, 2004). The 14 loci were merged into a concatenated dataset for analyses as well as treated independently, and with all insertion events included the concatenated matrix is 26,470 base pairs long. jModelTest (Posada, 2008) was used on all individual loci to choose the most appropriate model of substitution, with the Aikake Information Criterion applied to rank the models.

2.3 COMBINED DATA

All three kinds of data the morphological matrix, the concatenated 14-loci molecular matrix and the indel presence/absence matrix were combined into one dataset but kept as three partitions. In addition, the molecular data was partitioned separately into 14 partitions, thus reulting in a total of 16 partitions in the combined dataset. A separate combined data matrix was generated that included the ten fossil taxa for which morphological characters were the only available data.

2.4 PHYLOGENETIC ANALYSES

Phylogenetic analyses using different optimality criteria and analytical frameworks were performed on all datasets when relevant. The morphological data matrix was analyzed in Paup*4.0d98 (X86) (Swofford, 2008) using a parsimony optimality criterion. Trees were identified by a heuristic search using tree-bisection-reconnection (TBR) branch swapping with *Gallus gallus* as the root. Random additions

were replicated 1000 times. A strict consensus tree was calculated for three or more equally parsimonious trees. Support was measured by the nonparametric bootstrap, with a total of 1000 replications with each replicate subject to 10 random additions replications. Separate analyses were performed on the morphological data, with and without the fossil taxa.

Phylogenetic analyses of the molecular data were performed using three criteria: 1) a maximum parsimony analysis in Paup*4.0d98 (X86) (Swofford, 2008) with the same settings as the morphological data, except that *Struthio camelus* replaced *G. gallus* as the outgroup taxon for rooting purposes; 2) a maximum likelihood analysis in RAxML-III (Stamatakis *et al.*, 2008) using a GTR model with per-site rate categories. The GTR is the default substitution model in RAxML-III; and 3) a Bayesian analysis in MrBayes v3.2.0 (Huelsenbeck & Ronquist, 2001). The results from jModelTest for each individual locus showed that GTR, TIM3 and TVM were the most commonly chosen models of substitution. MrBayes does not incorporate TIM3 and TVM models so GTR+G was used for all the loci. This model was always one of the five most suitable models according to jModelTest, thus the risk of over-parameterization is not high. Two runs were performed simultaneously, each with six heated chains for 10 million generations, saving each 1000^{th} generation. Convergence of the two runs and stationarity was evaluated in TRACER v1.3 (Rambaut & Drummond) with the first 10% of trees discarded as burn-in and TreeAnotator v1.6.2 was used to calculate the maximum clade credibility tree for each run.

For the combined morphological, molecular, and indel data a parsimony analysis was performed in Paup*4.0d98 (X86) (Swofford, 2008), retaining the individual settings from the separate morphological and molecular analyses. As before, trees were identified by a heuristic search using tree-bisection-reconnection (TBR) branch swapping. Random additions were replicated 1000 times. Trees were rooted with *Struthio camelus*. A strict consensus tree was calculated on three or more equally parsimonious trees. Support was measured by a nonparametric bootstrap analysis, with a total of 1000 replications and each replicate was subject to 10 random additions replications.

Additionally, the combined dataset was analyzed using a Bayesian approach in MrBayes v3.2.0 (Huelsenbeck & Ronquist, 2001). A GTR+G model was used for the molecular as previously described. For the morphological and indel character datasets a simple JC model analog with a Dirichlet distribution was used. Two runs were performed simultaneously, each with six heated chains for 10 million generations, saving each 1000^{th} generation. Convergence of the two runs and stationarity were evaluated in TRACER v1.3 (Rambaut & Drummond) with the first 10% of trees discarded as burn-in. TreeAnotator v1.6.2 was used to calculate the maximum clade credibility tree for each run.

3. RESULTS

3.1 MORPHOLOGICAL DATA

A total of 134 osteological characters were identified, described and coded, including 45 cranial and 89 postcranial (See **Appendix II** for character list). The results from the parsimony analysis of the 134 morphological characters, for the 29 extant taxa only, showed that all but one of the characters were parsimony informative. The heuristic search led to nine equally parsimonious trees when all the characters were treated as unordered. When 15 characters were treated as ordered, the number of equally parsimonious trees rose to 15, and the strict consensus tree had a higher number of collapsed clades but the clades that had bootstrap support higher than 50 were the same on both trees. The strict consensus tree from the analysis with 15 ordered characters is displayed in **Figure 2** with bootstrap scores.

The morphological data were unsuccessful in resolving a monophyletic Caprimulgiformes. The morphological data were successful however, in resolving some relationships among the caprimulgiform taxa. There was strong support for the caprimulgids (represented by 5 species) and nyctibiids (represented by *Nyctibius)* being sister groups (**Figure 2**). Six characters are synapomorphies for this clade: (9) presence of a cone-like protrusion at the caudal margin of the foramen nerve optici, (14) separation of the nasal processus from the maxilla, forming a distinctive narrow ridge, (20) pronounced lateral convexity of the jugal argus, (41) caudal end of mandible short and compressed, especially the cotyla lateralis and processus medialia, (42) presence of an intraramal joint in the mandible with the caudal half of mandible greatly widened; and (53) articular face of the cranialmost incorporated vertebral element of synsacrum is circular or subcircular.

The Apodioidea (a clade with Aegothelidae as sister group to the Apodi) received low bootstrap support (**Figure 2**) but was supported by five synapomorphies: (37) absence of pneumatic foramina on the caudal surface of processus oticus of quadrate, (39) significant curvature of intermediate and rostralmost part of caudal pars of mandible, (73) dorsomedial curvature of acrocoracoid process with respect to coracoid main axis, (82) tuberculum ventralis of humerus extends laterally and downwards and conceals fossa pneumotricipitalis; and (95) shape of dorsal condyle of ulna generally rounded but with flat distal margin (change from complete rounded shape).

Within Apodioidea there was strong support for the trochilids (represented by *Phaethornis, Colibri* and A*mazilia*) being the sister group to the Apodidae (represented by *Apus* and *Streptoprocne*) and Hemiprocnidae (**Figure 2**). The clade containing these three families (Apodi) was supported by six synapomorphies: (77) crista articularis sternalis of coracoid is broad, (79) humerus very short and rigid, (89) processus supracondylaris dorsalis of humerus is present and well developed, (92) fossa olecrani of humerus is prominent and separates condyles, (98) ulna and radius highly abbreviated; and (133) trochlea I of tarsometatarsus is present, an indicator of pamprodactyly.

The clade containing Apodidae and Hemiprocnidae was supported by three synapomorphies: (60) perforations in corpus of sternum are present, (87) crista delto*pectoralis* of humerus is present and very sharply angled outwards like a hook and (99) sulcus tendinis of radius is deep. The trochilid clade was supported by ten synapomorphies: (6) orbit decreased in size, only moderately longer than internal antorbital fenestra, (16) maxilla very long, 1.5 to 3 times longer than cranium, (48) processus ventralis corporis of axis robust and tricurfated, (72) loss of ventral curvature

of scapula, (73) loss of dorsomedial curvature of acrocoracoid process of coracoid, (74) omal extremity of coracoid divided in two by large foramen, (82) loss of the lateral extension of tuberculum ventralis of humerus, (83) distinct distal protrusion on caput humeri, (84) presence of tuberculum musculi pronator superficialis of humerus and (105) intermetacarpal space of carpometacarpus is wider than metacarpal III. Finally the podargid taxa, *Batrachostomus* and *Podargus* formed a monophyletic clade (**Figure 2**) supported by three synapomorphies: (103) deep fossa intratrochealis of carpometacarpus, (117) decrease of pubis length such that it does not extend further caudally than ischium; and (119) antitrochanter of pelvis protrudes laterally and dorsally.

Levels of homoplasy were high in the analysis, with the average consistency index for all 15 trees at only 0.28 and the retention index at 0.58. Only seventeen characters received a consistency index of 1.0, with the remainder scoring 0.5 or less. With the exception of one character (44), which is a synapomorphy for the Galloanserae, all of the characters that have a high consistency index are synapomorphies for relationships within Caprimulgiformes, in particular within the Apodioidea but also for the clade containing Caprimulgidae and Nyctibiidae. The high levels of homoplasy are unsurprising because the morphological characters were primarily identified with respect to their utility to resolve relationships among the caprimulgiform families and the matrix itself included a taxonomically diverse sampling of outgroups. A larger sample of characters and taxa would have been required for a strong test of monophyly such as in the more extensive character set of Livezey and Zusi (2006, 2007) in which the Caprimulgiformes was indeed monophyletic.

In an analysis of the morphological matrix that enforced caprimulgiform monophyly and included a single outgroup taxon, *Gallus gallus*, the utility of the morphological data is more apparent. A parsimony analysis with fifteen ordered characters resulted in five equally parsimonious trees. The strict consensus tree is displayed in **Figure 3** with bootstrap values. The levels of homoplasy were lower with this taxon sampling, the average consistency index for the five trees is 0.49 and the retention index is 0.68. Forty-five characters had a consistency index of 1.0.

The analysis produces a nearly fully resolved Caprimulgiformes. The podargids are the sister to the remainder of the order. The podargid genera share eleven synapomorphies of which only two were synapomorphies for the family in the analysis that included the other neoavian taxa (**Figure 2**) (characters (117) and (119)). The nine new synapomorphies are: (2) rectangular foramen magnum; (12) hook at tip of beak forms suddenly; (15) basipterygoids present; (19) jugal arcus short and thick; (23) processus dorsolateralis nasalis enlarged; (45) prominent angulus mandibulae; (69) median clavicular process of furcula present as a prominent extension; (97) dorsal cotyle of ulna extended laterally; and (112) lamina ellipsoidalis lateralis of ilium present. These characters are strong autapomorphies for the family.

The remaining families Apodidae, Hemiprocnidae, Trochilidae, Aegothelidae, Caprimulgidae, Nyctibiidae and Steatornithidae form a monophyletic clade with >80 bootstrap support (**Figure 3**). This clade is supported by twelve synapomorphies: (4) ecethmoidal bone moderately developed and protruding laterally; (26) reduced processus palatus maxillaris; (35) condylus medialis of processus mandibularis of quadrate is long and lateromedially compressed; (39) significant curvature of intermediate and rostralmost

part of caudal pars of mandible; (57) uncinate process of costal bones long and slender and always interlock with parallel costa; (66) caudolateral process of sternum reduced to being short and stout; (68) loss of extension of xiphal area of sternum; (94) prominent external tricipital groove of humerus; (95) shape of dorsal condyle of ulna generally rounded but with flat distal margin (change from complete rounded shape); (107) proximal end of digit 2 reduced in width; (108) loss of distal extension of digital facet of digit 2; and (110) wide ischiopubic space. *Steatornis* is the sister-group of all others in this clade and the node receives moderately strong bootstrap support. The clade containing the remaining six families is nevertheless supported by thirteen synapomorphies: (3) prominent foramen veni occipitalis externus; (4) highly developed ecethmoidal bone; (12) loss of hook at tip of beak; (18) presence of ventromedial fenestra on rostrum maxillae; (20) pronounced lateral convexity of jugal arcus; (22) extreme rostral position of nasal aperture; (24) loss of prominent angulus tomialis maxillaris; (25) loss of pneumacity of corpus ossis of maxillae; (27) loss of medial keel of interpalatine synostosis; (29) very long and thin rostrally extending palatine process; (30) distinct processus rostromedialis of palatines; (38) loss of prominent joint between frontal and nasal bones; (63) diminutive rostral spine of sternum; (103) shallow fossa intratrochealis of carpometacarpus; and (106) ossial division of fossa dorsalis of phalanx proximalis digitalis majoris.

The monophyly of the clade containing Caprimulgidae and Nyctibiidae (**Figure 3**) is strongly supported by eleven synapomorphies, of which four were found in the previous analysis (characters (9), (41), (42) and (53)) but seven are different: (11) prominent lacrimal; (25) regain of pneumacity of corpus ossis; (28) coincident position of

angulus caudomedialis relative to pars lateralis of palatines; (43) decrease in length of dentaries which are less than ½ of total mandible length; (45) prominent angulus mandibulae; (51) decrease in number of presacral vertebrae from 18 to 17 and (68) long and slender xiphal area of sternum. The Caprimulgidae are supported by four synapomorphies: (26) prominent processus palatus maxillaris; (58) two costal bones of synsacrum; (110) narrow ischiopubic space; and (115) conspicuous, deep infracristal concavity of ilium.

The monophyly of Apodioidea is supported by thirteen synapomorphies, three of which were recovered in the previous analysis (characters (37), (73) and (82)) but ten are different: (2) circular foramen magnum; (46) absence of incisure of condyloid fossa of atlas; (59) sternum much longer than wider; (66) loss of caudolateral process of sternum; (76) presence of foramen nervi supracoracoidei; (78) processus lateralis of coracoid decreased in size; (104) carpometacarpus straight, not twisted laterally; (111) subhorizontal position of ala preacetabularis ilii with respect to planum transversum synsacri; (129) loss of crista lateralis of hypotarsus; and (132) large vascular foramen of tarsometatarsus.

The Apodi receive very high bootstrap support and are defined by twelve synapomorphies of which six are new: (6) orbit decreased in size, only moderately longer than internal antorbital fenestra; (13) loss of complete ossification of ventral side of upper jaw; (20) jugal arcus straight, not pronounced lateral convexity; (58) number of costal bones of synsacrum increases from one to two; (63) rostral spine of sternum extremely large and fork-like; (72) loss of ventral curvature of scapula; and (127) deep incisure intercondylae on distal end of tibiotarsus. Also receiving very high bootstrap support are

the trochilids (**Figure 3**), defined by twelve synapomorphies, eight being the same as before (characters (16), (48), (73), (74), (82), (83), (84) and (105), whereas five are different: (7) hourglass-shaped interorbital region of subraorbital margins; (22) nasal aperture not positioned in an extreme rostral position; (40) length of symphysial part of mandible between one fifth and one third of total length of mandible; (51) seventeen or less presacral vertebrae; and (85) external condyle of humerus broader than internal condyle.

The analysis of the dataset including the ten fossil taxa, with fifteen characters ordered resulted in 24 equally parsimonious trees. The strict consensus tree with bootstrap values is depicted in **Figure 4.** Levels of homoplasy are similarly high as in the analysis without the fossil taxa, with an average consistency index for all 24 trees of 0.25 and a retention index of 0.58. Only twelve characters received a consistency index of 1.0, with the remainder scoring 0.5 or less. The only fossil taxa that are placed with >50% bootstrap support, are *Paraprefica* which is placed within the clade containing Caprimulgidae and Nyctibiidae, and the primitive stem-hummingbirds *Jungornis* and *Eurotrochilus*. The clade containing the two trochilid fossils and the extant hummingbirds is supported by four synapomorphies: (16) increase in the length of the maxilla to 1.5-3 times the length of the cranium; (72); loss of ventral curvature of scapula; (83) presence of distinct distal protrusion on caput humeri; and (84) presence of tuberculum musculi pronator superficialis on humerus. Only one synapomorphy supports *Eurotrochilus* as the sister taxon to the extant hummingbirds: (82) loss of lateral and downward extension of tuberculum ventralis on humerus.

Some of the unsupported topological patterns seen on the highest scoring tree are in agreement with previous research, especially the placement of *Argornis* and *Parargornis* as primitive apodiform taxa (Karhu, 1999; Kristoffersen 2002; Mayr, 2003; Dyke *et al.*, 2004; Mayr, 2010) and *Eocypselus* as a primitive apodioid (Mayr, 2010). On the other hand, *Fluvioviridavis* and *Masillapodargus* are surprisingly placed as the sister-taxa of *Steatornis* and not affiliated with the podargids as previous studies of these fossils have suggested (Mayr, 1999, 2009; Nesbitt *et al.*, 2011).

3.2 MOLECULAR DATA

Concatenating the 14 nuclear markers resulted in a 26,470bp data matrix for 32 taxa. When all autapomorphic insertion events greater than 3bp in length were removed it resulted in a 22,213bp data matrix. The presence of insertion/deletion events in the nuclear markers varied greatly. Only one marker (*EGR1*) had no indels of significance. A considerable number of indels were non-autapomorphic and phylogenetically informative. These were not removed from the matrix, and were additionally scored as characters in a separate character matrix (See **Appendix III**). There was no topological difference among the trees that resulted from the phylogenetic analyses of the two concatenated data matrices. The bootstrap support values were slightly higher on the trees from the matrix when the noninformative insertion events were removed, suggesting that they may add some noise to the analysis.

The results of the complete concatenated molecular dataset when all of the outgroup taxa are included (for a total of 32 taxa with *Struthio camelus* used to root the tree) show a highly supported monophyletic Caprimulgiformes. This result is congruent

in the Maximum Likelihood, Maximum Parsimony and Bayesian analyses (**Figures 5-7**). The Caprimulgiformes are placed within the Neoaves with the Galloanserae as their sister. The Neoaves form a comb-shaped clade with most of the major lineages appearing nearly simultaneously as inferred from the maximum likelihood analysis. The branch-lengths are extremely short and few nodes receive high support. The taxa placed as the closest relatives to the caprimulgiforms are *Phoenicopterus*, *Treron*, *Eurypyga* and *Coccyzus* but with no support.

The relationships among the caprimulgiform families are far from being resolved by the molecular data. The clades separating the modern families range from having no or very low bootstrap support (high 40s or low 50s) to very high bootstrap support (100) on the likelihood and parsimony trees (**Figures 5-6**). The posterior probability values on the Bayesian tree are higher, as expected (**Figure 7**). *Steatornis* is consistently placed basally within the clade, although its exact placement is unresolved in the different analyses. The remaining taxa form two clades. One includes the nightjars (Caprimulgidae) and the potoos (Nyctibiidae) as sister taxa. The other includes the frogmouths (Podargidae) as the sister taxon to a highly supported Apodioidea (Aegothelidae and Apodi) clade. The relationships within the Apodi are strongly supported in all analyses, with the hummingbirds (Trochilidae) being the sister-group to a clade containing the swifts (Apodidae) and tree-swifts (Hemiprocnidae).

The fourteen nuclear loci were also analyzed separately and as with the concatenated data, with and without the removal of autapomorphic insertion events. The individual gene trees can be found in **Appendix V**. Individually the nuclear loci performed very poorly, with overall lack of resolution the most common pattern. Among

the outgroup taxa, Galloanserae are consistently sister to Neoaves. Within Neoaves is predominantly a non-resolved basal polytomy. Despite thorough sampling the caprimulgiform taxa are also poorly resolved for the most part, consistent with their early, near-simultaneous origins. The monophyly of the Caprimulgiformes, which is highly supported in the concatenated tree, is only recovered in three of the fourteen individual gene trees (*CLTC, CRYAA* and *MUSK*) and never with strong bootstrap support. Two additional gene-trees show a nearly monophyletic Caprimulgiformes: in one *Steatornis* is the only taxon excluded (*GH1*), and in the other *Coccyzus* is embedded within the caprimulgiform taxa (*RHO*). In the remaining gene trees the major lineages within the Caprimulgiformes are scattered within Neoaves without any particular pattern, and most of the nodes near the neoavian base are without any support.

The only consistent topological pattern is the monophyly of the Apodoidea, which is present in most of the gene trees with strong bootstrap support. Other topological patterns among the caprimulgiform lineages are present in some of the gene trees, rarely with bootstrap support (see **Appendix V)**.

The concatenated tree suggests a sister group relationship between the Apodioidea and the frogmouths (Podargidae) albeit with low support. This relationship is found in only two gene trees (*EEF2* and *FGB*), and in a third (*RHO*) with the outgroup taxon *Coccyzus* in the mix. The monophyly of the potoos (Nyctibiidae) and nightjars (Caprimulgidae), a pattern strongly supported by morphological characters, appears in three gene trees (*FGB, MUSK* and *RHO*) resulting in a moderately supported sister-group relationship in the concatenated tree (more strongly supported on the Bayesian tree than the likelihood tree). The basal position of *Steatornis* is only seen in one gene tree (*GH1*).

This explains why its position within Caprimulgiformes is not fully resolved on the concatenated tree.

Scoring the presence/absence of insertion/deletion events in the molecular data larger than 3bp in length resulted in a matrix of 59 characters. The matrix was analyzed in a parsimony analysis both separately (see **Figure 8**) and when added to the combined molecular and morphological dataset (resulting in a 22405 character dataset - see **Figure 9**). The analysis of the indel matrix on its own did not produce a monophyletic Caprimulgiformes, but the group was placed in a clade with the neoavian taxa *Eurypyga*, *Coccyzus*, *Treron* and *Phoenicopterus*, a pattern also seen in the likelihood results of the molecular data and (with the exception of *Coccyzus*) in the results of Hackett *et al* (2008). This clade is supported by a single deletion event in *EGR1*. This suggests that the insertion/deletion events are phylogenetically informative at this taxonomical level when they are scored as independent characters. The indel events that support particular monophyletic clades on the combined tree are summarized in **Appendix IV.** The majority of these events were within the Apodi, in which all major nodes have at least one indel event supporting them. The Apodoidea are also supported by a number of indel events. Indel events also support the monophyly of the caprimulgiform families Caprimulgidae, Nyctibiidae and Podargidae, and one deletion event in *GH1* supports the clade that contains Caprimulgidae and Nyctibiidae.

3.3 COMBINED DATASET

The full molecular, morphological, and the indel datasets were combined, leading to a 22, 405 character dataset. A parsimony search in Paup*4.0d98 (X86) resulted in a single most parsimonious tree in which 8209 of the 22, 346 characters were parsimony informative. Adding the morphological characters led to a slightly higher consistency index compared to results from the molecular dataset only (from 0.54 to 0.575), and the homoplasy index was slightly lower (from 0.46 to 0.42). The most parsimonious tree from the analysis of the combined dataset is shown in **Figure 9** with bootstrap values represented on the nodes.

In the Bayesian analysis in MrBayes, 10 million generations were sufficient for the two independent runs to converge and reach stationarity with all ESS values having high scores (>200). After a 12% burn-in, 8750 trees remained. The maximum credibility tree was calculated in TreeAnnotator and is displayed in **Figure 10**.

On both the parsimony and Bayesian tree, the Caprimulgiformes are monophyletic with robust support. The relationships within the group are better resolved than in the analyses of the individual datasets and are mostly congruent in the two analyses. *Caprimulgidae* and *Nyctibiidae* form a distinct, well-supported clade on both the parsimony and Bayesian trees. This is congruent with the results from the morphological data as well as the moderately supported results of the molecular data. The strong signal from the morphological characters amplifies the weaker molecular signal resulting in a strongly supported clade in the combined analyses. The Apodoidea are also strongly supported, as are all the relationships within it.

There is incongruence between the parsimony and Bayesian analyses regarding the position of both the podargids and *Steatornis*. On the parsimony tree the two families are sister-taxa in a reasonably strongly supported clade that forms a basal polytomy within the whole group along with Apodioidea and the caprimulgid/nyctibiid clade. On the Bayesian tree however, the podargids are the sister-group to Apodoidea, which is supported by a high posterior probability scores. *Steatornis* is placed as the most basal member of the Caprimulgiformes, albeit that position is not well supported. Collapsing this node results in a basal polytomy consisting of *Steatornis*, the caprimulgid/nyctibiid clade, and the apodoid/podargid clade.

Topological patterns among the remaining neoavian taxa are much more strongly supported on the Bayesian tree than the parsimony tree. The sister-group to the Caprimulgiformes is a clade containing *Phoenicopterus, Treron* and *Coccyzus*. These two clades are the well-supported sister-group to the sunbittern, *Eurypyga*. The remaining Neoaves are all grouped together in another highly supported clade. As there are numerous important neoavian groups missing in this study, the neoavian relationships will not be described in further detail.

4. DISCUSSION

4.1 SYSTEMATIC RELATIONSHIPS OF THE CAPRIMULGIFORMES

The results from the combined molecular and morphological dataset presented here provide a more concise picture of the relationships among caprimulgiform families than has been attained in previous analyses. The monophyly of the 'traditional' Caprimulgiformes is clearly unfounded as has been previously suggested on multiple occasions (Mayr *et al.*, 2003; Barrowclough *et al.,* 2006; Hackett *et al.*, 2008; Mayr, 2010; Han *et al.*, 2010; Nesbitt *et al.*, 2011) with the Apodi (the three families traditionally placed in the separate order Apodiformes) embedded in a clade containing the other five caprimulgiform families.

This revised Caprimulgiformes (including Apodi) is strongly supported as monophyletic by the concatenated 14-loci molecular data set alone and when combined with morphological characters. Only three of the fourteen molecular markers used in this study support this clade individually, and not strongly so. The other markers do not provide strong alternatives however, and yield mostly non-resolved polytomies at the Neoavian base. It is common that individual nuclear markers fail to provide resolution for the Neoaves (Fain & Houde, 2004; Ericson *et al.*, 2006; Poe & Chubb, 2007; Hackett *et al.*, 2008). Larger multi-locus datasets, in particular those that incorporate introns (Chojwnoski *et al.*, 2008) generally are more successful in providing higher resolution, although the results are not always congruent between studies (Hackett *et al.*, 2008; Pratt *et al.*, 2009; Pacheco *et al.*, 2011).

In this study, the taxon and character sampling of morphological data was not sufficient to test the monophyly of this clade. The anatomical diversity of neoavian birds that evolved extremely rapidly has led to considerable homoplasy (such as the presence/absence of a basipterygoid process, postorbital process, enlarged ethmoid, etc.) and this has complicated the use of morphological data by itself for higher-level avian systematics (Mayr, 2010). An additional difficulty for establishing the monophyly of the Caprimulgiformes from morphological data is that the sistergroup to the order is not known. The only study that has successfully obtained a monophyletic Caprimulgiformes using exclusively morphological data is that of Livezey and Zusi (2006, 2007). But, they also suggest reciprocal monophyly of the traditionally defined Apodiformes and Caprimulgiformes, and the two orders were placed (with low support) as a sister-group to a large group of land-birds including trogons, mousebirds, piciforms, coraciiforms and passeriforms. Neither of those topological patterns is corroborated by studies using molecular data, including this study.

The morphological data in this study independently provide strong support for some caprimulgiform relationships (**Figure 2**) and are highly congruent with most previous morphological studies (Mayr, 2010; Nesbitt *et al.*, 2011). Additionally, there is a greater agreement between the molecular and morphological data than seen in previous studies, and when the two datasets are combined a nearly completely resolved Caprimulgiformes is obtained (**Figures 9-10**).

The only unresolved relationship within the Caprimulgiformes in the combined analysis is at the very base resulting in a three-way polytomy. A possible cause for this polytomy is the problematic taxon *Steatornis,* which has been called “one of the most

challenging of avian genera with respect to phylogenetic position, irrespective of method" (Livezey & Zusi, 2006). Most studies place *Steatornis* at the base of the Caprimulgiformes, generally unresolved (Ericson *et al.*, 2006; Hackett *et al.*, 2008) or with very low support (Livezey & Zusi, 2006; Mayr, 2010). The lack of shared morphological characters with the other caprimulgiform lineages and a high number of autapomorphies limit the usefulness of morphological data for resolving its position. Molecular characters are even less successful, with the few individual gene trees that provide any resolution for its placement in this study being highly incongruent with one another. This results in a completely unresolved placement of *Steatornis* within Caprimulgiformes in all datasets in this study.

The second lineage in the basal caprimulgiform polytomy leads to the clade containing Caprimulgidae and Nyctibiidae. This clade has consistently been supported by previous morphological studies (Livezey & Zusi, 2007; Mayr, 2010; Nesbitt *et al.*, 2011), but not molecular ones in which the position of Nyctibiidae is generally unresolved (Johansson *et al.*, 2001; Ericson *et al.*, 2006; Hackett *et al.*, 2008; Braun & Huddleston, 2009). In this study, the sister-relationship between these two families is the prevalent topological pattern in the trees from both sources of data (**Figures 2, 5-7**), admittedly with low to moderate support from the molecular data. The incongruence between the different gene trees and the general lack of resolution regarding the placement of the Nyctibiidae (see **Appendix V**) is mostly solved by concatenation. The strong support for this relationship from the morphological data provides important reinforcement when all the data are combined (**Figures 10-11**), resulting in a well supported clade on the tree.

The third main group within the Caprimulgiformes contains the Apodoidea as the sistergroup to the Podargidae. This relationship is not supported by the morphological data on its own with the position of Podargidae completely unresolved (**Figure 2**), but the molecular data support it and this placement is maintained with high support in the Bayesian analysis of the combined data (**Figure 11**). This relationship was also seen in the study of Mayr *et al.* (2003) although it is only present in their Bayesian analysis of the molecular data, which consisted of three nuclear genes, but not in their combined dataset. Other studies have placed Podargidae as a sister-group to Caprimulgidae (Barrowclough *et al.*, 2006), in a clade containing both Caprimulgidae and Apodioidea (Hackett *et al.*, 2008) or have been unable to resolve its position (Ericson et *al.*, 2006; Braun & Huddleston, 2009). The parsimony analysis of the combined dataset in this study is in disagreement with the Bayesian analysis and places the podargids as the sister group to *Steatornis.* This is a similar result to Nesbitt *et al.* (2011) who also combined morphological and molecular characters in one dataset, albeit only two molecular markers were used in their study and they did not run a Bayesian analysis on their data. Because the Bayesian analysis incorporates models of substitution for the multiple molecular markers and performs better than the parsimony analysis in resolving relationships on the whole tree, its results should perhaps be interpreted as the more robust of the two.

The relationships within the Apodoidea, including Aegothelidae being the sistergroup to the Apodi, and the relationships within the Apodi (with Trochilidae the sister to a clade containing Apodidae and Hemiprocnidae) are consistent among all datasets and are highly congruent with results from multiple previous studies using

various data sources (Mayr *et al.*, 2003; Barrowclough *et al*., 2006; Ericson *et al.*, 2006; Hackett *et al.*, 2008; Braun & Huddleston, 2009; Mayr, 2010; Nesbitt *et al.*, 2011).

The taxonomic placement of the fossil taxa on the morphological tree is similar to previous studies with some exceptions. The only published phylogeny that includes the majority of the fossil taxa included in this study is the one by Mayr, which summarizes phylogenies from a number of previous studies and incorporates over 50 morphological characters (Mayr, 2009). The only topological patterns that are identical in Mayr's tree and the tree in **Figure 4** are the placement of *Eurotrochilus* and *Jungornis* as stem-trochilids with *Eurotrochilus* as the sister-taxon to the extant trochilids. *Argornis* and *Parargornis* are placed as stem-apodiform taxa on the tree in this study, forming a basal polytomy within Apodoidea along with *Aegotheles,* but in Mayr's study (2003, 2009) they are placed as stem-trochilids. *Eocypselus* is the sister-taxon to *Aegotheles* in this study but without support. Mayr (2003, 2009) places it as a basal apodoid, intermediate between *Aegotheles* and the Apodi. This study neither supports nor refutes that hypothesis.

Aegialornis is also positioned as a stem-apodiform on Mayr's tree (2009), but its position is unresolved in this study, as is the position of *Protocypselomorphus* (which also is unresolved on Mayr's tree). The fossil taxon *Fluvioviridavis* was recently re-evaluated and placed as a stem-podargid, though not as close to the crown taxa as *Masillapodargus* (Nesbitt *et al.*, 2011). This podargid-clade (called Podargiformes in the study), with two extant genera and two extinct, is the sister-clade to Steatornithidae in their study using a combined dataset. The results in this study fail to resolve the position

of the two podargid-fossils, and in fact *Fluvioviridavis* and *Masillapodargus* are placed (without support) as sister-taxa to *Steatornis* but not the podargids.

Further study of all these and other fossils not included here [such as the steatornithid *Prefica* Olson, 1987, and the enigmatic archaeotrogons (Mourer-Chauviré, 1980; Mayr, 2009)] as well as improved character sampling and scoring should lead to a better understanding of their placement on the caprimulgiform tree. The results presented here are not sufficiently robust to support definitively alternate hypotheses regarding the systematic status of the fossils sampled.

4.2 TAXONOMY OF THE CAPRIMULGIFORMES

The results from this study have implications for the higher-level taxonomy of the orders and families involved, which has been in a state of uncertainty since the publication of Sibley and Ahlquist's landmark study (1990) that challenged the traditional ordinal classification of birds. It is clear from the results presented in this study, as well as from multiple other studies (i.e. Ericson *et al.*, 2006; Hackett *et al.*, 2008; Braun & Huddleston, 2009; Mayr, 2010; Nesbitt *et al.*, 2011), that the previously recognized Caprimulgiformes is not monophyletic and therefore cannot be accepted as a taxonomic unit without some changes.

The Apodiformes, as the group was previously defined, remains monophyletic, and thus it can be argued that the order can keep its status. Relationships within the 'apodiform' families (Apodidae, Hemiprocnidae and Trochilidae) are well established as well. It has been proposed (Sangster, 2005; Barrowclough *et al.*, 2006: Braun & Huddleston, 2009) that the owlet-nightjars (Aegothelidae) should be included within the

Apodiformes, as they are consistently found to be their sister-group. Retaining the ordinal status of Apodiformes implies the paraphyly of traditional Caprimulgiformes, however. Therefore, the simplest solution may be to combine the two and form one large order that includes all the families in question. Mayr names this taxonomic assemblage Strisores in his review of avian systematics (Mayr, 2011), a name also used by Nesbitt *et al.* (2011), who also suggested that the traditional Apodiformes retain their ordinal name, and that the podargids and their related fossil taxa be placed in a new order, Podargiformes. They did not place the other caprimulgiform families in a particular order but at least three additional orders would be required for that. A simpler solution might be to use the term Caprimulgiformes (given by Ridgway in 1881) for all eight families and this is what I suggest. The old "Apodiformes" could be named Apodi (Peters, 1940), a name previously used only for Apodidae and Hemiprocnidae, whereas the clade containing both Apodi and Aegothelidae could be elevated to the superfamily Apodoidea. Other names that have been suggested for that clade are Daedalornithes (Sangster, 2005) and Apodimorphae (Sibley *et a*l., 1988; Mayr, 2010).

Mayr (2010) used the name Caprimulgi for the clade containing Caprimulgidae and Nyctibiidae. In his study as well as in Nesbitt *et al.* (2011), these two families formed a sister clade to the Apodoidea. The name Cypselomorphae was used for this clade (Mayr, 2010; Nesbitt *et al.*, 2011). This study does not support the Cypselomorphae, as the molecular and combined data support a sister-group relationship of Apodoidea and Podargidae. The name Cypselomorphae was coined by Huxley in 1867 for swifts and their relatives, and thus should not be used for a group that does not contain the Apodi. The podargids could replace the Caprimulgi in Cypselomorphae, but this would create

confusion. All of the caprimulgiform families can retain their original names (Aegothelidae, Apodidae, Caprimulgidae, Hemiprocnidae, Nyctibiidae, Podargidae, Steatornithidae and Trochilidae), and by pooling them all in a single order, Caprimulgiformes, there is no need to name every single subclade within the order.

Thus the following classification is suggested for the group based on the results of this study:

1. Order **Caprimulgiformes** Ridgway, 1881

1.2 Family **Steatornithidae** Bonaparte, 1842

1.3 Family **Caprimulgidae** Vigors, 1825

1.4 Family **Nyctibiidae** Chenu and des Murs, 1851

1.5 Family **Podargidae** Bonaparte, 1838

1. 6 Superfamily **Apodoidea**, new taxon

1. 6.1 Family **Aegothelidae** Bonaparte, 1853

1.6.2 Family **Apodidae** Olphe-Galliard, 1887

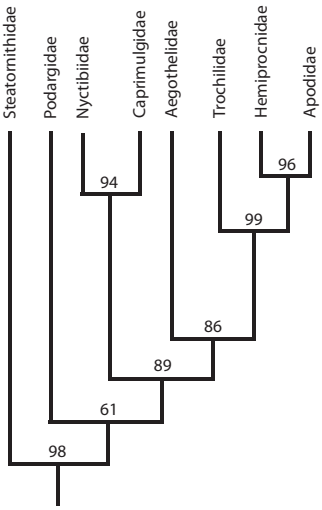
1.6.3 Family **Hemiprocnidae** Oberholser, 1906

1.6.4 Family **Trochilidae** Vigors, 1825.

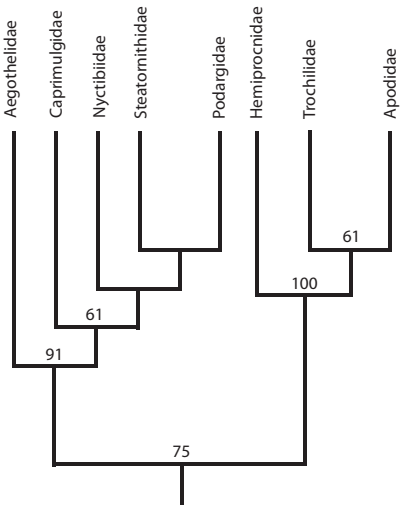
5. CONCLUSIONS

Resolving the relationships among the basal lineages of the Neoaves radiation remains one of the more confounding problems in avian systematics. The early evolution of the Caprimulgiformes, which are placed among the basal neoavian orders (i.e. Hackett *et al*, 2008), occurred as part of this radiation. This has made the systematics of this group so difficult, in particular at the family level. In this study a resolved phylogeny from a combined molecular and morphological data set is presented. It corroborates the recent expansion of the order that now includes the Apodi, a highly diverse assemblage of birds. Perhaps most importantly, there is evidence for congruence between the molecular and morphological data regarding contentious relationships such as the sister-relationship of the potoos (Nyctibiidae) and the nightjars (Caprimulgidae) that has not been seen before. Combining molecular and morphological data provides the best resolved tree, and our data suggest that morphological characters can enhance the signal from the sequence data. The high degree of incongruence among the individual gene trees cannot be ignored, however, and this emphasized the importance of having a varied molecular data set when addressing these higher-level systematic problems. More data sampling, both molecular and morphological, is encouraged for the group, including finding more robust morphological characters for the diverse fossil fauna. Additionally, even though the monophyly of Caprimulgiformes is well supported in our molecular data set, its placement on the neoavian tree remains unresolved and its closest sister-group is not known with certainty.

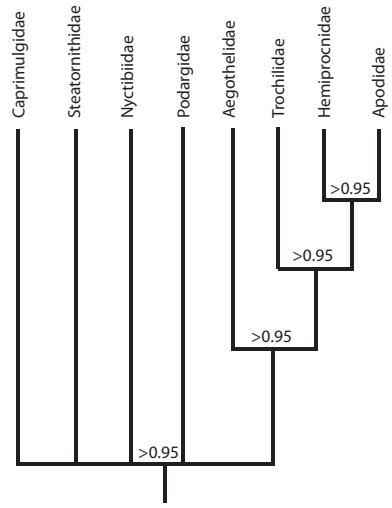
6. FIGURES



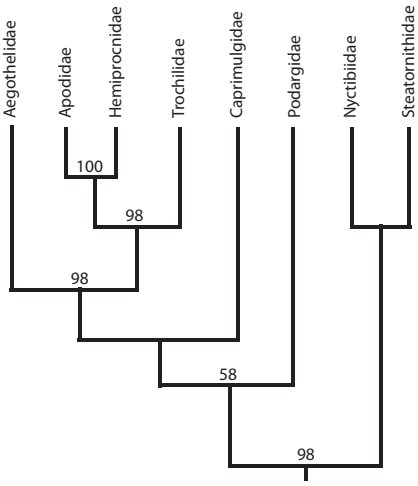
Most parsimonious tree resulting from analysis of 69 morphological characters (Mayr, 2010)



Subclade of a most parsimonious tree resulting from a analysis of 2954 morphological characters for all birds and other archosaurs (Livezey & Zusi, 2007)



Results from a Bayesian analysis of five nuclear genes (5007bp). Nodes with <0.95% posterior probability have been collapsed (Ericson et al., 2006)



Results from a ML analysis of a 19-locus data set (Hackett et al., 2008)

FIGURE 1 - Caprimulgiform relationships as depicted in previous studies.

FIGURE 1

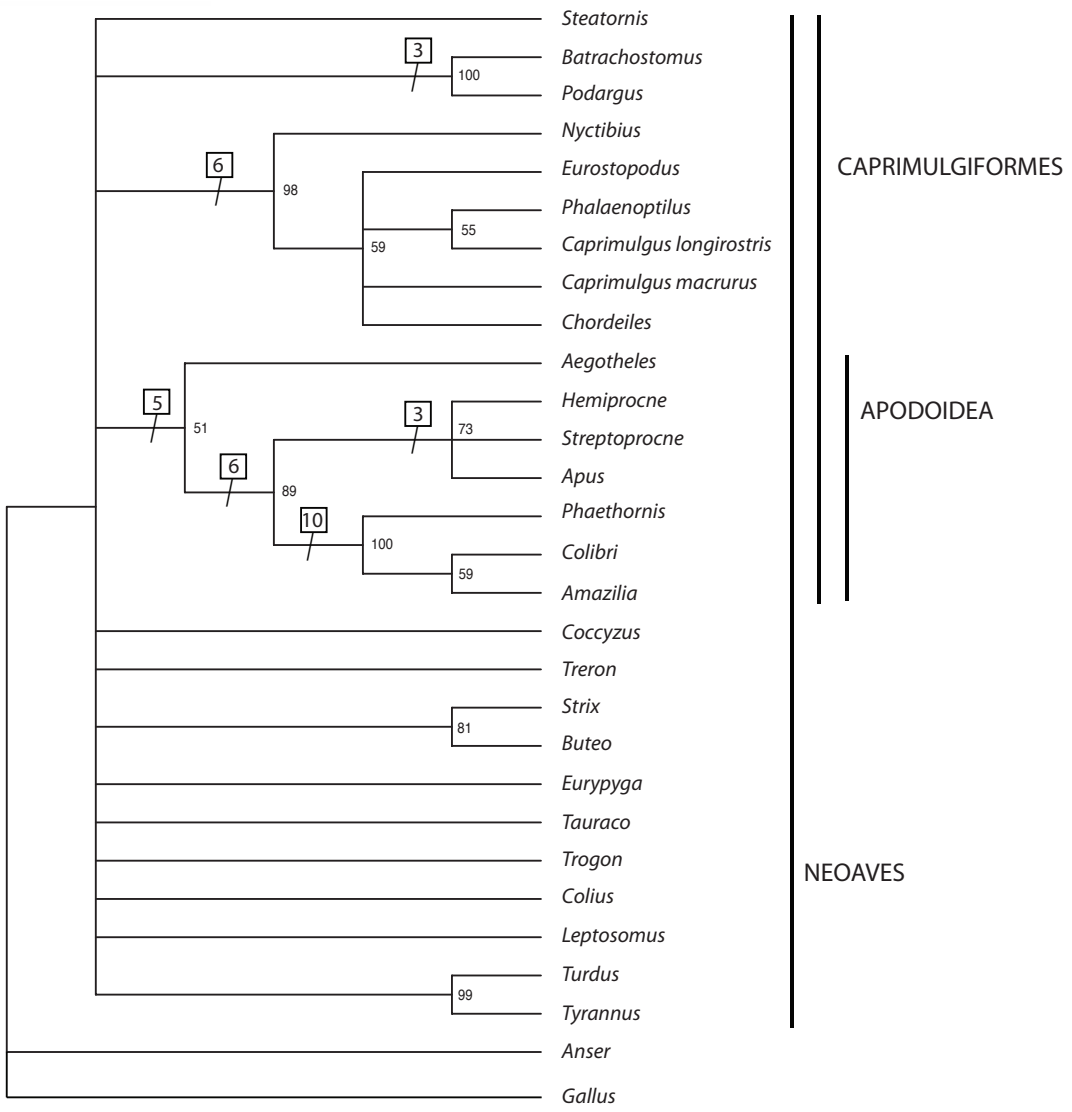


FIGURE 2: A parsimony strict consensus tree of the Caprimulgiformes plus thirteen outgroups based on a 134 character morphological dataset. Bootstrap values higher than 50 are displayed. Numbers in squares indicate the number of synapomorphies that support particular clades within the Caprimulgiformes.

FIGURE 2

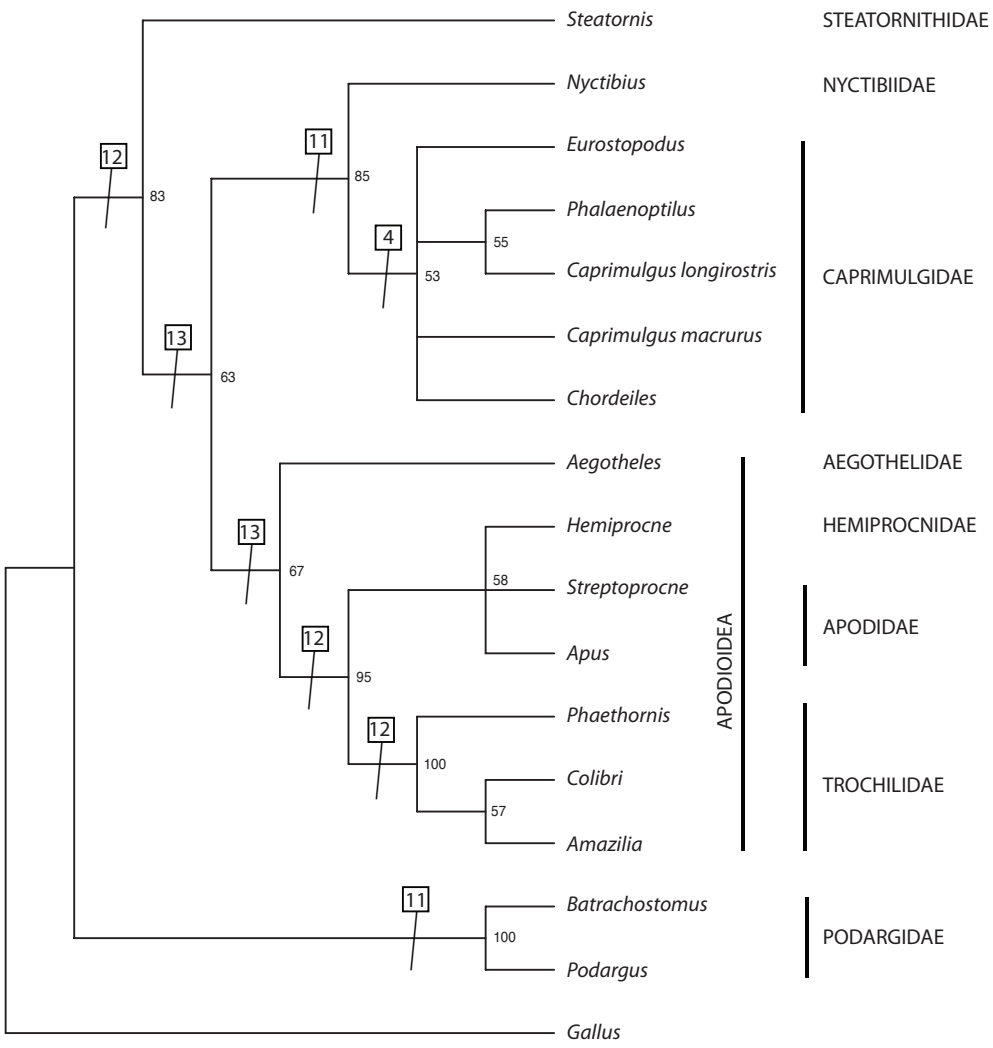


FIGURE 3: A parsimony strict consensus tree of the Caprimulgiformes with only a single outgroup taxon included, based on a 134 character morphological dataset. Bootstrap values higher than 50 are displayed.
Numbers in squares indicate the number of synapomorphies that support particular clades.

FIGURE 3

FIGURE 4: A parsimony strict consensus tree of the Caprimulgiformes, including ten fossil taxa and thirteen outgroup taxa based on a 134 character morphological dataset.The names of the fossil taxa are colored purple. Bootstrap values higher than 50 are displayed and numbers in squares indicate the number of synapomorphies that support particular clades. The Caprimulgiformes are not monophyletic on this tree.

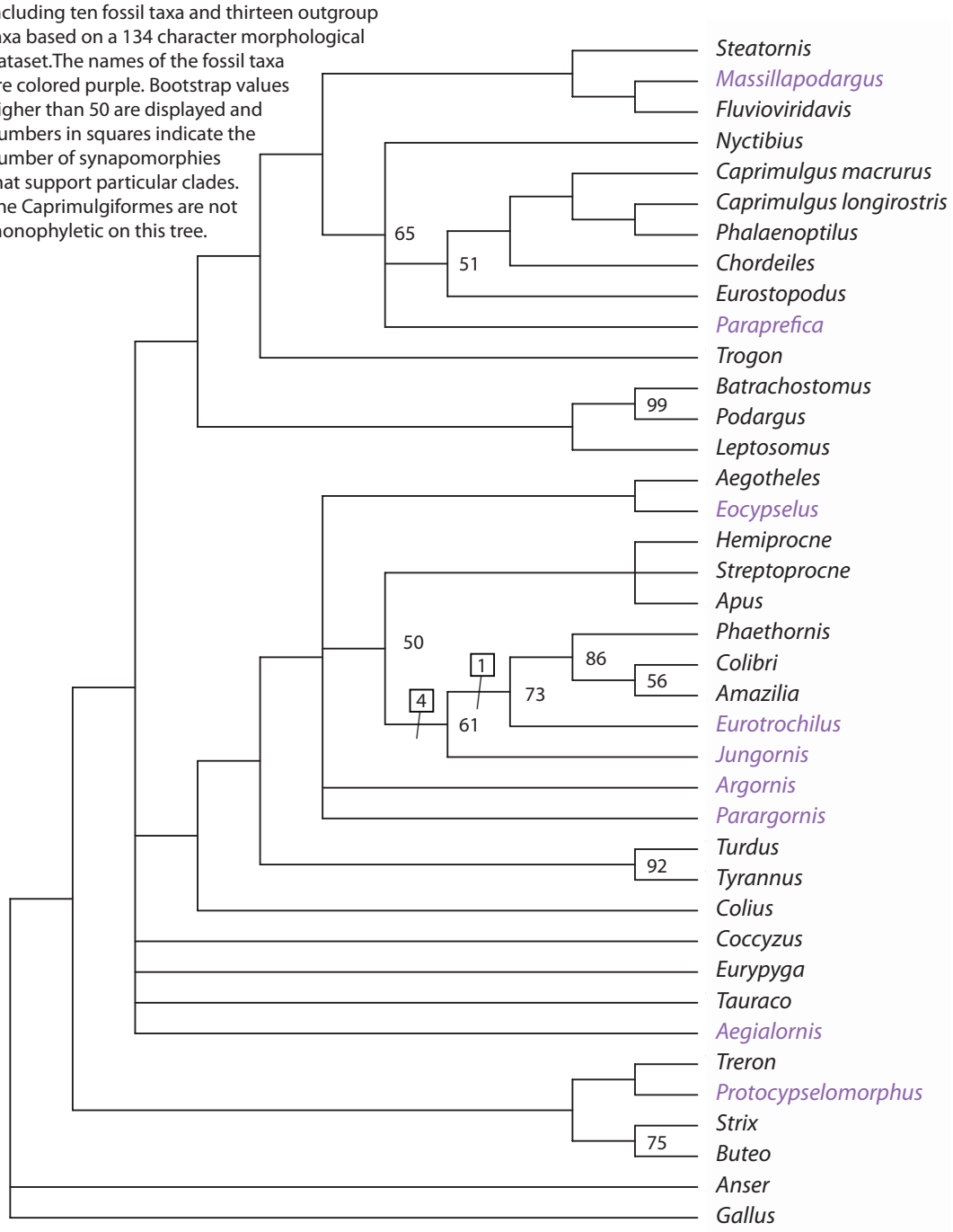


FIGURE 4

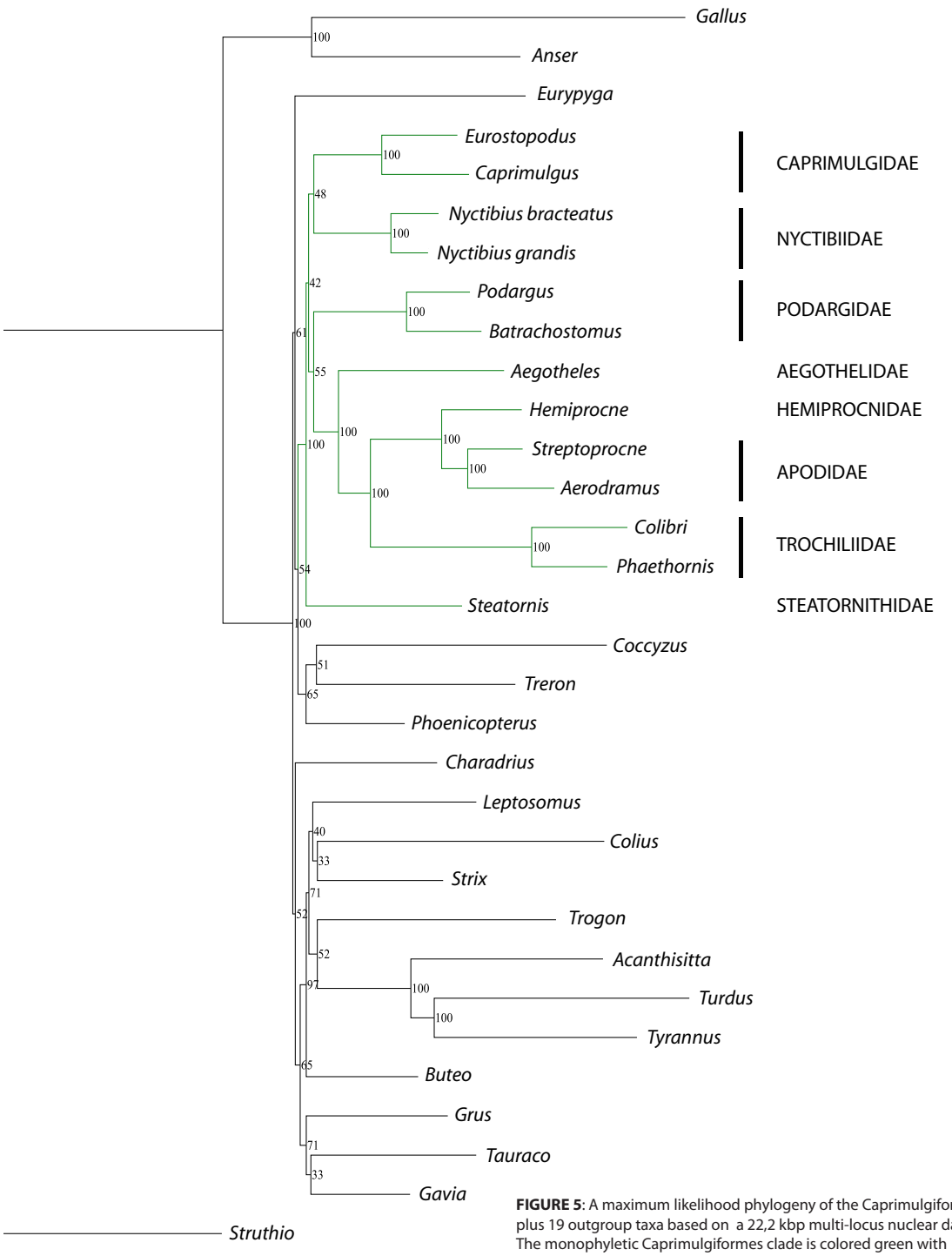


FIGURE 5: A maximum likelihood phylogeny of the Caprimulgiformes plus 19 outgroup taxa based on a 22,2 kbp multi-locus nuclear dataset. The monophyletic Caprimulgiformes clade is colored green with family names displayed.
Bootstrap values are displayed on the nodes.

FIGURE 5

FIGURE 6: A parsimony strict consensus tree of the Caprimulgiformes plus 19 outgroup taxa based on a 22,2 kbp multi-locus nuclear dataset. The monophyletic Caprimulgiformes clade is colored green. Bootstrap values are displayed on the nodes.

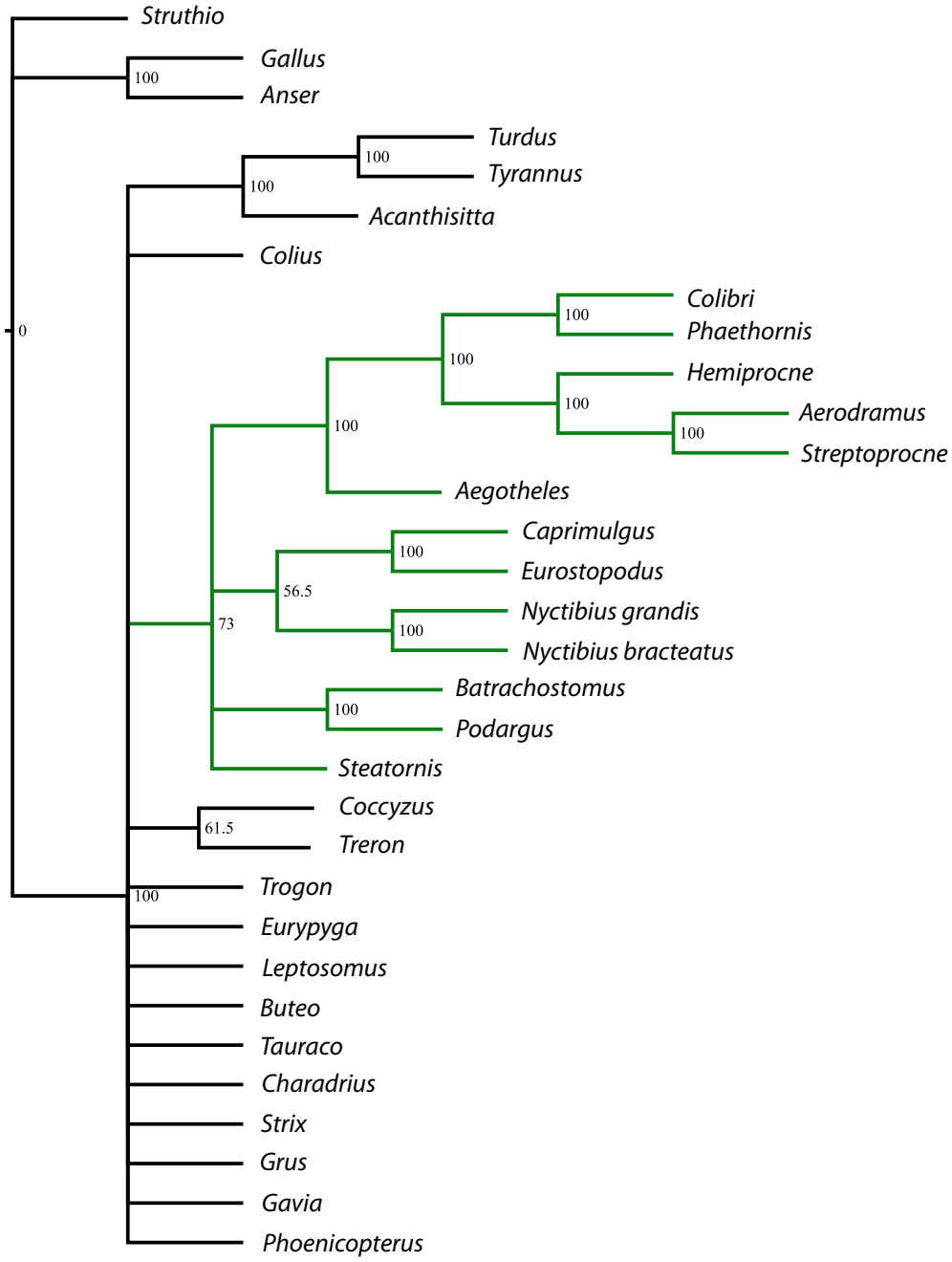


FIGURE 6

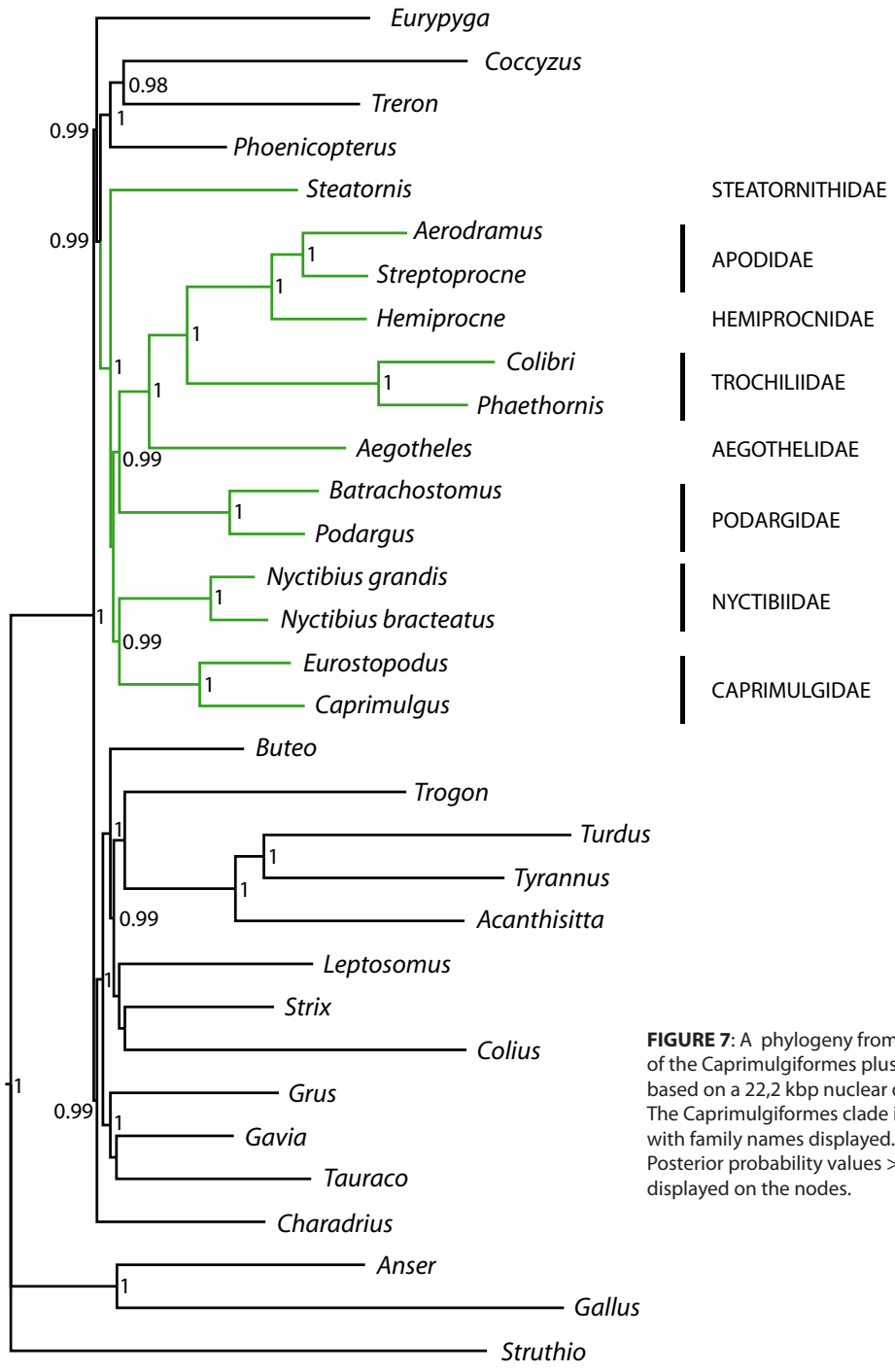


FIGURE 7: A phylogeny from a Bayesian analysis of the Caprimulgiformes plus 19 outgroup taxa based on a 22,2 kbp nuclear dataset. The Caprimulgiformes clade is colored green with family names displayed. Posterior probability values >0.95 are displayed on the nodes.

FIGURE 7

FIGURE 8: A maximum parsimony tree of the Caprimulgiformes and 19 outgroup taxa based on a 59 character indel presence/absence dataset. The caprimulgiforms are not monophyletic on this tree. Bootstrap values higher than 60 are displayed on the nodes. Number of insertion/deletion events that support particular clades are depicted as ticks on the branches with each tick representing a single insertion/deletion event.

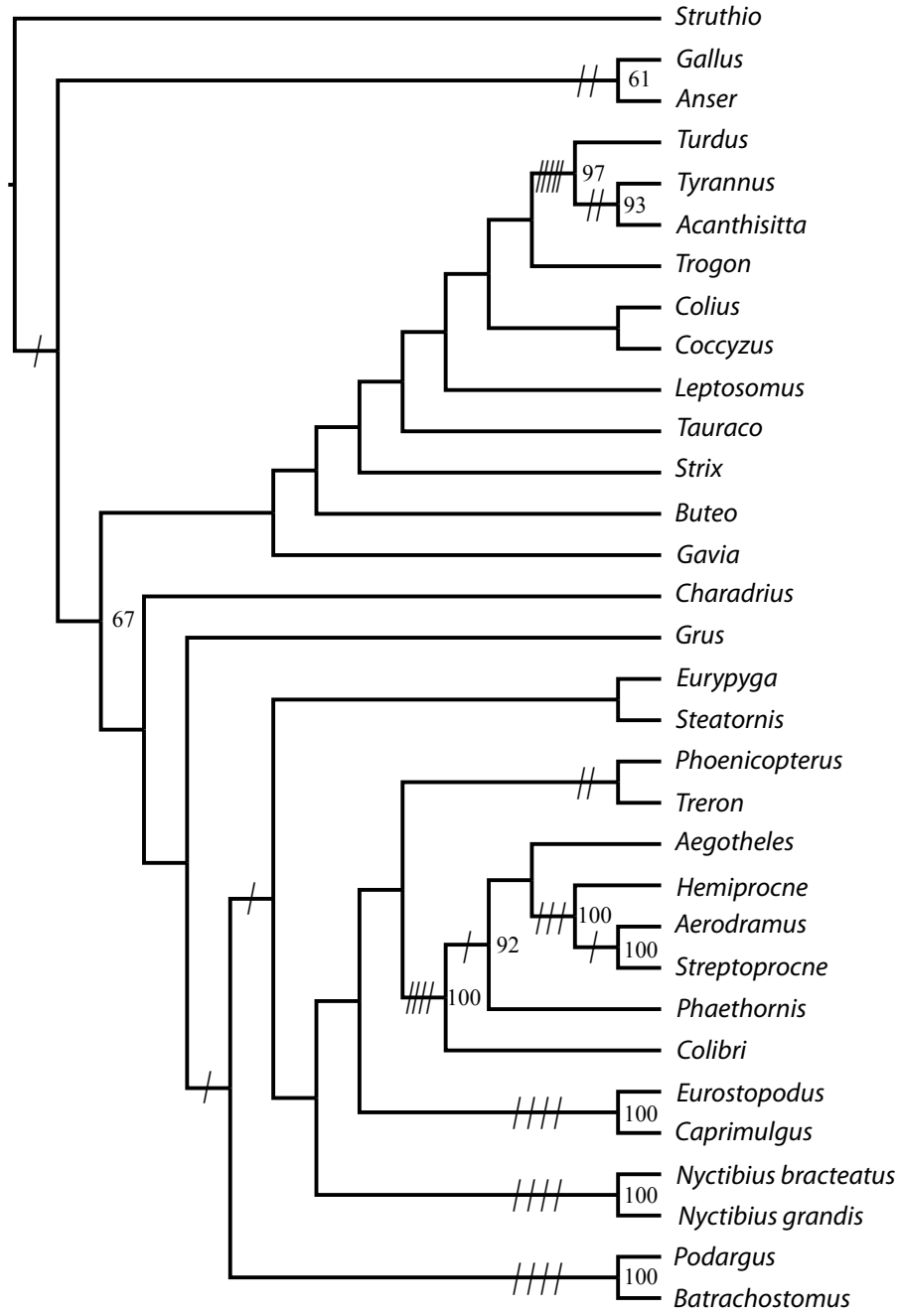


FIGURE 8

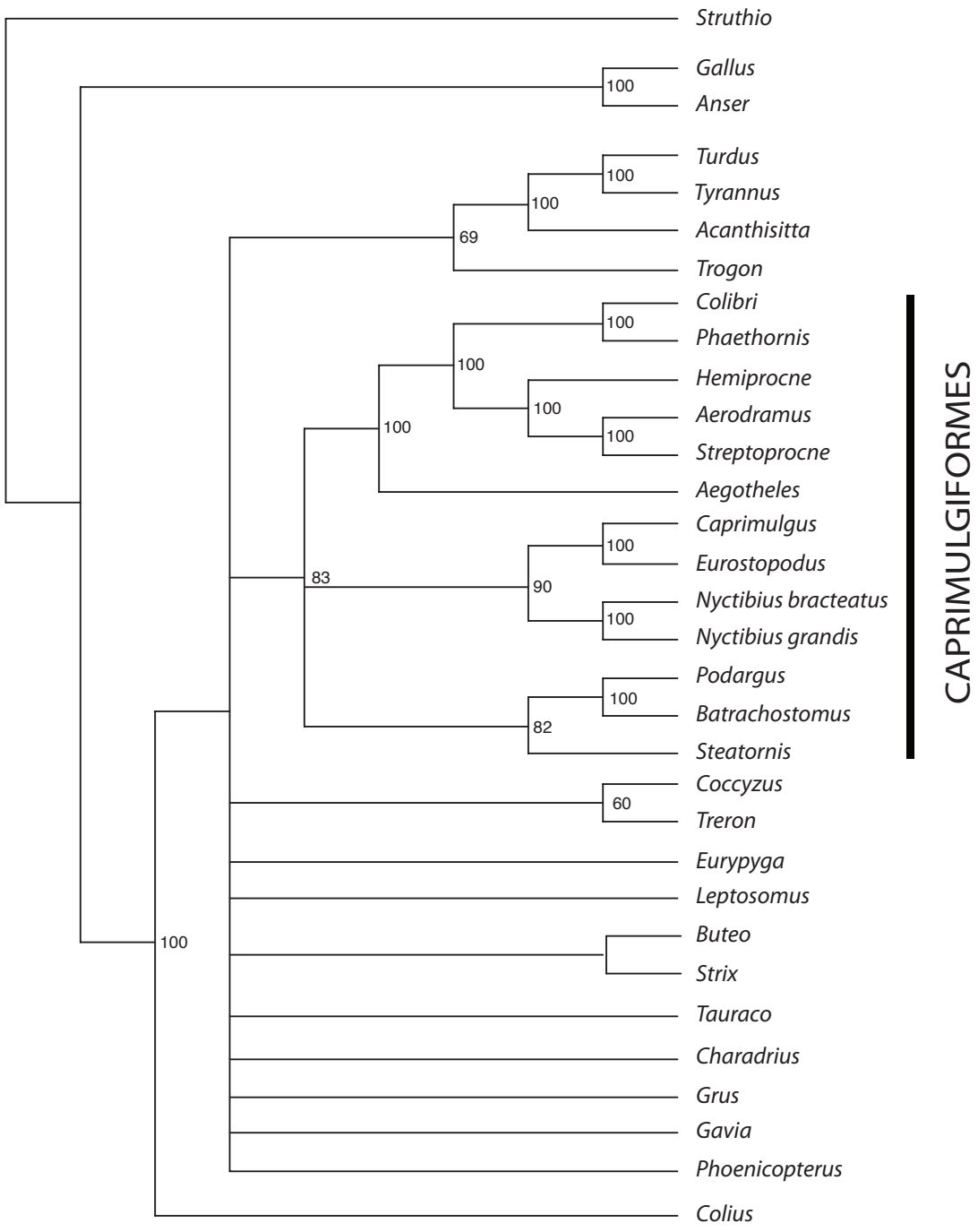


FIGURE 9: A parsimony strict consensus tree of the Caprimulgiformes plus 19 outgroup taxa based on a 22,405 character combined dataset (molecular, morphological and indel data). Bootstrap values higher than 60 are displayed on the nodes.

FIGURE 9

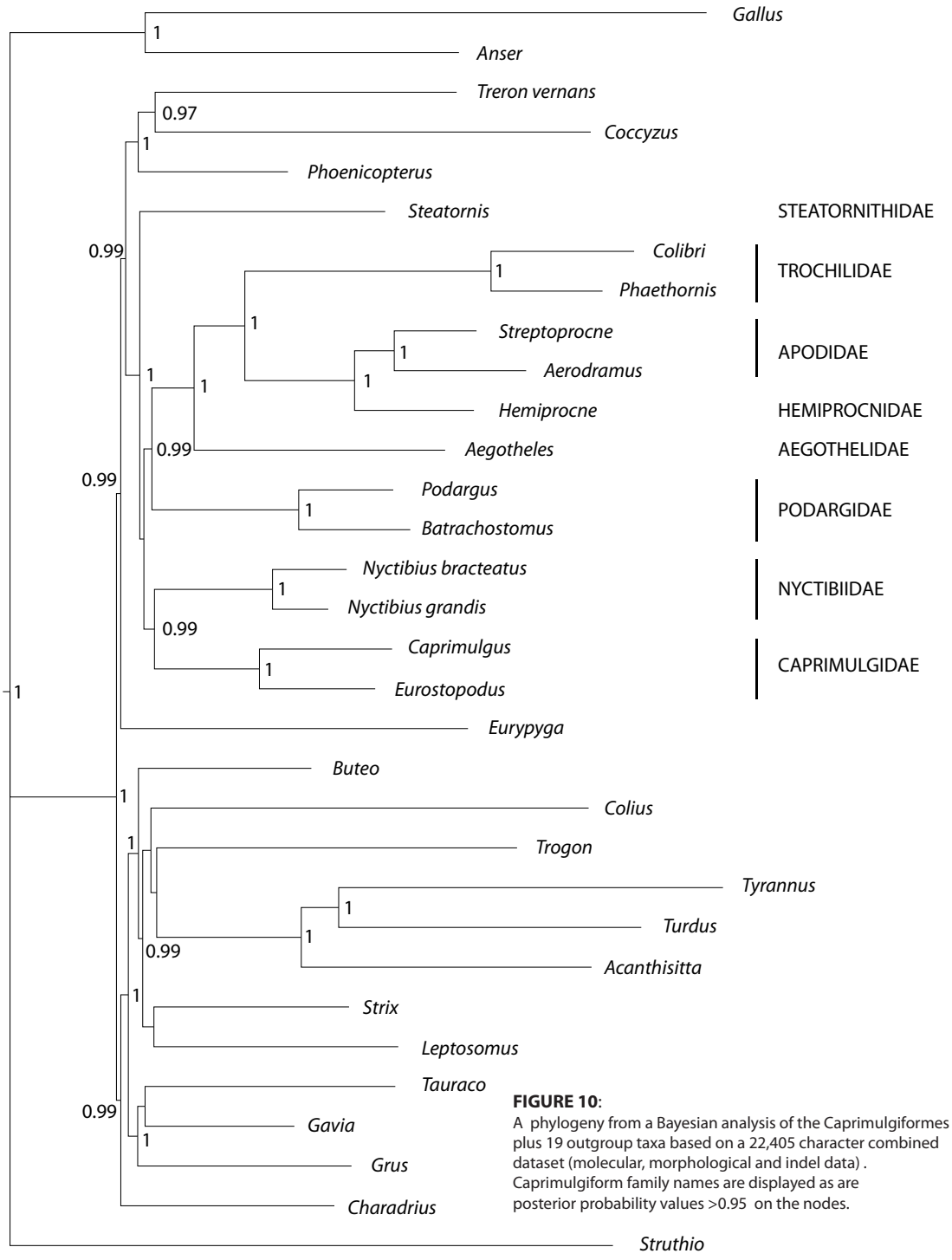


FIGURE 10:
A phylogeny from a Bayesian analysis of the Caprimulgiformes plus 19 outgroup taxa based on a 22,405 character combined dataset (molecular, morphological and indel data) . Caprimulgiform family names are displayed as are posterior probability values >0.95 on the nodes.

FIGURE 10

7. TABLES

TABLE 1

Insertion and deletion events that support major clades (not a finite list – see Figure 8 for prevalence of indel events in non-caprimulgiform taxa).

CLADE	GENE	INDEL EVENTS
Nyctibiidae	ALDOB	10 bp insertion event; 3 bp insertion event
	GH1	10 bp insertion event
	MUSK	48bp deletion event
	PCBD1	8bp deletion event
Caprimulgidae + Nyctibiidae	GH1	12-14bp deletion event
Caprimulgidae	ALDOB	5bp insertion event
	MYC	3bp insertion event
	PCBD1	6bp insertion event
	TGFB2	7bp insertion event
Podargidae	MYC	3-4bp insertion event
	PCBD1	8bp insertion event
	RAG2	3bp insertion event
	TGFB2	3-8bp insertion event
Apodidae + Hemiprocnidae	EEF2	286bp insertion event
	GH1	11bp deletion event; 6bp insertion event
	PCBD1	8-11bp deletion event; 160bp deletion event
	TGFB2	9bp deletion event
Trochilidae	EEF2	11bp insertion event
Apodiformes + Aegothelidae	EEF2	552 bp deletion event
	FGB	6-23bp insertion event; 4-9bp insertion event
	MYC	12bp insertion event
	RAG1	15bp deletion event
Apodidae	EGR1	101bp deletion event
Caprimulgiformes, Apodiformes, Columbiformes, *Eurypyga*, *Phoenicopterus*	EGR1	4bp deletion event

TABLE 2: Taxonomic patterns and presence/absence of monophyletic clades in individual gene trees

	ALDOB	CLTC	CRYAA	EEF2	EGR1	FGB	GH1	MUSK	MYC	PCBD1	RAG1	RAG2	RHO	TGFB2
CAP		X	(X)					(X)						
AA	X	X	X	X		X	X	X	X	X	X	(X)	X	(X)
A/C														
A/N														
A/P														
A/S														
AA/C			(X)				(X)							
AA/N														
AA/P						(X)								
AA/S								X						
C/N						(X)		X					(X)	
C/P											(X)			
C/N/P														
C/S														(X)
N/P			(X)											(X)
N/S										(X)				
N/P/S														
P/S														
AA basal														
C basal		X												
N basal														
P basal														
S basal							(X)							

CAP: Caprimulgiformes, AA: Apodiformes/Aegothelidae, A: Apodiformes, C: Caprimulgidae, N: Nyctibiidae, P: Podargidae, S: Steatornithidae. X: Presence of clade/pattern. (X): Presence of clade/pattern without support.

TABLE 2

8. APPENDICES

APPENDIX I

SPECIMEN LIST

List of skeletal specimens used in generation of morphological data – all specimens from AMNH collections unless otherwise noted.

List set-up
Order or family name

- Species name
    - Specimen number
    - Sex
    - Location where specimen collected

Caprimulgiform taxa

Aegothelidae

- *Aegotheles cristatus*
    - SMITHSONIAN – No. 620228
    - Female
    - Australia - Queensland

Apodidae

- *Streptoprocne zonaris mexicana*
    - No. 7889
    - Male
    - Chiapas, Mexico

Caprimulgidae

- *Caprimulgus longirostris*
    - No. 25962
    - Male
    - Depto. La Paz, Bolivia
- *Caprimulgus macrurus*
    - No. 22951
    - Female
    - Singapore: Tampines
- *Chordeiles minor*
    - No. 15930
    - Female
    - Mid Union, Colorado, Plainfield
- *Phalaenoptilus nuttallii*

    - No. 17986
    - Female
    - Maricopa Co., Phoenix, Arizona
- *Eurostopodus macrotis*
    - SMITHSONIAN – No. 613058
    - Female
    - Luzon, Philippines

Hemiprocnidae

- *Hemiprocne mystacea*
    - SMITHSONIAN – No. 560829
    - Female
    - Indonesia – Jaiblo District

Nyctibiidae

- *Nyctibius grandis*
    - SMITHSONIAN – No. 615095
    - Male
    - Panama: Bocas del Toro

Podargidae

- *Batrachostomus javensis*
    - No. 9189
    - Female
    - Thailand
- *Podargus strigoides*
    - No. 12462
    - Male
    - NY Zoo

Steatornithidae

- *Steatornis caripensis*
    - No. 22733
    - Female
    - Venezuela: Bol.,C. Guyana

Trochilidae

- *Amazilia fimbriata*

    - No. 12091
    - Female
    - Venezuela: Edo. Gualico
- *Colibri coruscans*
    - No. 25963
    - Female
    - Bolivia: Depto. La Paz
- *Phaethornis superciliosus*
    - No. 10239
    - Female
    - Peru: 59 km W. Pucallpa

Outgroup taxa

GALLOANSERAE

Galliformes
- *Gallus gallus*
    - No. 18553
    - Male
    - Captive bird

NEOAVES

Accipitriformes
- *Buteo jamaicensis*
    - No. 27122
    - Female
    - Hillsborough County, New Hampshire

Coliiformes
- *Colius colius*
    - No. 23334
    - Female
    - Orange Free State, South Africa

Columbiformes
- *Treron vernans*
    - No. 27556
    - Female
    - Malaysia: Sabah

Cuculiformes
- *Coccyzus americanus*

    - No. 16871
    - Male
    - Staten Island, NY

Eurypygiformes
- *Eurypyga helias*
    - No. 3750
    - ?
    - Captive at Joseph's Farm

Leptosomatiiformes
- *Leptosomus discolor*
    - No. 10083
    - Male
    - Madagascar

Musophagiformes
- *Tauraco erythrolophus*
    - No. 27959
    - Male
    - Captive

Passeriformes
- *Turdus falcklandii*
    - No. 27785
    - Male
    - Prov. de Rio Negro, Argentina
- *Tyrannus tyrannus*
    - No. 24542
    - Male
    - Huntington, Suffolk County, New York

Strigiformes
- *Strix occidentalis caurina*
    - No. 26463
    - Male
    - California: Humboldt County

Trogoniformes
- *Trogon violaceus*
    - No. 19422
    - Male
    - Est. Bolivar, Venezuela

APPENDIX II

LIST OF MORPHOLOGICAL CHARACTERS

1. Paroccipital process. Protruding downwards. No, not protruding / arguably absent (0), yes, protruding slightly downwards (1), yes, protruding extensively downwards. -> Potentially ordered. [Similar to Nesbitt et al 2011, 23 and Mayr 2009, 11].
2. Foramen magnum. Shape. Circular (0), oval with narrow dorsal part (1), rectangular (2).
3. Foramen veni occipitalis externus. Prominent, no (0), yes (1).
4. Ecethmoidal bone. Little developed but not absent (0), moderately developed, protruding laterally (1), highly developed (2). -> Ordered (0(1(2))).
5. Ecethmoidal bone. Connected to frontal with a slender processus. No (0), yes (1).
6. Orbit. Moderately longer than internal antorbital fenestra (0), expanded and much larger than internal antorbital fenestra (1).
7. Supraorbital margins: Concave, interorbital region hourglass-figured. No (0), yes (1).
8. Postorbital processus. Prominent. No (0), yes (1), yes and additionally connected to arcus parameat. (2). [Same as Nesbitt et al 2011, 20 and Mayr 2005, 13].
9. Cone-like bony protrusion at caudal margin of foramen nervi optici: absent (0) present (1). [Same as Mayr 2009, 12 and Nesbitt et al 2011, 24].
10. Frontal. Very narrow due to highly enlarged eye socket. No (0), yes. Very narrow (1).
11. Lacrimal. Absent or vestigial (0), present and prominent (1). [similar to Mayr 2009, 3 – also Nesbitt et al 2011, 8]
12. Prominent hook at tip of beak. No (0), yes, forms suddenly (1), yes, forms gradually, quite long (2).
13. Ventral side of upper jaw completely ossified. No (0), yes (1).
14. Premaxilla. Nasal processus clearly separated from maxilla, forming a distinctive narrow ridge. No (0), yes (1).
15. Basipterygoid: absent (0), present (1).
16. Maxilla - dorsal face. Relative length to that of cranium: 0.5-1.5 (0), 1.5-3.0 (1), >3 (2). Ordered (0(1(2))).
17. Maxillae: Triangular dorsoventral and lateromedial form and dorsoventrally compressed. No (0), yes (1).
18. Rostrum maxillae: Ventromedial fenestra. Absent (0), present (1).
19. Jugal arcus: Long and slender (0), short and thick (1).
20. Jugal arcus: Pronounced lateral convexity. No (0), yes (1). [Similar to Nesbitt et al 2011, 25].
21. Jugal arcus: Pronounced ventral convexity. No (0), yes (1).
22. Nasal aperture. Extreme rostral position. No (0), yes (1).
23. Enlarged processus dorsolateralis nasalis. No (0), yes (1) [probably same as Nesbitt 2011, 9 which is modified from Livezey and Zusi 2007, 383]
24. Prominent angulus tomialis maxillaris. No (0), yes (1). [Modified from Livezey

and Zusi, 2007, 408 – also in Nesbitt et al 2011, 6]

25. Maxillae - corpus ossis. Pneumacity. Absent (0), present (1) present and highly prominent (2).
26. Processus palatus maxillaris. Reduced (0), prominent (1).
27. Palatines - interpalatine synostosis, medial keel. Absent (0), present (1).
28. Palatines - position of angulus caudomedialis relative to pars lateralis. Coincident (0), caudal (1). [Perhaps same as Nesbitt et al 2011, 14]
29. Palatine process extends rostrally, very long and thin. No (0), yes (1). [Same as Nesbitt et al 2011, 18 and Mayr 2009, 6].
30. Palatines - processus rostromedialis. Absent or minute (0), distinct (1).
31. Palatines - lateral extensions. Absent (0), present (1), present and greatly enlarged (2). Potentially ordered. [Mayr 2009, 8 and Nesbitt et al 2011, 13]
32. Palatines - pterygoid processus. Absent (0), present but short (1) present, long and slender (2). Ordered (0(1(2))).
33. Pterygoids very long and slender (0) or short and rather thick (1).
34. Pterygoid - prominent dorsolateral process at basipterygoid articulation. Absent (0), present (1). [Similar to Nesbitt et al 2001, 22 and Mayr 2009, 10].
35. Quadrate - condylus medialis of processus mandibularis long and lateromedially compressed. Larger than condylus lateralis and parallel with pterygoid. No (0), yes (1).
36. Quadrate - processus orbitalis. Absent (0), present, shorter in length than processus oticus (1) present, similar in length as processus oticus (2), Ordered (0(1(2))). [same as Mayr 2009, 13 and Nesbitt et al 2011, 27].
37. Quadrate - processus oticus. Pneumatic foramina on caudal surface. Absent (0), present (1). [Same as Mayr 2009, 15 and similar to Nesbitt et al 2011, 29].
38. Prominent joint between frontal and nasal bones: Absent (0), present (1). [Mayr and Clarke 2003, 5 and Nesbitt et al 2011, 7].
39. Mandible - Intermediate and rostralmost part of caudal pars. Significant curvature. No (0), yes (1). [Similar to Nesbitt et al 2011, 33 and Livezey and Zusi 2006, 673].
40. Mandible - symphysial part. Length of proportion of total length of mandible. Short, less than one fifth (0), medium, btw one fifth and one third (1), long, more than one third (2). Ordered (0(1(2))).. [Similar to Mayr 2009, 16 and Nesbitt et al 2011, 30].
41. Mandible - caudal end quite short and compressed, esp. cotyla lateralis and processus medialis. No (0), yes (1). [Similar to Mayr 2009, 18 and Nesbitt et al 2011, 37].
42. Mandible - presence of intraramal joint. Caudal half of mandible greatly widened. No (0), yes (1).[Similar to Mayr 2009, 17 and Nesbitt et al 2011, 36].
43. Mandible - Dentaries - length. Less than 1/2 of total mandible length (0), more than 1/2 of total mandible length (1).
44. **Mandible, long and strongly mediolaterally compressed processus retroarticularis: absent (0), present (1). From Cracraft (1988) and Mayr & Clarke (2003). A synapomorphy for Galloanserae.**
45. Prominent angulus mandibulae: Absent (0), present (1).
46. Atlas. Incisure of condyloid fossa. Absent (0), present (1).

47. Axis. Zygapophysis caudalis dorsally at same height as processus spinosus No (0), yes (1).
48. Axis. Processus ventralis corporis. Slender, caudal end not bifurcated (0), robust, caudal end bifurcated (1) robust and tricurfated (2).
49. Cervical vertebrae. Transversal foramina in main arcus. Present in all vertebrae (0), present in all but atlas (1), present in all but atlas and axis (2). Unordered. [Related to Mayr 2009, 19 and Nesbitt et al 2011, 39].
50. Cervical vertebrae III-IV. Corpus-dorsal view. Slender (0), broad not much narrower than proc.transc or zyg.cand at widest (1).
51. Number of presacral vertebrae. 19 or more (0), 18 (1), 17 or less (2). [Same as Mayr 2009, 24 and Nesbitt et al 2011, 45].
52. Synsacrum. Cranialmost incorporated vertebrae element. Articular face. Type: Flat (0), concave (1)
53. Synsacrum. Cranialmost incorporated vertebrae element. Articular face, shape: circular or subcircular (0). Rectangular, more wide than deep (1).
54. Synsacrum. Dorsal side. Intertransversary fenestra, Absent (0), present but very small (1), present and comparatively large (2). Ordered (0(1(2))).
55. Number of caudal vertebrae (excluding pygostyle). Five or six or less (0), seven or eight (1).
56. Pygostyle. Lamina pygostylis, craniocaudally extended. No (0), yes (1).
57. Costal bones. Uncinate process. Shape. Sh1ort and sturdy (0), long and slender, always interlocking with parallel costa (1).
58. Costal bones of synsacrum. Number of pairs0: Zero (0), one (1), two (2). Ordered (0(1(2))).
59. Sternum. Shape, much longer than wider No (0), yes (1).
60. Sternum - perforations in corpus. Absent (0), present (1).
61. Sternum - large, single pneumatic foramen immediately caudal to cranial margin of median sulcus. No (0), yes (1).
62. Sternum - Craniolateral processus. Elongation: No elongation, quite short (0) somewhat elongated, not protruding greatly (1), very elongated, protruding greatly (2). Ordered (0(1(2)))..
63. Sternum - Rostral spine. Shape. Diminutive, medially invaginated (0), prominent, slightly invaginated (1), large, ridgelike (2) extremely large, fork-like (3). Unordered. [Similar to Mayr 2009, 29 and Nesbitt et al 2011, 54].
64. Sternum - External labrum. Shape. Even. No or only slight lateral extensions (0), lateral extensions (1).
65. Sternum - Internal labrum. Shape. Flat, not protruding (0), protruding laterally, forming slight extensions dorsally (1).
66. Sternum - Caudolateral process. Absent (0), present short and stout (1), present, long (2). Ordered (0(1(2))).
67. Sternum. Caudolateral incisure divided by trabecula intermedia. No (0), yes - slight protrudence (1), yes very prominent extension (2). Ordered (0(1(2))).
68. Sternum. Xiphal area. Very short, not extending (0), Extending but short and broad (1), extending, long and more slender (2). [Combines characters 55 and 56 from Nesbitt et al 2011].
69. Furcula. Median clavicular process. Absent (0), present as slight furrow (1),

present as prominent extension (2) very large and round extension (3).

70. Furcula. Extremitas omalis with laterally protruding facies articularis acrocoracoidea. No (0), yes (1). [Same as Mayr 2009, 25 and Nesbitt et al 2011, 46].
71. Furcula. Scapular tuberosity, elongated. No (0), yes (1).
72. Scapula. Ventral curvature. Absent, more or less straight (0), present (1).
73. Coracoid. Acrocoracoid process. Dorsomedial curvature with respect to coracoid main axis. No (0), yes (1).
74. Coracoid. Omal extremity divided in two by large foramen. No (0), yes (1).
75. Coracoid. Procoracoid processus. Absent (0), present, rudimentary(1), present, prominent (2). Ordered (0(1(2))).
76. Coracoid. Foramen nervi supracoracoidei. Absent (0), present (1). [Same as Mayr 2009, 27 and Nesbitt et al 2011, 48].
77. Coracoid. Crista articularis sternalis. Shape. Narrow (0), broad (1).
78. Coracoid. Processus lateralis. Diminutive (0), extended (1), forming a prominent hook (2). [Similar to Mayr 2009, 28 and Nesbitt et al 2011, 49].
79. Humerus. Very short and rigid. No (0), yes (1). [Similar to Mayr 2009, 37 and Nesbitt et al 2011, 63'.
80. Humerus. Clearly defined dorsal tuperculum of proximal extremity. No (0), yes (1).
81. Humerus. Ventral tubercle long and narrow and stretches further caudally than caput humerus. No (0), yes (1). [Similar to Mayr 2009, 34 and Nesbitt et al 2011, 58].
82. Humerus. Tuberculum ventralis. Extending laterally and downwards and concealing fossa pneumotricipitalis. No (0), yes (1).
83. Humerus. Caput humeri bearing a distinct distal protrusion. No (0), yes (1).
84. Humerus. Tuberculum musculi pronator superficialis. Absent (0), present (1).
85. Humerus. External condyle broader than internal condyle. No, it is narrower (0), no, they are similar (1), yes (2).
86. Humerus. Ectepicondylar prominence. Present and prominent. No (0), yes (1).
87. Humerus. Crista delto*pectoralis*. Shape. Short and not very wide (0), Ridgelike, quite wide (1) Hook like - sharply angled outwards (2). [Similar to Nesbitt et al 2011, 59'.
88. Humerus. Proximal extremity. Sulcus incisurae transverses. Diminished (0), prominent and deep (1). [Same as Mayr 2009, 33 and Nesbitt et al 2011, 61'.
89. Humerus. Processus supracondylaris dorsalis. Absent or poorly developed (0), present (1).
90. Humerus. Fossa pneumotricipitalis. Reduced in size (0), broad (1).
91. Humerus. Shape of corpus. Straight/linear (0), sigmoidal (1).
92. Humerus. Fossa olecrani. Absent or diminutive (0), prominent and broad, separating condyles (1).
93. Humerus – distal end. Fossa muscular brachialis. Shallow (0), deep and well defined (1). [Same as Mayr 2009, 36 and Nesbitt et al, 62].
94. Humerus. External tricipital groove. Prominent. No (0), yes (1).
95. Ulna. Dorsal condyle. Shape: Flat (0), generally rounded but with flat distal margin (1), overall rounded (2).

96. Ulna. Olecranon extended proximally. No (0), yes (1).
97. Ulna. Dorsal cotyle, extended laterally. No (0), yes (1).
98. Ulna and Radius. Highly abbreviated. No (0), yes (1).
99. Radius. Sulcus tendinis deep. No (0), yes (1).
100. Radius, Tuberculum bicipitale radii. Prominent, slightly extended laterally. No (0), yes (1).
101. Carpometacarpus. Intermetacarpal space. Nar0row, similar in width to metacarpal II (0), wider than metacarpal III (1).
102. Carpometacarpus. Metacarpal I processus equally long as carpal trochlea. No (0), yes (1).
103. Carpometacarpus. Fossa intratrochealis. Shallow (0), deep (1).
104. Carpometacarpus twisted laterally so distal and proximal ends are not parallel. No (0), yes, slightly, less than 45° (1), yes, very, more than 45° (2).

105. Very long digits in first phalanx. Equal in length to carpometacarpus and radius/ulna. No (0), yes (1).
106. Phalanx proximalis digitalis majoris. Ossial division of fossa dorsalis, Absent (0), present (1).
107. Digit 2. Proximal end almost twice the width of distal end. No (0), yes (1).
108. Digit 2. Distal extension of digital facet. Absent (0), present (1). [Similar to Nesbitt et al 2011, 75].
109. Synsacrum and ala preacetabularis ilii truncated. No (0), yes (1).
110. Ischiopubic space. Absent (0) very narrow (1), wide (2). Ordered (0(1(2))).
111. Ilium. Ala preacetabularis ilii. Position with respect to planum transversum synsacri. Subhorizontal (0), oblique (1).
112. Ilium. Ala preacetabularis ilii. Dorsal flanks high-ridged and extending frontally. No (0), yes (1).
113. Ilium. Ala preacetabularis ilii. Lamina ellipsoidalis lateralis. Absent (0), present (1).
114. Ilium. Ala postacetabularis ilii. Overall width. Similar to width of ischium (0), considerably wider than ischium (1).
115. Ilium. Infracristal concavity. Distinct but shallow (0), Conspicuous, quite deep (1).
116. Ischium. Shape of corpus. Flat/linear (0). Concave (1).
117. Ischium and pubis. Pubis extends further caudally than ischium. No (0), yes (1).
118. Pelvis. Ilio-ischiatic fenestra. Shape elliptical (0), oval (1), circular or irregular (2).
119. Pelvis. Antitrochanter, protruding laterally and dorsally. No or only laterally (0), yes (1).
120. Pelvis. Processus marginales caudalis ilii. Protruding. No (0), yes, slightly (1), yes, greatly, quite long (2).
121. Pelvis. Caudalmost processii transversii of synsacrum, connect to first pair of caudal vertebrae. No (0), yes (1).
122. Pelvis. Caudalmost pair of synsacral foramina intertransversarii noticeably

larger than other foramina intertransversarii. No (0), yes (1).

123. Femur. Crista trochantericus. Sharp and straight (0), irregularly shaped and short (1).
124. Length of femur relative to tibiotarsus. About 50% of tibiotarsus or slightly longer (0). Longer than 75% of the length of tibiotarsus (1).
125. Tibiotarsus. Proximal end. Crista cnemialis, reduced. No (0), yes (1).
126. Tibiotarsus. Foramen interosseum distale. Absent or highly reduced (0), present (1).
127. Tibiotarsus. Distal end. Incisure intercondylae. Shallow (0), deep (1).
128. Tarsometatarsus. Abbreviated length. No (0), yes (1). [Similar to Mayr 2009, 51 and Nesbitt et al 2011, 85].
129. Tarsometarsus. Hypotarsus. Crista lateralis. Absent (0), present but nonprominent (1), present and prominent (2). Ordered (0(1(2))).
130. Tarsometatarsus. Hypotarsus. Crista medialis. Extending dorsally. No, in same plan as other cristae of hypotarsus (0), yes (1).
131. Tarsometatarsus. Hypotarsus. Prominent two canals. No (0), yes (1).
132. Tarsometatarsus. Vascular foramen. Rather small and narrow (0), large, oval (1).
133. Tarsometatarsus. Present trochlea I - indicator of pamprodactyly. No (0), yes (1).
134. Tarsometatarsus. Distal metatarsal trochlea. Highly divergent laterally. No (0), yes (1).

CHARACTER SCORES FOR ALL TAXA – FOSSIL TAXA INDICATED BY LETTER F

Steatornis
2101110100021000000000012?1?0000111201100010100010011101100001101000001001002010000011100001110000101110001121001011002111111012100 00

Batrachostomus
1200010100010110101000112 11?0010000201000011110101 1?2110100111112221??1002002000001010011000211000101200100011000001120000000010000 0

Podargus
2200010200010110101000112 11?0011100101000011111201112110100111112221001002002000010100110002110001012001001110000011100000000101000 0

Nyctibius_griseus
11?2?10110??1?0011011100100010201110001011011102121 02?1010002010111210100200020100001111011010100000110201010210100110010001000110100 1

Caprimulgus_macrurus
2112010010101100110111002100112100110010110111021 2???2?1120012001101210100000201100011110110111100001102010101100010110101010000101000 0

Caprimulgus_longirostris
2112110011101100010101001100112000100010110111021 2??1011200?2001201210100000201100011110110111100001102010100100011110100000000101000 0

Chordeiles
2112010010101100 1?010?0??1001120101000101101?00212?1101120011001101211100000201100010110110111100001101010101100000?0001001000010?000

Eurostopodus
2112110010101100 1?010?0011001120101100101101110212?0211120011101202?1110010100010111100101110000011020101011000101001100100001000000

Phalaenoptilus
21?2110010101100110101001100 1?2100100010110 1?1021201 1?11?0012001201211100000201100010110110011000001102010101100111110100000000111000

Aegotheles
1011110101011100110101000001112200111010001 00??2?11121?11??120110201 1?1100100?100??100010??1??0??1???0???02?100000??200??0000000100

Hemiprocne
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Streptoprocne
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Apus
0112000001000100010001000001111200111010001 00100211??2111211112000002110100110101102001101110??0000010010110

Phaethornis
0012001000000101010000000000?1100001210120 01?0???02??00?12101120000020000101101110120101001011001000000110102000101110000000001001??10

Colibri
00120010000001020100000000?1100001210110010012202O1?01?2101120000020000
11110011011201010010100010001001?0102000101111?00100001001?110
Amazilia
00120010000001010100000000?110000???01100100???12010????10?1200000???001
11101100112000100101000100000011010200010110000100001001?1?0
Treron
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02002000000002001000121100010010001011011011100010100000010000
Coccyzus
01120111001201000000000011001000001200010010000212??2000200012002212001O
02002000000211000101120100011020010001001001?0001?10000001000
Strix
0002010?00111100010001002?01101101120100000000021 1?10101110011002110101O
02100011000111001100011100110020100001010011110010101101101O0
Buteo
00121101011101000000000002?01101100120000007010010001001 1?101020000021010
02100010000201001100121100111020100001010111210010 1?110110100
Eurypyga
01100100000001?001000000000?1000??120101001001010011201107100201201201 10
02001011000101000100120100010020100021010101202007000101000 00
Trogon
00100110001107101000001110100000010201000010010210??101110001200222200 10
02002010000101000101120000010020000121011001201000100011110 01
Tauraco
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00101000000011000100020000011020000011000107202?0000100000000
Colius
01020100001001000100000007001?100012000000?000221011201121002410202100 10
01000001000211000100120100010020000?1001001000010007100000000
Leptosomus
20011111001101100010000120110000100200000010110210?12011?101110011100010
02102000000111000100020100011020100001010001102110007100101001
Turdus
02?201010000010001000000000110120002000000000002001111011100230000031110
01000000000211000000021000000020010021101011101100007000001000
Tyrannus
02?201100000010001000000117111120002010100010007110111111110023002003?110
01000000000211000000021000000020010020111001101?000?000001000
Anser
10?0010100?01110000000012??000111102010001011001001120017100121020?00110
00000010000201101100020000011020?000210100110001000000010110O
Gallus
00000102001201000000000001111001100200000000100?00112000110022012022001O
00000000000200001100020000010020010011010011201001100000101000

F: *Masillapodargus*
???????????1?10101??0?01????????????00001???????????0??0??1???111??????1??10
???????0?0????????0??0????????????????????????????0????0?

F: *Paraprefica*
???????????1?001?01??????????2?01?0??1011????????????????00?1???222????1?20??0
???00??11??10?????0??????0???1????????????????1?11???0?0

F: *Jungornis*
??120????????10111010
?111??20100??

F: *Argornis*
??10111001?
100??2?000??????0????????????????????????????????????

F: *Eurotrochilus*
??????????????01?????0????????????????????1?????????????????????????000????0021?01?
??11???01????????1??0???0????2??????????????0??0??????

F: *Aegialornis*
??100?
000??1?101??

F: *Parargornis*
???????????????000????1????????????????????????????????????0??????1????????11?01?
???????2?0????????0??0????????????????????????????020?0?1

F: *Protocypselomorphus*
?????????????????????1????????0?????????00??????????????1??1???1????????0?000?
?000??1?0?0???1??0??????1?????????????????????????101????

F: *Fluvioviridavis*
?????001000?10001011?0?11???0?0???11100100011????0??110????????????????????
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F: *Eocypselus*
???100?0??????0????????????????????????????????????1????0??2????20?0??10???10?
???????1??0?1???????1???0?????0?????????????0??000????

APPENDIX III

INDEL CHARACTER MATRIX

Struthio	0100001100001100000100010000000000000010000??000000001001000
Gallus	0100111001000100011100010010000000000100??000000000001001000
Anser	0000111001001100011100010010000000000100000000000000000?1000
Turdus	0000000011010000000000000?????1110000000010000100000000000000
Tyrannus	00000000101100000001001100000111000000001000010000000000000
Acanthisitta	00000000100110000000100110000011100000000100001000000000000
Trogon	00000000000000010000000001?????100000000000000000000000000000
Leptosomus	00000??????000000001100100000?000000000000000000000000?0000
Buteo	0000010100000010001011001000001000000000000000000000000000000
Strix	0000010100000000001011001000001000000000000000000000000000000
Colius	00000??????001000001100100000100000000000000000000000000000000
Tauraco	0000010000000000010110010000??????????000000000000000000
Charadrius	0000010100000000010100000000000000000100000000000000000?0000
Coccyzus	0000010000000100000100010000??????????000000000000000000
Grus	0000000000000000010000000000000000001000000000000000000000
Gavia	0000010100000100010110010000000000000100000000000000000000
Eurypyga	0000010000000100010100000010110000010000000000000000000000000
Phoenicopterus	0000010000000110011000010010100000000100000000001010000?0000
Treron	0000010000000000000100000010100000000000000000000010100000000
Podargus	0000010100000000010000000000100000000000000000000000010010100
Batrachostomus	00000??????000001000000?????000000000000000000000010010100
Steatornis	?????10100000000010110000010100000010000000000000000000000
Eurostopodus	00100101000?????????????????????000100000000010000001000000010
Caprimulgus	001001010000000000000000001010001000000000100000010000000010
N_bracteatus	100101010000010001000000001010001000100001001000000???0000
N_grandis	100100010000010001000000001010001000100001001000000000000000
Aegotheles	000000000000000000000100111010000000001000010000000001000000
Hemiprocne	000000000000000100000100011010000100001100010011000001?0001
Aerodramus	00000??????000010000010011111000011100110001001100000???0001
Streptoprocne	000000000000000010000010011111100001100001000100110000??00001
Phaethornis	???????????000001000010011101?????????????01????????010????
Colibri	000000000000000010000100001010000000000000010000000000100000

APPENDIX IV

APPENDIX IV
List of taxa used in analyses of molecular data and
affiliated nuclear sequences with GENBANK reference numbers.

	GENETIC MARKERS:	
TAXA	**ALDOB**	**CLTC**
Acanthisitta chloris	EU737790	EU738109
Aegotheles insignis	EU737791	EU728110
Aerodramus vanikorensis	EU737792	
Anser erythropus	EU737796	EU302707
Batrachostomus septimus	EU737803	
Buteo jamaicensis	EU737785	EU302710
Caprimulgus longirostris	EU737812	EU302711
Charadrius vociferus	EU737816	EU738132
Coccyzus americanus	EU737820	EU302713
Colibri coruscans	EU737822	EU302714
Colius colius	EU737824	
Eurostopodus macrotis	EU737840	EU738149
Eurypyga helias	EU737841	EU302724
Gallus gallus	EU737788	EU302727
Gavia immer	EU737847	EU738153
Grus canadensis	EU737850	EU738157
Hemiprocne mystacea	EU737853	EU738159
Leptosomus discolor	EU737858	
Nyctibius bracteatus	EU737873	EU738178
Nyctibius grandis	EU737874	EU738179
Phaethornis griseogularis		
Phoenicopterus chilensis	EU737892	EU302734
Podargus strigoides	EU737898	EU302735
Steatornis caripensis		EU738215
Streptoprocne zonaris	EU737917	EU302742
Strix occidentalis	EU737918	EU738216
Struthio camelus	EU737782	EU302743
Tauraco erythrolophus	EU737921	EU302744
Treron vernans	EU737926	EU302746
Trogon personatus	EU737927	EU302747
Turdus falcklandii	EU737928	EU738223
Tyrannus tyrannus	EU737929	EU738225

TAXA	CRYAA	EEF2
Acanthisitta chloris		EU738714
Aegotheles insignis	EU737637	EU738571
Aerodramus vanikorensis	EU737638	EU738572
Anser erythropus		EU738577
Batrachostomus septimus	EU737650	EU738584
Buteo jamaicensis	EU737632	EU738566
Caprimulgus longirostris	EU737659	EU738592
Charadrius vociferus	EU737664	EU738597
Coccyzus americanus	EU737668	EU738601
Colibri coruscans	EU737670	EU738603
Colius colius	EU737672	EU738605
Eurostopodus macrotis	EU737687	
Eurypyga helias	EU737688	EU738621
Gallus gallus	EF408909	EU738569
Gavia immer	EU737694	EU738627
Grus canadensis	EU737697	EU738631
Hemiprocne mystacea		EU738634
Leptosomus discolor	EU737705	EU738640
Nyctibius bracteatus	EU737718	EU738651
Nyctibius grandis	EU737719	EU738652
Phaethornis griseogularis		EU738666
Phoenicopterus chilensis	EU737734	EU738671
Podargus strigoides	EU737741	EU738678
Steatornis caripensis	EU737758	EU738697
Streptoprocne zonaris	EU737759	EU738698
Strix occidentalis		EU738699
Struthio camelus		EU738563
Tauraco erythrolophus	EU737762	EU738702
Treron vernans	EU737767	EU738706
Trogon personatus	EU737768	EU738707
Turdus falcklandii	EU737769	EU738708
Tyrannus tyrannus	EU737771	EU738709

TAXA	EGR1	FGB
Acanthisitta chloris	EU738893	EU739358
Aegotheles insignis		EU739359
Aerodramus vanikorensis	EU738895	EU739360
Anser erythropus	EU738899	EU739365
Batrachostomus septimus	EU738906	
Buteo jamaicensis	EU738888	EU739353
Caprimulgus longirostris	EU738915	EU739381
Charadrius vociferus	EU738920	EU739386
Coccyzus americanus		EU739386
Colibri coruscans	EU738926	EU739392
Colius colius	EU738928	EU739394
Eurostopodus macrotis	EU738946	
Eurypyga helias	EU738947	EU739413
Gallus gallus	EU738891	EU739356
Gavia immer	EU738953	EU739419
Grus canadensis	EU738957	EU739423
Hemiprocne mystacea	EU738960	EU739426
Leptosomus discolor	EU738966	EU739432
Nyctibius bracteatus		EU739447
Nyctibius grandis	EU738982	EU739448
Phaethornis griseogularis		EU739462
Phoenicopterus chilensis	EU739001	EU739466
Podargus strigoides	EU739008	EU739472
Steatornis caripensis	EU739027	EU739491
Streptoprocne zonaris	EU729028	EU739492
Strix occidentalis	EU739029	EU739493
Struthio camelus		EU739350
Tauraco erythrolophus	EU729032	EU739496
Treron vernans		EU739500
Trogon personatus	EU739038	
Turdus falcklandii	EU739039	
Tyrannus tyrannus	EU739041	EU739504

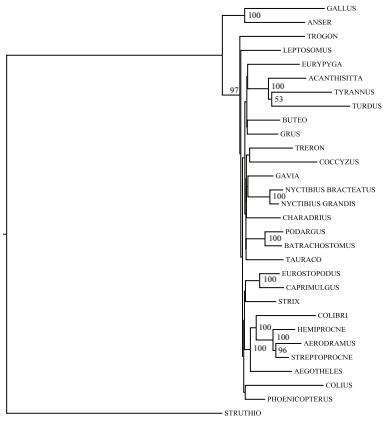
TAXA	GH1	MUSK
Acanthisitta chloris	EF521431	EU739756
Aegotheles insignis	EF521432	EU739757
Aerodramus vanikorensis	EF521433	EU739758
Anser erythropus	EF521438	EU739762
Batrachostomus septimus	EF521445	EU739769
Buteo jamaicensis	EF521426	EU739752
Caprimulgus longirostris	EF521453	EU739778
Charadrius vociferus	EF521457	EU739782
Coccyzus americanus		EU739786
Colibri coruscans	EF521462	EU739788
Colius colius	EF521463	EU739790
Eurostopodus macrotis	EF521481	EU739807
Eurypyga helias	EF521482	EU739808
Gallus gallus	EF521429	
Gavia immer	EF521488	EU739814
Grus canadensis	EF521492	EU739817
Hemiprocne mystacea	EF521495	EU739820
Leptosomus discolor		EU739826
Nyctibius bracteatus	EF521514	EU739840
Nyctibius grandis	EF521515	EU739841
Phaethornis griseogularis		
Phoenicopterus chilensis	EF521532	EU739857
Podargus strigoides	EF521539	EU739863
Steatornis caripensis	EF521558	EU739878
Streptoprocne zonaris	EF521559	EU739879
Strix occidentalis	EF521560	EU739880
Struthio camelus	EF521423	EU739749
Tauraco erythrolophus		EU739883
Treron vernans	EF521568	EU739888
Trogon personatus	EF521569	EU739889
Turdus falcklandii	EF521570	EU739890
Tyrannus tyrannus	EF521572	EU739892

TAXA	MYC	PCBD1
Acanthisitta chloris	EU738242	EU738407
Aegotheles insignis	EU738243	EU738408
Aerodramus vanikorensis	EU738244	EU738409
Anser erythropus	EU738249	EU738414
Batrachostomus septimus	EU738255	EU738421
Buteo jamaicensis	EU738237	EU738402
Caprimulgus longirostris	EU738263	EU738430
Charadrius vociferus	EU738268	EU738435
Coccyzus americanus	EU738272	EU738439
Colibri coruscans	EU738274	EU738441
Colius colius	EU738276	EU738443
Eurostopodus macrotis	EU738292	EU738459
Eurypyga helias	EU738293	EU738460
Gallus gallus	EU738240	EU738405
Gavia immer	EU738299	EU738466
Grus canadensis	EU738303	EU738470
Hemiprocne mystacea	EU738306	EU738473
Leptosomus discolor	EU738312	EU738479
Nyctibius bracteatus	EU738327	EU738494
Nyctibius grandis	EU738328	EU738495
Phaethornis griseogularis	EU738342	
Phoenicopterus chilensis	EU738347	EU738513
Podargus strigoides	EU738354	EU738520
Steatornis caripensis	EU738373	EU738539
Streptoprocne zonaris	EU738374	EU738540
Strix occidentalis	EU738375	EU738541
Struthio camelus		EU738399
Tauraco erythrolophus	EU738378	EU738544
Treron vernans	EU738383	EU738548
Trogon personatus	EU738384	EU738549
Turdus falcklandii	EU738385	EU738550
Tyrannus tyrannus	EU738387	EU738552

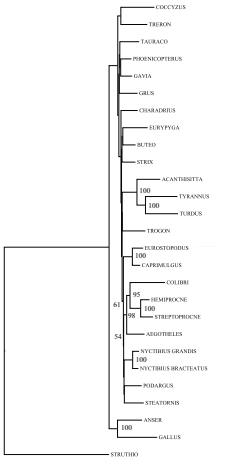
TAXA	RAG-1	RAG-2
Acanthisitta chloris	AY056975	sequenced in AMNH lab
Aegotheles insignis	DQ482636	sequenced in AMNH lab
Aerodramus vanikorensis		
Anser erythropus	DQ137227	
Batrachostomus septimus	DQ482613	sequenced in AMNH lab
Buteo jamaicensis	AY461394	sequenced in AMNH lab
Caprimulgus longirostris	DQ482621	sequenced in AMNH lab
Charadrius vociferus	AF143736	
Coccyzus americanus	DQ482640	sequenced in AMNH lab
Colibri coruscans	DQ482639	sequenced in AMNH lab
Colius colius		sequenced in AMNH lab
Eurostopodus macrotis	DQ482615	sequenced in AMNH lab
Eurypyga helias	DQ881806	sequenced in AMNH lab
Gallus gallus	AF143730	sequenced in AMNH lab
Gavia immer	AF143733	sequenced in AMNH lab
Grus canadensis	AF143732	sequenced in AMNH lab
Hemiprocne mystacea	DQ482637	
Leptosomus discolor	AY233361	
Nyctibius bracteatus		
Nyctibius grandis	DQ482612	sequenced in AMNH lab
Phaethornis griseogularis	DQ482638	sequenced in AMNH lab
Phoenicopterus chilensis	DQ881823	
Podargus strigoides	DQ482614	sequenced in AMNH lab
Steatornis caripensis	DQ482611	sequenced in AMNH lab
Streptoprocne zonaris		sequenced in AMNH lab
Strix occidentalis	DQ482641	sequenced in AMNH lab
Struthio camelus	AF143727	sequenced in AMNH lab
Tauraco erythrolophus	DQ482643	sequenced in AMNH lab
Treron vernans		sequenced in AMNH lab
Trogon personatus	AY625227	sequenced in AMNH lab
Turdus falcklandii	AY057039	sequenced in AMNH lab
Tyrannus tyrannus	AF143739	sequenced in AMNH lab

TAXA	RHO	TGFB2
Acanthisitta chloris	EU737164	EU737322
Aegotheles insignis	EU737165	EU737323
Aerodramus vanikorensis	EU737166	EU737324
Anser erythropus	EU737171	EU737329
Batrachostomus septimus	EU737178	EU737336
Buteo jamaicensis	EU737159	EU737317
Caprimulgus longirostris	EU737186	EU737345
Charadrius vociferus	EU737191	EU737350
Coccyzus americanus	EU737195	EU737354
Colibri coruscans	EU737197	EU737356
Colius colius	EU737199	EU737358
Eurostopodus macrotis	EU737213	EU737376
Eurypyga helias	EU737214	EU373377
Gallus gallus	EU737162	EU737320
Gavia immer	EU737220	EU737383
Grus canadensis	EU737224	EU737387
Hemiprocne mystacea	EU737227	EU373390
Leptosomus discolor	EU737233	EU737396
Nyctibius bracteatus	EU737247	EU737411
Nyctibius grandis	EU737248	EU737412
Phaethornis griseogularis		
Phoenicopterus chilensis	EU737264	EU737431
Podargus strigoides	EU737270	EU737438
Steatornis caripensis	EU737289	EU737457
Streptoprocne zonaris		EU737458
Strix occidentalis	EU727391	EU737459
Struthio camelus	EU737156	EU737314
Tauraco erythrolophus	EU737294	EU737462
Treron vernans		EU737467
Trogon personatus	EU737299	EU737468
Turdus falcklandii	EU737300	EU737469
Tyrannus tyrannus	EU737302	EU737471

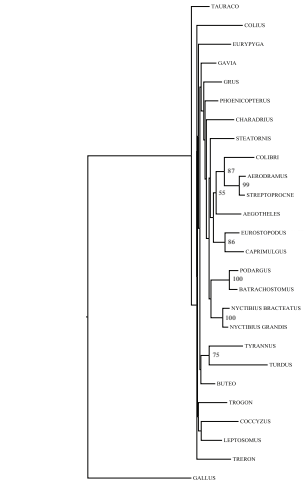
APPENDIX V - INDIVIDUAL GENE TREES



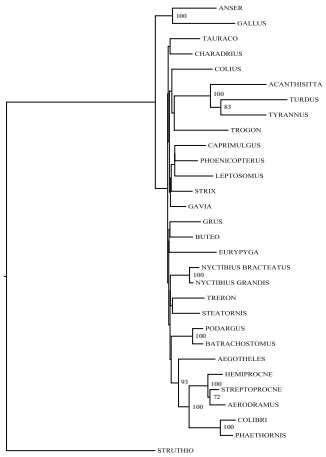
Highest-scoring tree from a Maximum Likelihood analysis of the nuclear exon ALDOB with 11 caprimulgiform taxa, 16 other neoavian taxa, 2 galloanseran taxa and rooted by a single paleognath taxon. Node numbers indicate bootstrap support.



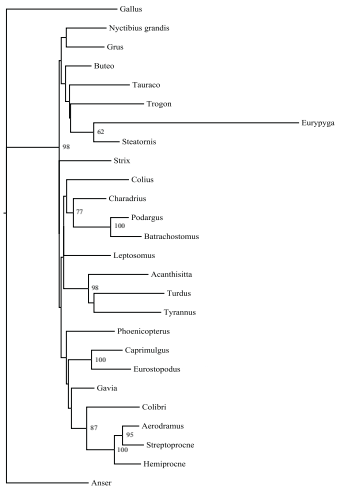
Highest-scoring tree from a Maximum Likelihood analysis of the nuclear exon CLTC with 10 caprimulgiform taxa, 14 other neoavian taxa, 2 galloanseran taxa and rooted by a single paleognath taxon. Node numbers indicate bootstrap support.



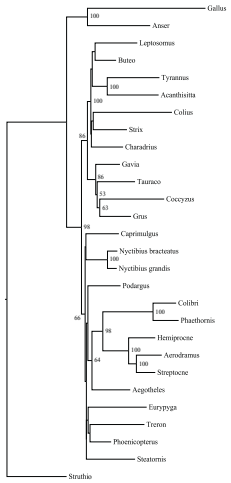
Highest-scoring tree from a Maximum Likelihood analysis of the nuclear exon CRYAA with 11 caprimulgiform taxa, 14 other neoavian taxa, and rooted by a single galloanseran taxon. Node numbers indicate bootstrap support.



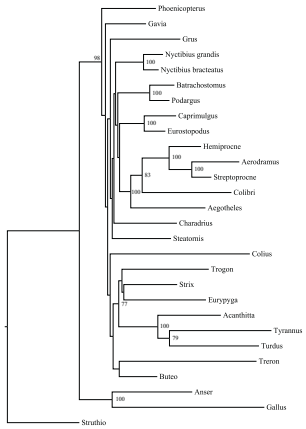
Highest-scoring tree from a Maximum Likelihood analysis of the nuclear exon EEF2 with 12 caprimulgiform taxa, 15 other neoavian taxa, 2 galloanseran taxa and rooted by a single paleognath taxon. Node numbers indicate bootstrap support.



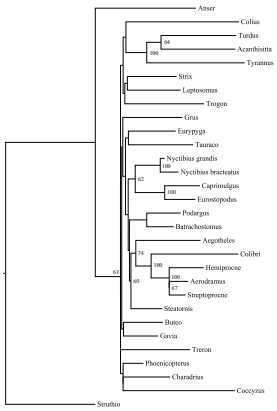
Highest-scoring tree from a Maximum Likelihood analysis of the nuclear exon EGR1 with 10 caprimulgiform taxa, 13 other neoavian taxa, rooted by 2 galloanseran taxa. Node numbers indicate bootstrap support.



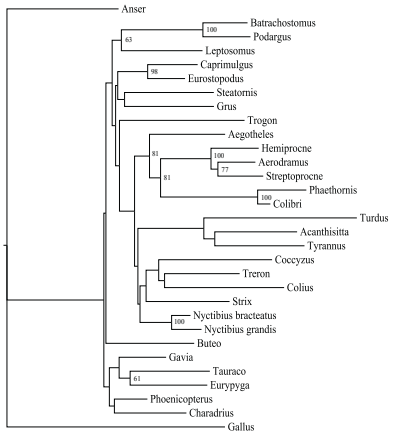
Highest-scoring tree from a Maximum Likelihood analysis of the nuclear exon FGB with 11 caprimulgiform taxa, 14 other neoavian taxa, 2 galloanseran taxa and rooted by a single paleognath taxon. Node numbers indicate bootstrap support.



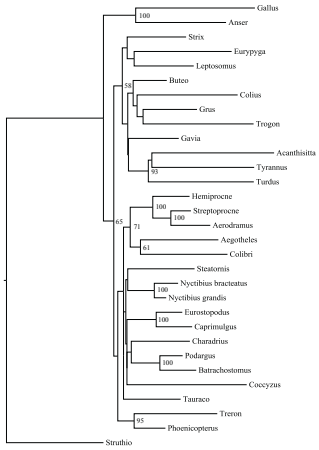
Highest-scoring tree from a Maximum Likelihood analysis of the nuclear exon GH1 with 12 caprimulgiform taxa, 13 other neoavian taxa, 2 galloanseran taxa and rooted by a single paleognath taxon. Node numbers indicate bootstrap support.



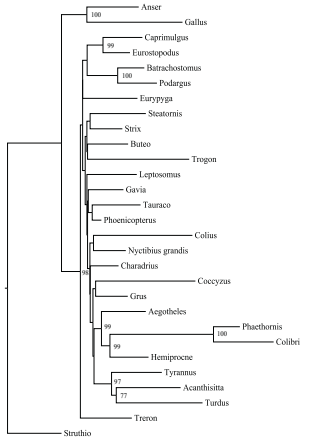
Highest-scoring tree from a Maximum Likelihood analysis of the nuclear exon MUSK with 12 caprimulgiform taxa, 16 other neoavian taxa, 1 galloanseran taxa and rooted by a single paleognath taxon. Node numbers indicate bootstrap support.



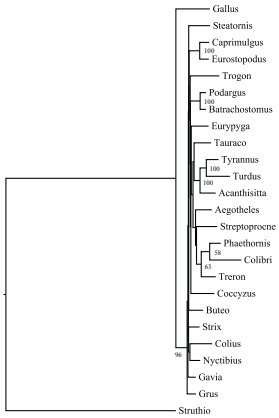
Highest-scoring tree from a Maximum Likelihood analysis of the nuclear exon MYC with 13 caprimulgiform taxa, 16 other neoavian taxa, rooted by 2 galloanseran taxa. Node numbers indicate bootstrap support.



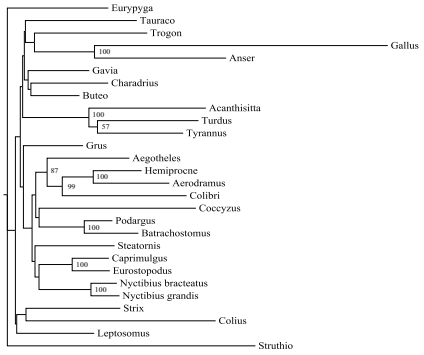
Highest-scoring tree from a Maximum Likelihood analysis of the nuclear exon PCBD1 with 12 caprimulgiform taxa, 16 other neoavian taxa, 2 galloanseran taxa and rooted by a single paleognath taxon. Node numbers indicate bootstrap support.



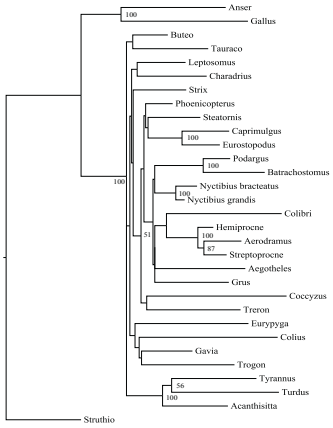
Highest-scoring tree from a Maximum Likelihood analysis of the nuclear exon RAG-1 with 10 caprimulgiform taxa, 16 other neoavian taxa, 2 galloanseran taxa and rooted by a single paleognath taxon. Node numbers indicate bootstrap support.



Highest-scoring tree from a Maximum Likelihood analysis of the nuclear exon RAG-2 with 10 caprimulgiform taxa, 13 other neoavian taxa, one galloanseran taxon and rooted by a single paleognath taxon. Node numbers indicate bootstrap support.



Highest-scoring tree from a Maximum Likelihood analysis of the nuclear exon RHO with 11 caprimulgiform taxa, 13 other neoavian taxa, one galloanseran taxon and rooted by a single paleognath taxon. Node numbers indicate bootstrap support.



Highest-scoring tree from a Maximum Likelihood analysis of the nuclear exon TGFB2 with 12 caprimulgiform taxa, 16 other neoavian taxa, one galloanseran taxon and rooted by a single paleognath taxon. Node numbers indicate bootstrap support.

CHAPTER 3

THE SYSTEMATICS OF THE NEW WORLD CAPRIMULGIDAE

1. INTRODUCTION

Avian systematics has undergone a revolution in the last couple of decades with the greatly increased use of genetic data for phylogenetics. The taxonomy of most avian taxa, from species to higher groups, has been in a process of re-evaluation with the result that major changes have been made to traditional classifications. Classical ideas about relationships among many higher taxa, as well as about their true species diversity, have been drastically challenged. Although there has been great progress in the field, some important clades have undeniably received less focus than others, and among those are the nightjars (Caprimulgidae). Nightjars are biologically important for multiple reasons. They are a cosmopolitan group found on all continents except Antarctica and have a relatively high species diversity for a non-passerine family with 89-90 biological species recognized (Cleere & Nurney, 1998; Holyoak, 2001; Dickinson *et al.*, 2003). The highest species diversity is in South America and Africa, but radiations extend into North America, South and Southeast Asia and Australia, with two species breeding in Europe and two species on Madagascar (Cleere & Nurney, 1998).

Despite relatively high species diversity, nightjars are quite homogenous morphologically. This is probably associated with their predominantly nocturnal and crepuscular lifestyle (Holyoak, 2001). They all have a relatively similar body-shape, with the most notable features being a very large gape, despite the bill itself being rather small and weak. Additionally, they can spread their lower jaw horizontally, an adaptation to catch insects in flight at night (Bühler, 1970). Their eyes are large and they possess a

unique feature also present in other caprimulgiform taxa, a tapetum in the retina, which is known to increase the detection rate of light that enters the eye, an adaptation to their crepuscular lifestyle (Nicol & Arnott, 1974; Lythgoe, 1979). Another unusual feature of nightjars is that the middle toe on each foot is unusually long and pectinate, which has been hypothesized to be associated with preening, in particular for the removal of dirt and parasites (Cleere, 1999). Nightjars have large wings and are generally strong fliers. Their plumage is dominated by brownish colors, but the patterns can be quite complex, and white or light-colored spots and other markings are common as are stripes of black and grey. Plumage can vary considerably within species and is often the main basis for subspecies description (Cleere, 1999, 2010; Holyoak, 2001). A few species have ear-like tufts on the back of their heads, in particular the eared-nightjars of the genera *Eurostopodus* and *Lyncornis*. A number of species in different genera have very striking secondary sexual characters in the form of long tail feathers, or in the case of the Standard- and Pennant-winged nightjars (*Macrodipteryx*), a greatly elongated and modified second primary. These species have polygamous mating systems which is unusual as most other nightjar species with known breeding systems are strictly monogamous (Holyoak, 2001).

Nightjars are known for their vocalizations, as that is often the only way to localize and identify them in their natural habitat. These vocalizations can be elaborate and complex, often in the form of patterned sequences performed repeatedly as part of territorial or mating behavior. They are frequently accompanied by various mechanical sounds produced by the wings as well as visual displays (summarized in Holyoak, 2001). Vocalizations have not been mapped consistently in nightjar species but variations have

been noted at and below the species level, suggesting that vocalizations may be important not only for identification in the field but potentially as informative characters for species delimitation and other systematic studies.

Systematic analyses are greatly needed for the Caprimulgidae inasmuch as an accurate understanding of their current diversity is lacking. Intraspecific diversity is high within the family with 47 species being divided into two or more subspecies and some into as many as 10 (Holyoak, 2001; Dickinson *et al.,* 2003, Cleere, 2010). Recently, suggestions have been made to elevate some subspecies to full species status on morphological and behavioral differences (Cleere, 2010; Chesser *et al.,* 2012), but genetic data are also needed to evaluate the taxonomic status of nearly all named taxa.

Phylogenetic studies of the caprimulgids have not received much attention and the majority of studies have investigated their relationship to the other caprimulgiform families (Aegothelidae, Nyctibiidae, Podargidae and Steatornithidae). Although the systematics of the caprimulgiforms have long been in flux, there is strong evidence that another order, Apodiformes, which includes three families of swifts and hummingbirds, is embedded within Caprimulgiformes (Cracraft *et al.*, 2004; Ericson., 2006; Hackett *et al.*, 2008; Braun & Huddleston, 2009; Mayr, 2010). Morphological evidence strongly suggests that the potoos (Nyctibiidae) are the sister-group to nightjars (Mayr, 2002; Livezey & Zusi, 2006, 2007; Mayr, 2010) but results from molecular data are inconsistent and usually lack strong resolution (Cracraft *et al.*, 2004; Ericson *et al.*, 2006; Hackett *et al.*, 2008; Braun & Huddleston, 2009). The monophyly of the Caprimulgidae has not been questioned with one notable exception as described below (Mariaux & Braun, 1996).

There are few generic-level phylogenetic studies within caprimulgids and analyses of species or subspecies are practically nonexistent. Previously published studies vary greatly in their taxon sampling. Mariaux & Braun (1996) included five caprimulgid species in their phylogeny of the order based on 656bp of cytochrome B (*CYTB*) sequence data. Their results were rather unusual, with the Aegothelidae embedded within the Caprimulgidae, splitting *Eurostopodus* from the remaining caprimulgids. This phylogenetic pattern was not well supported, has not been corroborated by other analyses, and is likely to be an artifact of poor character- and taxon-sampling (Mariaux & Braun, 1996). Barrowclough *et al* (2006) included 21 species (14 genera) of caprimulgids in a nuclear *RAG-1* phylogeny of the Caprimulgiformes. Their results exhibited good support for a monophyletic Caprimulgidae and for five major lineages within the family. The Australasian genus *Eurostopodus* was found to be sister to all remaining caprimulgids. Three New World clades were resolved as paraphyletic, with the nighthawks (*Chordeiles* and *Podager*) being the sister group to an Old World radiation. They suggested that their results indicate a Neotropical origin for the family, excluding *Eurostopodus*. The only genus that had multiple species sampled was *Caprimulgus*, and they showed it was clearly not monophyletic and divided into three unrelated groups. Another important result was that the traditional division of the family into the Chordeilinae and Caprimulginae, which were previously erected on morphological data (mainly skull characters), was not recovered by the *RAG-1* data (Barrowclough *et al.,* 2006).

Larsen *et al.* (2007) analyzed partial sequences of *CYTB* from 21 caprimulgid species in eight genera, including three subspecies of *Caprimulgus europeaus*. Their small data set did not support a monophyletic Caprimulgidae if *Eurostopodus* is included,

but there was also no strong support for the latter genus being more closely related to other caprimulgiforms. Corroborating the results of Barrowclough *et al.* (2006), Larsen *et al.* (2007) found evidence for geographically structured clades including an Old World clade and three to four New World clades, but relationships among them were not resolved. Their results also failed to support the split into the two subfamilies (Larsen *et al.,* 2007). The small character sampling raises questions about the validity of their results.

By far the most extensive analysis of the caprimulgids in terms of taxon sampling is that of Han *et al.* (2010). A total of 66 specimens of 55 species were sampled from 14 of the 16 recognized genera. Both mitochondrial (*CYTB*) and nuclear markers (*C-MYC* and *GH*) were amplified and sequenced, with the final alignment of all genes including 4226bp. Both the nuclear markers and concatenated data set supported a monophyletic Caprimulgidae. The most basal lineages consisted of the four species of *Eurostopodus* and the Malagasy *Caprimulgus enarratus*, and the authors placed the latter in a new genus *Gactornis*. The remaining caprimulgids formed a well-supported core clade that is further divided into four major groups having clear geographic patterns. There was an Old World clade containing species of *Caprimulgus* (including the type species *C. europaeus*) as well as *Macrodipteryx*. The three New World lineages comprise a clade of seven genera of primarily South American species (including species of "*Caprimulgus*"), a nighthawk clade (*Chordeiles* with the monotypic *Podager* imbedded inside it), and a mostly North and Central American clade of four genera (again with species of "*Caprimulgus"*). The relationships among these four core clades differed across individual gene trees and concatenated trees. As with previous studies the Caprimulginae and Chordeilinae were not

supported (Han *et al.*, 2010). A summary tree showing the main findings of Barrowclough *et al.* (2006) and Han *et al.* (2010) is depicted in **Figure 1**.

The previous studies outlined above provide a good framework for further analyses of relationships within the family. Despite a significant increase in taxon sampling in the study of Han *et al.* (2010) compared to previous work, the latter was far from complete at the species level. A total of 34 recognized species were not sampled in that study, 24 from the Old World and 10 from the New World (based on the species tally in Holyoak, 2001). Two subspecies of *Antrostomus (="Caprimulgus") vociferus* and two subspecies of *Lurocalis semitorquatus* were included in the study of Han *et al.* (2010), and three subspecies of *Caprimulgus europaeus* in Larsen's study (2007), but there was no further sampling of subspecies or any dense intraspecific sampling (such as from multiple localities in species with large ranges). Moreover, usually only one individual of each species was used for the phylogenetic analyses.

This study presents a molecular phylogeny of the nightjars with an emphasis on the New World taxa. The Old World taxa are principally members of a single radiation with the exception of the most basal lineages of the family (*Eurostopodus, Lyncornis* and *Gactornis*). The focus of this paper is therefore on the members of the three well-defined New World clades found in the studies of Barrowclough *et al.* (2006) and Han *et al.* (2010). The major goals of the current study are to 1) reexamine relationships at the genus/species level within the four core clades of the family, concentrating particularly on relationships among the species within the three New World clades; 2) use genetic evidence to reevaluate the species status of some of the New World taxa, and 3) use the

results from the genetic data to address the current taxonomy and nomenclature of both genera and species of New World nightjars and propose modifications where necessary.

As previous studies have demonstrated the non-monophyly of the genus *Caprimulgus*, any New World taxon placed in *Caprimulgus*, whose taxonomic status has not been officially changed, will be hereafter in this paper called "*Caprimulgus*".

2. METHODS

2.1 TAXON SAMPLING

Dickinson *et al.* (2003) recognized 89 species of caprimulgids in the Howard & Moore checklist, of which 44 are New World. Twenty-five of those New World species contain two or more subspecies giving a total of 101 subspecies. That plus the 19 monotypic species yields 120 named taxa in the New World (Dickinson *et al.*, 2003). Of the 44 traditionally defined species, 41 were sampled in this study. Of the 101 subspecies, 78 were sampled in this study. Three species-level taxa were not sampled due to lack of specimen availability:

- The Cayenne Nightjar ("*Caprimulgus" maculosus*), known only from the unique holotype from French Guiana. Possibly a misidentified "*Caprimulgus" nigrescens* according to Holyoak (2001).
- The Puerto Rican Nightjar ("*Caprimulgus" noctitherus*), a very rare and endangered species found in SW Puerto Rico. Similar in size and appearance to *Antrostomus vociferus*.

- The Jamaican Poorwill (*Siphonorhis americana*), an extremely rare species from Jamaica, last collected in 1859. Presumed to be near extinction if not extinct. Very similar to *Siphonorhis brewsteri* in size and appearance.

The samples included fresh tissue samples from museum collections as well as toe-pads from museum skins when fresh tissue samples were not available. The taxonomic coverage at the subspecies level is therefore about 77%, which is the densest sampling of New World nightjars in any phylogenetic study of the group.

A number of Old World nightjars were also sampled. The eared-nightjars of the genus *Eurostopodus* are considered to be basal within the family Caprimulgidae. However, previous research suggests that the genus is paraphyletic with respect to the remaining nightjar taxa (Han *et al.*, 2010). Of the seven traditionally recognized species of *Eurostopodus*, five were sampled in this study, with the Heinrich's Nightjar (*Eurostopodus diabolicus*) and the Papuan Nightjar (*Eurostopodus papuensis*) not included. Cleere (2010) recognizes nine species of eared-nightjars. He places two of them, *E. macrotis* and *E. temmincki* in a separate genus, *Lyncornis*, and this placement is used in this study. A thorough study of the eared-nightjars incorporating molecular data is needed. The Collared Nightjar (*Gactornis enarratus*) from Madagascar, which has also been placed in a basal position in previous studies was sampled in this study as were a number of Old World species that belong to the strictly Old World monophyletic clade (Barrowclough *et al.*, 2006; Han *et al.*, 2010). A total of 10 species were sampled from that clade (nine *Caprimulgus* and one *Macrodipteryx*). As the goal of this study was to specifically investigate the relationships among the New World taxa, greater taxon sampling within the well-established Old World clade was not necessary. Previous

studies do suggest that, with the exception of the eared-nightjars and *G. enarratus*, all of the Old World taxa constitute a monophyletic group. Finally, to root the whole nightjar tree, a number of species from closely related families were included: the swift *Apus affinis*, the tree-swift *Hemiprocne mystacea*, the hummingbirds *Colibri coruscans* and *Phaethornis griseogularis*, and finally the frogmouth *Podargus strigoides.*

Of the 96 species/subspecies sampled in this study, 57 were available as fresh tissue specimens (as well as all three outgroup taxa), whereas 39 were only available as museum skins, some as old as from the late 1800s. Two monotypic species were added by using *CYTB* sequences downloaded from Genbank including *Eleothreptus candicans* and *Antrostomus salvini*. When available, more than one specimen was sampled for a given taxon, especially if the taxon had a wide distribution. In those cases, specimens from different parts of their range were chosen if possible. Along with the 16 Old World taxa and non-caprimulgid outgroup taxa, the total number of individuals sampled in this study was 210.

2.2 CHARACTER SAMPLING

A DNA sequence dataset was produced by amplifying and sequencing four genetic markers, the two mitochondrial loci NADH dehydrogenase subunit 2 (*ND2*) and cytochrome B (*CYTB*), the nuclear exon recombination activating gene 1 (*RAG-1*) and the nuclear intron 9 from the aconitase gene (*ACO1*). The two mitochondrial markers and the nuclear intron were chosen to target genetic signal at the species level whereas *RAG-1* was chosen to resolve the relatively more basal nodes within the family, specifically among the four main radiations. DNA was amplified from fresh tissue specimens where

possible, but for 79 specimens DNA was extracted from toe-pads of museum skins. *ND2* was the only marker amplified and sequenced from these skin extractions, hence was the only marker sampled for all species (except the two Genbank sequences in which only *CYTB* was sampled). The other three markers were sampled from the fresh tissue specimens (summarized in **Table 1**).

Sequences of *ND2* were obtained for 163 individuals with the final complete sequence being 1041bp long. Additionally, five outgroup sequences were downloaded from GENBANK. For some of the older museum skin specimens, complete sequences were not obtained due to DNA degradation and severe difficulties for amplification. The shortest sequence was less than 300bp, and a number of genes have large gaps in the middle of the sequence, in some cases up to 400bp in length. Twenty-eight individuals have incomplete sequences but only five of those have less than 500bp of available sequence. The total number of individuals in the *ND2* matrix is thus 199 including the out-group taxa.

CYTB was sequenced for 58 specimens, all from fresh tissue. The final complete sequence was 1143bp long. The single codon deletion at positions 1135-1137 seen in *Nyctidromus albicollis* and *Gactornis enarratus* in the study of Han *et al.* (2010) was not encountered in the sequences produced in our study. Additionally, 27 sequences produced by the studies of Han *et al.* (2010) and Larsen *et al.* (2007) were downloaded from GENBANK. Among those were two taxa, *Eleothreptus candicans* and *Antrostomus salvini*, not sequenced in this study, as neither fresh tissue nor museum skins were available. Thus, *CYTB* is the only marker sampled for these two taxa. A total of 85 *CYTB* sequences including outgroups were analyzed in this study.

Intron 9 of *ACO1* was sequenced for 109 individuals from fresh tissue plus a partial sequence was successfully obtained from a museum skin specimen of *Antrostomus ridgwayi* Nelson, 1897, using the same protocol as for the fresh tissue specimens during amplification and sequencing. The final complete sequence was 871bp long but insertion/deletion events are quite common: a 1-base deletion event in all Caprimulgidae except the basal *Eurostopodus mystacalis* and *Gactornis enarratus* at base 136; a 1-base insertion event between bases 211 and 212 in *Caprimulgus pectoralis* and *Caprimulgus poliocephalus*; a 4-base deletion event from base 220 to 223 in *Hydropsalis climacocerca*; a 3-base deletion event from base 261 to 263 in *Gactornis enarratus* and *Podager nacunda*; a 1-base insertion event between bases 327 and 328 in *Nyctiprogne leucopyga*; a 6-base deletion event that all species in both the Nighthawk Clade and the Old World Clade share from base 442 to base 447; a 3-base deletion event in *Macrodipteryx vexillarius* from base 719 to 721; and finally there is a 1-base deletion event at base 819 in the following species: "*Caprimulgus" cayennensis*, "*Caprimulgus" longirostris* (including "*C". l. decussatus*), "*Caprimulgus" maculicaudus*, *Eleothreptus anomalus*, *Hydropsalis climacocerca* and *Hydropsalis torquata*.

RAG-1 was sequenced for 78 individuals, all from fresh tissue. The final complete sequence was 2,873bp long. Eight of the 82 sequences are incomplete. There is a single insertion/deletion event in the *RAG-1* data matrix, a six-base pair deletion event from base 1037 to base 1042 in all ten taxa that were sampled from the Old World clade.

2.3 LABORATORY METHODS

Genomic DNA was extracted from frozen tissue samples using the standard procedure implemented in the DNeasy Tissue Kit (Qiagen, Valencia, California). For the

museum skin specimens, small pieces (approximately 1-2 mm in diameter) of toe-pad skin was cut off, rinsed in sterilized water and extracted via the same process as the tissue samples, with the exception that 30 μl of diluted DTT (dithiothreitol) was added into the sample at the beginning of the extraction process along with the ATL buffer and the proteinase K to aid with the tissue digestion process. To increase the final DNA concentration in the toe-pad extractions, samples were eluded in 100 μl of AE buffer while samples from fresh tissue specimens were eluded in 200 μl.

DNA was amplified via polymerase chain reaction (PCR). General external and internal primers were used for all four genetic markers (**Table 2a**) For the toe-pad samples, multiple internal *ND2* primers had to be designed (**Table 2b)**. Amplification of fresh tissue specimens for *ND2, RAG-1,* and *ACO1 I-9* followed the same step-down PCR procedures. Amplification of fresh tissue specimens for *CYTB* followed a different procedure (listed in **Table 3**). Amplification of toe-pad samples from museum specimens required extensive optimization procedures with independent primer-pairs treated differently, especially annealing temperatures (see **Table 3**).

All PCR products were cleaned using single-step enzymatic cleanup (EXOSAP) which removes unwanted dNTPs and primers from PCR products and cycle sequenced with the same primers as were used in each amplification process using the BigDye Terminator Cycle Sequencing Kit (Applied Biosystems, Foster City, California).
The cycle-sequencing reaction is described in **Table 3**. The cycle sequencing product was cleaned by 70% alcohol precipitation and spun in a centrifuge until the alcohol was removed. 35 μl of de-ionized water were added to each well on the sequencing plate and

the sequences were run on a 3730 Automated DNA Sequencer (Perkin-Elmer, ABI) sequencer.

2.4 DATA ANALYSIS

Sequences were assembled, edited and aligned in Geneious 4.6.5 (Drummond *et al.*, 2010). The sequence matrix for each of the four loci was aligned separately using the Muscle Alignment Feature (Edgar *et al.*, 2004) as implemented in Geneious 4.6.5 with default parameters, and later the four matrices were concatenated. The concatenated data set was partitioned by locus. Additionally the *ND2, CYTB* and *RAG-1* data sets were partitioned by codon position. All data sets were also analyzed in a non-partitioned state. Phylogenetic analyses were performed on all datasets: separate and concatenated.

Maximum Likelihood analyses were performed on the whole data set (210 individuals) as well as the individual partitions in RAxML (Stamatakis *et al.*, 2008) on the open RAxML BlackBox cluster server (http://phylobench.vital-it.ch/raxml-bb/). RAxML incorporates bootstrap analyses for support in their tree-search analyses using their rapid bootstrap (RBS) heuristics. Bootstrap inferences are conducted under the GTR+CAT model of rate heterogeneity, however the final trees are scored under GTR+Γ, which is the standard RAxML tree-search algorithm. To ensure these default settings suited the data, PHYML as implemented in jModelTest (Posada, 2008) was used on all individual locus data-sets to calculate what model of substitution was most suitable for each data-set, with the Aikake Information Criterion used to rank the models based on suitability. According to the results from jModelTest 0.1.1 the best fitting base substitution model for three of the four individual loci data-sets (for *CYTB* it was the

second best behind TIM3+ I + Γ) as well as the concatenated data set is the General Time Reversible model with gamma distributed rate heterogeneity and a proportion of invariant sites (GTR + Γ + I). Thus using the default settings for Maximum Likelihood in RAxML (Stamatakis *et al.*, 2008) is justified.

Bayesian analyses were performed in Beast v1.6.2 (Drummond and Rambaut, 2007) on the whole data set as well as the individual partitions. Base substitution models were chosen for individual loci and the concatenated data set based on the results from the jModelTest analysis. For the coding *ND2, CYTB* and *RAG-1* matrices, the data were partitioned into codon positions. The analysis was run for 15 million generations with tree samples taken every 1000 generations. Stationarity was evaluated in TRACER v1.3 (Rambaut & Drummond, 2007) with the first 20% of trees discarded as burn-in.

Maximum parsimony analyses were performed in TNT (Goloboff *et al.*, 2003) on the non-partitioned concatenated data set only, representing all sampled taxa. The parsimony analysis was performed to verify general topological patterns and was not performed on the individual gene partitions. Traditional heuristic tree searching methods were implemented with TBR branch swapping, as well as sectorial searching, ratcheting and tree fusing. Trees were retrieved by a driven search using 100 initial addition sequences and requiring that the minimum length tree be found a total of 10 times. All characters were equally weighted and non-additive, and gaps were treated as missing data. The results of these searches were subsequently resubmitted to TNT for TBR branch swapping. Support values for nodes were also calculated in TNT through standard bootstrap resampling employing 100 iterations, each subjected to five iterations of

ratcheting and three rounds of tree fusing after an initial five rounds of Wagner tree building.

3. RESULTS

Overall there was a high level of congruence among the results from the various phylogenetic analyses but there were minor differences present. Due to variation in taxon sampling across gene trees, not all topological relationships can be compared directly. The *ND2* and *CYTB* trees (**Figures 2** and **3**) resolve relationships near the tips of the tree with higher confidence than the nuclear trees (**Figures 4** and **5**) whereas the nuclear trees, in particular the *RAG-1* tree (**Figure 4**), better resolve the deeper nodes. In general, the trees resulting from the analysis of all four concatenated markers are the best resolved overall. The tree from the likelihood analysis of the concatenated dataset is depicted in **Figures 6-11**. **Figure 6** demonstrates relationships among major groups whereas **Figures 7-11** show the relationships between species within those groups (Old World taxa, nighthawks, poorwills, South American radiation). **Figure 12** depicts the whole tree from the parsimony analysis of the concatenated dataset.

The basal caprimulgid taxa of the genera *Eurostopodus, Lyncornis* and *Gactornis* are not sampled equally on the individual gene trees. The best sampling is on the ND2 tree (**Figure 2**) in which *Lyncornis macrotis* and *L. temmincki* are placed as the sister-group to all nightjars. However, in the analysis of the concatenated four-marker dataset (**Figure 7**) it is *Eurostopodus* that is the sister, thus which of the two clades is the sister-group to the remaining caprimulgids is not resolved with confidence. *Gactornis enarratus* is strongly supported as the sister-group to all nightjars excluding *Eurostopodus* and *Lyncornis* using the individual markers (*ND2*, *RAG-1* and *ACO1 I9*) (**Figures 2, 4** and **5**) and the concatenated data.

The clade containing the four radiations is strongly supported by all markers and the concatenated data. However, the individual markers do not all resolve the relationships of the four clades and there are clear topological differences among them. The *RAG-1* data are most successful in resolving the relationships (**Figure 4**), placing the South American clade as the sister-group to the other three and the poorwills are the sister to a clade containing the nighthawks and the Old World radiation. This is also the pattern seen on the tree from the analysis of the concatenated data (**Figure 6**). *ND2* is completely unsuccessful in resolving the relationships (**Figure 2**), and although *CYTB* does a better job (**Figure 3**), it is incongruent with the *RAG-1* results as it has a monophyletic New World caprimulgid clade. The topological patterns on the *ACO1 I9* tree (**Figure 5**) are not well resolved but are similar to the patterns seen on the *RAG-1* tree (**Figure 4**).

Placement of individual taxa within the four core radiations is mostly congruent among the four gene trees. The few exceptions usually relate to unresolved placements that are in most cases resolved in the analysis of the concatenated data. It is usually the same taxa that are not well-resolved, for example "*Caprimulgus" parvulus* and "*Caprimulgus" whitelyi,* which are members of the large *Hydropsalis*-radiation in the South American clade, as well as *Siphonorhis brewsteri,* the basal species in the Poorwill clade whose position is less resolved by the mtDNA markers (**Figures 2-3**) compared to *RAG-1* (**Figure 4**).

Generally the results from the total-evidence concatenated data set provide a robust phylogeny for the three major radiations of New World nightjars and by far the most taxonomically complete phylogenetic tree available for this group. Thus, the

concatenated tree will be used to evaluate and discuss the phylogenetic relationships and the taxonomic status of each genus, species and subspecies study in the subsequent Discussion. The individual gene trees will be referenced when there is clear incongruence among them that might cause lack of resolution in the concatenated tree and when important diagnostic characters are seen in the individual genes.

4. DISCUSSION

4.1 MAJOR NIGHTJAR LINEAGES

The analysis presented here clearly support the findings of previous studies (Barrowclough *et al.*, 2006; Larsen *et al.*, 2007; Han *et al.*, 2010). The division of the family into the subfamilies Chordeilinae and Caprimulginae is not supported and the basal lineages in all individual gene trees and the concatenated tree are members of the genera *Eurostopodus* and *Lyncornis* (previously *Eurostopodus*) as well as a single species from Madagascar, *Gactornis enarratus*. The recognition of *Lyncornis* as a separate genus is supported, as the "old" *Eurostopodus* is not monophyletic. *Lyncornis* contains the Southeast Asian *L. macrotis* and its relative *L. temmincki*. *Lyncornis macrotis* is polytypic with five subspecies distributed from India, Myanmar, Thailand, Cambodia and Vietnam to the Philippines and Sulawesi (Holyoak, 2001; Dickinson *et al.*, 2003). It is highly likely that some of these subspecies represent valid species but that remains unstudied. *Lyncornis temmincki* is allopatric to *L. macrotis* and is found on Sumatra and Borneo and the southernmost part of the Malaya Peninsula. *Eurostopodus* includes species that breed in Australia and Papua New Guinea: *Eurostopodus archboldi*, *E. argus*, and *E. mystacalis* are the three species sampled in this study but Cleere (2010) recognizes four more species that breed in Papua New Guinea, Solomon Islands and New Caledonia. They are likely to belong to this clade as well. *Eurostopodus* is the sister to the remaining nightjars (**Figure 7**), which is also seen in the study of Han *et al.* (2010), but in both studies the support for this topology is low. Improved character and taxon sampling is required to clarify the exact placement of *Eurostopodus* and *Lyncornis*. The

position of *Gactornis enarratus* as a single-species lineage sister to the core nightjar clade, first seen in Han *et al.* (2010) is supported in this study with confidence (**Figure 7**).

The remainder of nightjar diversity can be split into four major radiations that seemingly diversified over a narrow window of time. These four radiations have been consistently seen in all molecular phylogenetic studies of nightjars (Barrowclough *et al.*, 2006; Larsen *et al.*, 2007; Han *et al.*, 2010) and the results of this study are no different. The four core clades are:

A) **The Nighthawk Clade** – the genera *Chordeiles* and *Podager*. North, Central and South America (see **Figure 8**).

B) **The Poorwill Clade** – the genera *Antrostomus* (previously *Caprimulgus*), *Nyctiphrynus*, *Phalaenoptilus,* and *Siphonorhis*. Predominantly North and Central America and the Caribbean with a few South American taxa (see **Figure 9**).

C) **The South American Clade (abbr. SA Clade)** – the genera *Eleothreptus*, *Hydropsalis, Lurocalis*, *Macropsalis*, *Nyctidromus, Nyctiprogne,* and *Uropsalis* as well as species that were previously placed in the genus *Caprimulgus* but are now subsumed in *Nyctidromus* and *Hydropsalis* (see **Figures 10** and **11**)

D) **The Old World Clade**. The genera *Caprimulgus* and *Macrodipteryx*. Africa, Europe, Middle East, South and Southeast Asia (see **Figure 7**).

It has proven difficult to resolve with confidence the topological relationships among these four core clades, and data sets from different studies are not always

congruent with one another. The most robust relationship seems to be that the Nighthawk Clade and the Old World Clade are sister-groups. This is supported by the *RAG-1* data of Barrowclough *et al.* (2006) as well as the combined three-marker data set of Han *et al.* (2010). This is also the case with the combined data set in this study in which this relationship receives high bootstrap support (**Figure 7**). There is even a deletion event in the *ACO1-I9* data set that is unique to these two clades.

The *RAG-1* data strongly support that the SA-Clade is the sister-group to the other three (**Figure 4**) and this topological pattern is also seen on the concatenated tree, albeit with no bootstrap support (**Figure 7**). This is the same topology seen in the tree of Barrowclough *et al.* (2006), which is unsurprising as their tree is based on *RAG-1* sequences only. The concatenated ML tree in the study of Han *et al.* (2010) places the Poorwill Clade as the most basal of the four but this pattern is without bootstrap support. Higher sampling of nuclear markers is needed to resolve these relationships with high confidence. Regardless of which clade is the sister to the remainder, the Poorwill Clade or the SA Clade, it is evident that there are three independent radiation events in the New World and that the Old World seems to have been re-colonized from the New World unless the three New World radiations were all the result of independent colonization events.

4.2 RELATIONSHIPS WITHIN THE NIGHTHAWK CLADE

Within the highly supported Nighthawk clade (see **Figure 8**), the relationships among the traditionally defined species are consistent with previous studies (Barrowclough 2006, Han 2010), but the mitochondrial data (**Figures 2-3**) suggest that

some of the traditionally defined species can be split into two or more phylogenetic species.

The *Nacunda* Nighthawk (*Podager nacunda*) and the Least Nighthawk (*Chordeiles pusillus*) are sister taxa with very strong support and are the sister-group to the other nighthawks (**Figure 8**). This implies that the genus *Chordeiles* is paraphyletic. As *Chordeiles minor* is the type for the genus *Chordeiles* (Oberholser, 1914), *C. pusillus* can be moved into the genus *Podager.*

The two subspecies of *Podager nacunda* show some genetic separation in the mitochondrial data (**Figures 2-3**), which is unsurprising as their allopatric ranges are roughly split by the Amazon River. However, the branches leading to these two sub-clades are extremely short. Morphological differences between the two are present, with males of the nominate form *P. n. nacunda* having a darker crown and breast with black feathers more prominent than *Podager nacunda minor*. A more detailed investigation of the genetic structure and morphological variation in this species is needed.

Only three of the six recognized subspecies (Dickinson *et al.*, 2003) of *Podager pusillus* are sampled in this study. The overall range of *P. pusillus* in South America is not well defined and fragmented and mostly consists of relatively small areas each inhabited by a single subspecies. The individuals sampled in this study belong to the subspecies *Podager pusillus esmereldae* and *P. p. septentrionalis* which have adjoining ranges in Northern South America and *P. p. novaesi* which has a small range in the state of Maranhaõ, Brazil (Holyoak, 2001). The *ND2* data indicate that *P. p. novaesi* is separated from the other two subspecies (**Figure 2 – as *Chordeiles pusillus***). *P. p. novaesi* is morphologically distinct from other subspecies of *P. pusillus*, as it has distinct

brick-red and light-brown colored back-feathers. *P. p. esmereldae* and *P. p. septentrionalis* are very similar in their plumage patterns, although *P. p. esmereldae* has a larger white throat-patch and is also the largest of all the subspecies. *Podager pusillus saturatus*, which was not sampled, has considerably darker plumage than the other subspecies. Intraspecific diversity within this species should be studied further with all subspecies sampled.

The remaining nighthawk species all belong to the genus *Chordeiles* and they form a monophyletic clade (**Figure 8**). There are two main species-groups. One contains the Sand-colored Nighthawk (*Chordeiles rupestris*), a monotypic species with a continuous range in the Amazon rainforest (Holyoak, 2001 and the Lesser Nighthawk (*Chordeiles acutipennis*) which is polytypic with seven subspecies distributed throughout a large range extending from SE United States and Northern Mexico south to coastal Peru as well as Brazil south of the Amazon basin (Holyoak, 2001; Dickinson *et al.*, 2003). Both the ND2 (**Figure 2**) and ACO1 I9 (**Figure 5**) indicate that *Chordeiles acutipennis* should be split into two phylo-species. There is over 2% divergence in the ND2 sequences (14 homologous substitution events) that separate individuals of the northernmost subspecies *C. a. texensis* from other subspecies of *C. acutipennis* and they are placed in a strongly supported clade on the concatenated tree (**Figure 8)**. Individuals of *C. a. texensis* are noticeably larger in size and have a lighter plumage than most other subspecies of *C. acutipennis*. It is therefore recommended that *C. a. texensis* be elevated to full species status as *Chordeiles texensis*.

Among the remaining six subspecies of *Chordeiles acutipennis*, two Central American subspecies *Chordeiles acutipennis micromeris* and *C. a. littoralis* are distinct

from the remaining South American subspecies on the concatenated tree (**Figure 2**), but the bootstrap support for this is rather low and not all individuals are placed with confidence in this separate clade. These two subspecies are both morphologically different from the other four (but not as much with respect to each other), and are actually more similar to *C. texensis*, as they are larger in size and with lighter-colored plumage than the nominate form C. *a. acutipennis* (with by far the largest range of all the subspecies throughout northern South America), *C. a. aequatorialis* (in Ecuador), and *C. a. exilis* (in coastal Peru). Both *C. a. aequatorialis* and *C. a. exilis* are noticeably lighter in plumage than the nominate form but there are no strong genetic differences among them. Better sampling of individuals (including missing subspecies *C. a. crissalis*) and increased sequence data should clarify whether any of these six subspecies represent distinct taxa, as was the case with *C. texensis*. Thus, all six subspecies remain in *Chordeiles acutipennis.*

The third species-group contains the Common Nighthawk (*Chordeiles*) and the Antillean Nighthawk (*Chordeiles gundlachii*). *Chordeiles minor* is the only nighthawk species that breeds predominantly in North America, with its breeding range covering most of the continent from Canada to Panama. There are nine described subspecies, but with the exception of *C. m. panamensis* in Panama, their distributional ranges are not clearly separated from one another (Dickinson *et al.*, 2003). In particular, the seven subspecies breeding in North America lack clear range limits in that numerous hybrid zones have been suggested based on observations of morphology (Selander, 1954: Holyoak, 2001). These zones have not been tested, as no studies on the genetic diversity of *C. minor* are currently available. In addition to having a large, homogeneous breeding

range, *C. minor* is a long-distance migrant that winters in South American continent. Information about wintering localities and breeding site-fidelity are scarce. It is known that migrants cross the Gulf of Mexico as well as Central America but the final destinations of those two migration pathways are not well understood since the wintering range of the species extends through a large part of South America (summarized in Holyoak, 2001). The results from this study show that there is little to no genetic structure within the species and what there is does not follow subspecies lines (eight of the nine subspecies were sampled including *C. m. panamensis*) or even clear biogeographic patterns.

In the two markers that were best sampled for *C. minor*, *ND2* and *ACO1-I9*, there are 12 polymorphic sites, 10 in *ND2* and two in *ACO1-I9*. However, how these polymorphisms are distributed among the sampled individuals does not follow any particular pattern resulting in a basal polytomy in both the individual gene trees (**Figures 2-5**) and the concatenated tree (**Figure 8**). This lack of genetic diversity suggests either a recent expansion of its range or that gene flow is high between populations. In this study, sampling was too sparse to test for the presence and directionality of gene flow in the species. The morphology of the nine subspecies is variable and not always distinct enough to separate them, especially between taxa with adjacent distributional ranges. The characters that seem to be most variable are size and plumage color, in particular darkness/paleness of the plumage.

Finally, the Antillean Nighthawk (*Chordeiles gundlachii*) is found in the Northern Caribbean. It is closely related to *C. minor*, and was even formerly considered to be conspecific with it (Peters, 1940; Meyer de Schauensee, 1970). The two species are very

similar in their morphology, and the slight plumage differences that separate them are not consistently present. Two individuals of *C. gundlachii* were sampled in this study, one from Florida and the other from the Bahamas, but the results from the two individuals are strikingly different. The nuclear data does not demonstrate that *C. gundlachii* is a distinct species as it falls within *Chordeiles minor* (**Figures 4-5**). The *ND2* data tell the same story about the Florida individual thus suggesting it may be a wrongly identified *C. minor chapmani* (**Figure 2**). But, the *ND2* sequence of the individual from the Bahamas is different from the Florida individual (3.5% divergent) as well as all the other *C. minor* individuals such that it is placed as their sister taxon. This is also the result on the concatenated tree (**Figure 8**). Therefore the data suggest that the status of *C. gundlachii* will remain unclear until additional sampling is undertaken, especially from other parts of its range (such as Cuba or Jamaica). No changes in its taxonomy are suggested at this time.

4.3 RELATIONSHIPS WITHIN THE POORWILL CLADE

The second of the three major nightjar radiations in the New World contains a collection of mostly North and Central American species of which many are known as poorwills. Based on traditional taxonomy, there are seventeen species in four genera, *Siphonorhis, Nyctiphrynus, Phalaenoptilus* and *Antrostomus*. There are only four species that breed on the South American continent, a surprisingly low number. On the other hand, of the three nightjar radiations, the poorwills are by far the most successful group to colonize the islands of the Caribbean with species found on all of the Greater Antilles (Cuba, Hispaniola, Puerto Rico and Jamaica) (Holyoak, 2001; Dickinson *et al.*, 2003).

4.3.1 BASAL POORWILL GENERA

The genus S*iphonorhis* is the sister to the other poorwill genera (see **Figure 9**) with strong support. This is congruent with the results of Han *et al.* (2010). In both studies, only the Least Poorwill (*Siphonorhis brewsteri*) was sampled. It is a monotypic species, breeding on Hispaniola. The Jamaican Poorwill (*Siphonorhis americana*) which by all accounts is extinct (it hasn't been collected since 1859, and sighting reports since then are few and unconfirmed), is very similar morphologically to *S. brewsteri*, and thus is likely to be its sister species (Holyoak, 2001).

The genus *Nyctiphrynus* consists of four traditionally described species (*N. mcleodii*, *N. ocellatus*, *N. rosenbergi,* and *N. yucatanicus*) and is the strongly supported sister-group of the clade containing *Antrostomus* and *Phalaenoptilus* (**Figure 9**). The Chocó Poorwill (*Nyctiphrynus rosenbergi*) is the sister species of the remaining *Nyctiphrynus* species, which is in agreement with the results of Han *et al.* (2010). Among the three remaining species*, N. mcleodii* is the sister of *N. ocellatus* and *N. yucatanicus*. This is also congruent with the results of Han *et al.* (2010), and they found an indel in their nuclear data that supported this relationship (Han *et al.*, 2010). These are surprising findings as *N. yucatanicus* and *N. mcleodii* are both found in Mexico whereas *N. ocellatus* is found isolated in SE Brazil, Bolivia and Peru (although a little known subspecies *N. o. lautus* has been found in Nicaragua) (Holyoak, 2001; Dickinson *et al.*, 2003).

The Common Poorwill (*Phalaenoptilus nuttallii*) is the only member of its genus and is placed as the sister taxon to a large clade containing the genus *Antrostomus* (**Figure 9**). This result is congruent with the results of Han *et al.* (2010) and

Barrowclough *et al.* (2006). Its intraspecific diversity is of potential interest, as there are five traditionally recognized subspecies (Dickinson *et al.*, 2003) and their distributions coincide with well known biogeographic areas in the SW United States and Northern Mexico. Five of the six subspecies were sampled in this study with *ND2* sequenced for all individuals. The *ND2* sequences are nearly identical with less than 6 polymorphic sites, and the only attainable topological pattern that receives medium support on both the ND2 tree and the concatenated tree (**Figures 2** and **9**) is that the subspecies *P. n. dickey* is distinct from the remaining individuals sampled (0.7% divergence in *ND2*). This subspecies is found on the Southern half of the Baja Peninsula, south of the well-known biogeographical boundary at 30ºN (Lindell *et al.*, 2006). Only one individual of *P. n. dickeyi* was sampled and the *ND2* sequence is the only data available for this individual. *P. n. dickey* is not morphologically distinct and in fact the morphology of all the subspecies is similar. *P. n. californicus* has a slightly darker plumage than the rest (see also Ridgway, 1914) and *P. n. huyei* a slightly lighter plumage but the subspecies are not easily diagnosable from one another (see Dickey, 1928). Thus, the results suggest that *Phalaenoptilus nuttallii* is a single species.

4.3.2 THE *ANTROSTOMUS* CLADE

The remaining diversity of the poorwills is contained in a strongly monophyletic clade that includes ten traditionally defined species (of which nine are sampled in this study). All were previously assigned to *Caprimulgus* but have recently been moved into the genus *Antrostomus* (Han *et al.*, 2010; Chesser *et al.*, 2012). *Antrostomus* can be split into two species-groups (**Figure 9**), the Whip-poor-will (*Antrostomus vociferus*) and its

allies, on the one hand, and the Chuck-will's-widow (*Antrostomus carolinensis*) and its allies, on the other. The latter species-group includes six traditionally recognized species: *Antrostomus badius, A. carolinensis, A. cubanensis, A. rufus, A. salvini* and *A. seriocaudatus*.

Within the *carolinensis*-species group the Rufous Nightjar (*Antrostomus rufus*) is one of two *Antrostomus* species whose distribution is limited to the South American continent where its five subspecies are widespread (Dickinson *et al.*, 2003). Four are sampled in this study, the nominate *Antrostomus rufus rufus*, *A. r. rutilus*, *A. r. minimus*, and *A. r. otiosus*. Holyoak (2001) recognized a sixth subspecies, *A. r. noctivigulus*, which is also sampled here. *Antrostomus rufus rufus* is found in northeastern Brazil towards the southern tributaries of the Amazon, as well as in the Guianas but *A. r. rutilus* replaces it in southeastern Brazil. The remaining subspecies have poorly delimited distributions and are mostly known from sporadic point localities in Colombia, Panama, Venezuela, Amazonian Brazil as well as some of the southernmost Lesser Antilles (Holyoak, 2001; Dickinson *et al.*, 2003). The only subspecies missing in the study is *A. r. saltarius* from Argentina.

The results of this study indicate that *Antrostomus rufus* is split into at least two independent lineages (**Figure 9**). One includes individuals of the subspecies *minimus* and *otiosus* and the other individuals of *rufus*, *rutilus* and *noctivigulus*. These genetic results are only based on the *ND2* sequences, as the majority of the specimens sampled were museum skins. There is about 2% divergence between these two lineages in the *ND2* sequence. This result is consistent with the observations of Wetmore & Phelps (1953), who recognized *otiosus* as a separate species. However, Robbins and Parker (1997)

suggested plumage and vocal differences are not distinct enough to justify the elevation of *otiosus* to full species status. A taxonomic change is not suggested for *A. rufus* based on the limited results in this study, but a more rigorous test of species limits is suggested with more sampling of individuals and molecular markers as well as a closer look at their morphology. Too few museum skins were available to allow for a detailed comparison of morphology in this study.

The sister taxa of *Antrostomus rufus* are the Chuck-will's Widow (*Antrostomus carolinensis*) and the Greater Antillean Nightjar (*Antrostomus cubanensis*). *A. cubanensis* and *A. carolinensis* are sister-taxa on the concatenated tree but without bootstrap support (**Figure 9**). According to Holyoak (2001) and Dickinson *et al.* (2003) there are three subspecies of *A. cubanensis*: *cubanensis* which breeds on Cuba, *ekmani* on Hispaniola, and *insulaepinorum* on Isla de la Juventud south of Cuba. Cleere (2010) elevated two of these subspecies to full species status, naming them Cuban Nightjar (*A. cubanensis*) and Hispaniolan Nightjar (*A. ekmani*) respectively. All three are similar in their morphology, with slight differences in plumage patterns. Song differences have been noted (Garrido & Reynard, 1994) and due to their separated ranges on large islands it is possible that they are genetically distinct and might be separate phylo-species. Unfortunately, these species are poorly sampled in this study with only old museum-skins available. Due to the highly degraded state of the DNA extracted from toe pads of these skins, only a fraction of *ND2* was sequenced and just from one of the two subspecies (*ekmani)*. Despite the low amount of DNA sequence, this individual is placed in a clade with *A. carolinensis* and *A. rufus* with moderate bootstrap support (low posterior probability values however) but the relationships among the three are not resolved on the concatenated tree (**Figure 9**).

The Chuck-will's Widow (*Antrostomus carolinensis*) is one of the larger nightjars and breeds in the southeastern United States from Texas to Florida and north to southern New England. It is also a long-distance migrant that winters in Central America as well as the most northwestern tip of South America (Holyoak, 2001; Dickinson *et al.*, 2003). It is monotypic and there is no indication of strong genetic structure within its geographic range.

Like the Rufous Nightjar (*Antrostomus rufus*), the Silky-tailed Nightjar (*Antrostomus seriocaudatus*) is endemic to South America where it breeds in lowland forests in Brazil, Bolivia, Paraguay and Northern Argentina. Its sister species is the Yucatan Nightjar (*Antrostomus badius*) (**Figure 9**). These two species thus breed far away from one another as *A. badius* breeds in the Yucatan Peninsula of Mexico (Holyoak, 2001; Dickinson *et al.*, 2003). The Tawny-collared Nightjar (*Antrostomus salvini*) is similar in morphology to *A. badius* and also breeds in Eastern Mexico (Gulf of Mexico excluding the Yucatan). In the study of Han *et al.* (2010), *Antrostomus salvini* was sampled whereas *A. badius* was not, and they found *A. salvini* to be the sister species to *A. seriocaudatus.* A tissue or skin specimen of *A. salvini* was not sampled in this study but the *CYTB* sequence produced by Han *et al.* (2010) was downloaded from Genbank and added to the dataset. Instead of being placed with *A. badius* and *A. seriocaudatus* in the concatenated dataset as was expected, *A. salvini* was found to be the sister taxon to the *A. carolinensis*-species group as a whole (**Figure 9**). As there is only *ND2* available for *A. badius*, there was no overlapping data with *A. salvini* and relationships at the base of the *carolinensis*-species group are poorly supported. It is possible that *A. salvini, A.*

badius and *A. seriocaudatus* all belong to a single clade but this needs to be verified by additional data.

The two individuals of *Antrostomus seriocaudatus* sampled in this study represent the two described subspecies. *A. s. seriocaudatus* breeds in the Atlantic Forest of south-eastern Brazil as well as into Paraguay and north-eastern Argentina but *A. s. mengeli* has a disjunct breeding distribution in northern Brazil as well as eastern Peru and north-western Bolivia (Holyoak, 2001; Dickinson *et al.*, 2003). The sampling does not enable evaluation of whether the two are distinct phylo-species, which might be the case since their vocalizations are said to be distinct (Hardy & Straneck, 1989).

The *vociferus*-species group contains the Whip-poor-will (*Antrostomus vociferus*) and its allies. The Whip-poor-will has a disjunct breeding distribution, with one subspecies, the nominate *vociferus* breeding in Eastern United States and sporadically in south-Eastern Canada while the remaining five subspecies (*arizonae*, *setosus*, *oaxaceae*, *chiapensis* and *vermiculatus*) breed in a broadly linear set of parapatric ranges from south-western US through Mexico and into Guatemala and Honduras (Holyoak, 2001; Dickinson *et al.*, 2003). The nominate form differs from the other subspecies in its vocalizations (Davis, 1972) whereas the morphology is similar among all the subspecies. In a recent supplement to the American Ornithologists' Union *Check-list of North American Birds*, the nominate form was recognized as a separate species *Antrostomus vociferus* keeping the common name Whip-poor-will, and the remaining subspecies were pooled into a single species the Mexican Whip-poor-will (*Antrostomus arizonae*) (Chesser *et al.*, 2012).

The results in this study are in agreement with these recent taxonomic changes. Both mitochondrial and nuclear markers support that the traditional Whip-poor-will is in fact two phylo-species (**Figure 9**) with the divergence being over 5% in the *ND2* data set (**Figure 2**). This is also fully congruent with the results of Han *et al.* (2010). There is no strong evidence for further genetic structuring among the subspecies that are now within *Antrostomus arizonae* although two of them (*setosus* and *vermiculatus*) were not included in this study. There is an indication of genetic structure within the nominate *A. vociferus* among individuals from different parts of its range in eastern USA in the *ND2* (**Figure 2**) and *ACO1* data (**Figure 5**), which should be investigated with more data.

The sister species to the *Antrostomus vociferus*/*A. arizonae* clade is the Dusky Nightjar (*Antrostomus saturatus*) (**Figure 9**), also known as the Dusky Whip-poor-will (Cleere, 2010). It is a rather secretive, medium-sized nightjar that is only found in the montane forests of Costa Rica and Western Panama. It is similar to the other Whip-poor-wills in size and general morphology, with a slightly more dark plumage (Holyoak, 2001).

One species that is not sampled in this study (due to the paucity of available specimens) but which is likely to be placed in the vicinity of *Antrostomus vociferus* and the other Whip-poor-wills is the Puerto Rican Nightjar (*Antrostomus noctitherus*), also known as the Puerto Rican Whip-poor-will (Cleere, 2010). It is a critically endangered species with a very small range in southeastern Puerto Rico. It has previously been considered a subspecies of *A. vociferus* (Peters, 1940) although its vocalizations are considerably different (Reynard, 1962). It is very similar in morphology to *A. vociferus* and *A. arizonae*.

The final species in the poorwill clade is the Buff-collared Nightjar (*Antrostomus ridgwayi*). Like many of the other species in the clade it breeds in Mexico and Central America (Holyoak, 2001; Dickinson *et al.*, 2003). It is predominantly found in arid woodland and scrubland type habitats. Its placement within the *Antrostomus*-clade is poorly resolved and is incongruent among different data sets (**Figures 2-5, 9**). It is not placed within either of the two species-groups (*carolinensis*-group and *vociferus*-group) but how the three are related is unclear. The results of Han *et al.* (2010) strongly place it as the sister species to the *carolinensis*-group but in this study is it either placed as the sister species to the *vociferus*-group (**Figure 9**) or outside both those groups (**Figure 12**), in each case with low bootstrap support. There are two recognized subspecies of *A. ridgwayi*, the nominate form that breeds in western Mexico and *A. r. troglodytes* that breeds in Guatemala, Honduras and Nicaragua (Dickinson *et al.*, 2003). The two individuals sampled here represent these two subspecies.

4.4 RELATIONSHIPS WITHIN THE SOUTH AMERICAN CLADE

The largest of the three New World core clades has its diversity almost entirely limited to South America, hence it is termed the South American (SA) Clade (**Figures 10-11**). Only one taxon, *Nyctidromus merrilli,* extends its range as far north as the border of Mexico and the USA, while a few other species extend their range into the southern part of Central America. A total of 21 biological species belong to this clade in eight genera (Holyoak, 2001; Dickinson *et al.*, 2003). Intraspecific diversity is high within many of the species, in particular the ones that have large ranges. In this study, 29

phylogenetic species are identified within this clade and numerous species are moved into different genera.

There are four strongly supported lineages at the base of the SA clade. Three represent single genera: *Lurocalis*, *Nyctiprogne* and *Nyctidromus* (**Figure 10**). A fourth clade, the *Hydropsalis* clade, includes the remaining five genera (*Eleothreptus, Hydropsalis, Macropsalis, Uropsalis* and taxa previously assigned to "*Caprimulgus*") (**Figure 11**). Relationships among these four groups are not resolved on the concatenated tree where there is a polytomy at the base of the SA clade (**Figure 10**) because of incongruence among the individual gene trees. The *RAG-1* data place *Lurocalis* as the sister-group to the other three (**Figure 4**), but on the *ND2* and *ACO1 I9* trees (**Figures 2** and **5**), *Nyctiprogne* is the basal group. *Nyctidromus* is the sister-group to the *Hydropsalis*-clade on the *ND2* tree with low support while *RAG-1* and *ACO1 I9* fail to resolve this relationship. Relationships within these four clades are for the most part much better resolved.

4.4.1 *NYCTIPROGNE*

The species in *Nyctiprogne* and *Lurocali*s are commonly called nighthawks and have been placed in the subfamily Chordeilinae with the other nighthawk genera as they lack rectal bristles and have 13 secondaries (*Nyctiprogne* may only have 12 – see Ridgway, 1914) as do members of *Chordeiles*. As the results shown here (see also Han *et al.* (2010) and Barrowclough *et al.* (2006)), indicate that the subfamily Chordeilinae is a polyphyletic assemblage and that *Lurocalis* and *Nyctiprogne* belong in the SA Clade (**Figure 10**).

Traditionally there is only one described species of *Nyctiprogne*, the Band-tailed Nighthawk (*Nyctiprogne leucopyga*). The Bahian Nighthawk on the genus *Chordeiles* (as *C. vielliardi* - see Holyoak, 2001 & Cleere and Nurney, 1998) has recently been placed in the genus *Nyctiprogne* (*Nyctiprogne vielliardi*) (Whitney *et al.*, 2003; Cleere, 2010) on the basis of morphology, but this species is only known from a handful of specimens. This study provides the first genetic evidence confirming this hypothesis, as an individual of *Chordeiles vielliardi* is placed with high support within *Nyctiprogne* (**Figure 10**).

The results also suggest that the species *Nyctiprogne leucopyga* should be split into two unrelated phylo-species, as it is paraphyletic with respect to *N. vielliardi* (**Figure 10**). Traditionally, *Nyctiprogne leucopyga* is polytypic with five subspecies recognized (Holyoak, 2001; Dickinson *et al.*, 2003). Three of these subspecies have small ranges in Venezuela in close vicinity to one another: *pallida* along the lower banks of the Orinoco River, *exigua* on the upper right bank of the Orinoco and *latifascia* in the far south of Venezuela close to the source of the Rio Negro. The remaining two subspecies have much larger ranges, the nominate form *leucopyga* in French Guiana and throughout the Amazon basin in Brazil and *majuscula* in the Mato Grosso of Brazil and into southeastern Bolivia (Dickinson *et al.*, 2003). Three of the five subspecies were sampled in this study; *latifascia, leucopyga* and *pallida*.

The results from this study show that the subspecies *Nyctiprogne leucopyga latifascia* forms a distinct clade that is the sister-group to *N. vielliardi* and the two remaining subspecies of *N. leucopyga* (*leucopyga* and *majuscula*) (**Figure 10**). There is over 8% divergence in the ND2 sequences of the two *N. leucopyga* groups (**Figure 2**),

whereas the divergence between *N. vielliardi* and the *leucopyga/majuscula* clade is only 2.6 %. There is also 7% divergence between the two groups in the *CYTB* sequence, while it is only 0.7% in the *ACO1 I9* sequence. Only *ND2* is available for *N. vielliardi*.

It has been suspected that *N. leucopyga* may not be a single species and in particular that *N. l. latifascia* may be a separate species (Friedmann, 1945). The morphological diversity within *Nyctiprogne* is very limited, with subtle plumage differences among the recognized subspecies, but *latifascia* is distinct from the rest, being overall darker in color and less vermiculated (Friedmann, 1945). Differences in vocalizations have also been observed (Naka, 2012).

Based on the strong genetic evidence, as well as the morphological and vocal traits, *latifascia* should be elevated to full species status as *Nyctiprogne latifascia* (Friedmann, 1945). The status of *N. leucopyga exigua* and *N. l. pallida* remains uncertain. Based on their distribution in Venezuela, it is possible that they are closely related to *N. latifascia,* in particular *N. l. exigua*, whose range is parapatric to *N. latifascia* in southern Venezuela. However, the morphology of both *exigua* and *pallida* is more similar to the other *leucopyga* subspecies, *leucopyga* and *majuscula*, than it is to *latifascia.* Thus, their status remains uncertain for now.

4.4.2 *LUROCALIS*

Two species of the genus *Lurocalis* are recognized (Dickinson *et al.*, 2003): the Short-tailed Nighthawk (*Lurocalis semitorquatus*) and the Rufous-bellied Nighthawk (*Lurocalis rufiventris*). The genus *Lurocalis* is strongly monophyletic as indicated by the

genetic results (**Figure 10**), and it is further characterized by the morphological trait of having a short, squared tail and a short tarsus that is partially feathered on the front (Holyoak, 2001). The reciprocal monophyly of the two distinct species is supported strongly by the two mitochondrial loci and *RAG-1* but not by *ACO1* (**Figures 2-4**). The two species have been grouped together as a single species in the past (i.e. Peters 1940, Sibley & Monroe, 1990) but the evidence here strongly suggests the presence of separate species.

Lurocalis rufiventris is monotypic and breeds in montane forests of the Northern Andes from Venezuela through Colombia, Ecuador, Peru and Bolivia (Holyoak, 2001). Its total distributional range is not well defined and could be less fragmented than locality reports indicate. *Lurocalis semitorquatus* on the other hand is polytypic with five subspecies (Holyoak, 2001; Dickinson *et al.*, 2003). The geographic ranges of these subspecies are not well known in detail. There are two Central American subspecies, *stonei* in Guatemala and Honduras, and *noctivagus* in Panama and Costa Rica. *L s. schaeferi* is only found in lower subtropical zones of the Rancho Grande region in Venezuela, and the nominate form *semitorquatus* is known from numerous, but scattered localities ranging from Northern Colombia and Venezuela to the Guianas and extreme NW Brazil. Finally, *L. s. nattereri* has by far the largest range, in Brazil south of the Amazon all the way south to Paraguay and northern Argentina (Holyoak, 2001; Dickinson *et al.*, 2003). In this study, three of the five subspecies were sampled, with *noctivagus* and *schaeferi* missing. There is some genetic structure within both *ND2* and *CYTB* but it is not congruent (**Figures 2-3**) and has no support on the concatenated tree (**Figure 10**).

4.4.3 *NYCTIDROMUS*

The third main group within the SA Clade contains the Pauraque (*Nyctidromus albicollis*), one of the most widespread and better known of the New World nightjars, and its relatives. Three of the nightjar species in this group are traditionally placed in the genus "*Caprimulgus"*: the Scrub Nightjar ("*Caprimulgus" anthonyi*), the Pygmy Nightjar ("*Caprimulgus" hirundinaceus*) and the Blackish Nightjar ("*Caprimulgus" nigrescens*). This study is the first on nightjar relationships that includes "*C". hirundinaceus*. Han *et al.* (2010) included the other two, which they placed with *N. albicollis* whereas Barrowclough *et al.* (2006) only included *N. albicollis*. In the phylogeny of Han *et al.* (2010), *albicollis* and *anthonyi* are sister-taxa and *nigrescens* is the sister to them. The results presented here support a sister relationship between *hirundinaceus* and *nigrescens* (**Figure 10**) and these, in turn, are sister to *anthonyi* and *albicollis* (which is further split into three species, see below). The placement of *hirundinaceus* is only supported by *ND2* as it is the only marker sampled for the species, but the support is robust (**Figure 2**). As all three species require a new genus name instead of *Caprimulgus*, the simplest solution is to move them to *Nyctidromus*.

The Scrub Nightjar (*Nyctidromus anthonyi*) is a monotypic species with a limited breeding distribution in the arid lowlands of Ecuador and Peru. The Blackish Nightjar *(Nyctidromus nigrescens*) likewise is monotypic and is one of the few nightjar species that can be described as a true Amazon species, with a relatively uniform distribution throughout the lowland tropical rainforests of the Amazon basin (Holyoak, 2001;

Dickinson *et al.*, 2003). Four individuals of *nigrescens* were sampled from different parts of its range but little genetic structure was seen (**Figure 10**).

The little-known Pygmy Nightjar (*Nyctidromus hirundinaceus*) is polytypic with three subspecies (Dickinson *et al.*, 2003): *hirundinaceus*, *ceare* and *vielliardi*, but only a single specimen each of the latter two was sampled. The distributional ranges of the subspecies are not well established and morphological diversity is poorly documented. The species is endemic to the caatinga shrubland in Eastern Brazil (Stotz *et al.*, 1996; Holyoak, 2001).

The Pauraque (*Nyctidromus albicollis*) is, on the other hand, well-known and well represented in museum collections. According to Holyoak (2001) there are six recognized subspecies of *N. albicollis*. Their combined range covers a large area from the southern United States to southern Brazil. Three subspecies are found in Mexico, *merrilli* in NE Mexico and SW Texas, *yucatanensis* along the western coast and in the Yucatan peninsula, and *insularis,* which is only found on the Tres Marias Islands off the western coast. The nominate form, *albicollis* has by far the largest range extending from Guatemala into South America through Colombia, Venezuela, the Guianas, the majority of Northern and Central Brazil as well as parts of Ecuador, Peru and Bolivia. It is replaced by *derbyanus* in southernmost Brazil and Paraguay. The sixth subspecies is *gilvus* in the coastal regions of northern Colombia (Holyoak, 2001). Dickinson *et al.* (2003) include a seventh subspecies *N. a. intercedens* by separating the populations of *albicollis* that are found in Central America from El Salvador to Costa Rica from the South American populations. Six subspecies are sampled in this study with only *gilvus* missing.

All *Nyctidromus albicollis* individuals sampled are monophyletic (**Figure 10**), and there is considerable genetic structure within the species complex. This structure is seen in all four markers (**Figures 2-5**), but is better supported by the mitochondrial markers (**Figures 2-3**). As can be seen on the tree resulting from the analysis of the concatenated dataset (**Figure 10**) there are at least three groups within *N. albicollis*. One includes individuals from the southernmost part of the species range: an individual of *derbyanus* from southern Brazil as well as two individuals of *albicollis* from Bolivia and eastern Brazil. The second contains the remaining individuals of the nominate form from Guyana, Venezuela, Ecuador, Peru and Panama. The third group contains individuals from the northern parts of the range clade: the three Mexican subspecies (*merrilli*, *insularis* and *yucatanensis*), as well as two individuals from Panama that are assigned to *intercedens*. Thus *Nyctidromus albicollis* should be split into three phylogenetic species with members of the nominate subspecies *albicollis* north of the Amazon retaining the *N. albicollis* name (as the type is from Guyana – Holyoak, 2001), whereas individuals from the southernmost part of the range of *albicollis* including Brazil south of the Amazon as well as individuals of *derbyanus* should be placed in the reinstated species *Nyctidromus derbyanus*. The four Central American and Mexican subspecies form the third phylo-species, *Nyctidromus merrilli*.

The external morphology of the Pauraque has been studied extensively (Hartert, 1892; Griscom 1929; Grant, 1965). Hartert (1892) suggested that there is clinal variation in plumage morphology, with individuals in the wet tropics being darker and smaller in size than individuals in more arid regions. However, morphological variability also falls along subspecies-lines and the three phylo-species proposed in this study differ in

morphology from one another. *N. albicollis* is the smallest of the three phylo-species. It is overall the darkest with a soot-grey head but also has distinct brown markings on its back and coverts. *N. derbyanus* is the largest of the three phylo-species and most conspicuously reddish-brown in color with the crown, back and coverts rustic-brown. *Nyctidromus merrilli* is intermediate in size and the plumage is both lighter and greyer than in the other two phylo-species, with a slate-gray coloration on the crown and back being particularly noticeable. There are also conspicuous black patterns on the coverts of *merrilli*, which in both *albicollis* and *derbyanus* tend to be browner. Some individuals in arid areas of Mexico are slightly more reddish in color, but overall the three named forms within *N. merrilli* (*insularis*, *merrilli* and *yucatanensis*) are similar to one another. The only subspecies of the 'old' *Nyctidromus albicollis* that was not sampled, *N. a. gilvus*, is similar in size to the nominate form but considerably lighter in color. Genetic data are needed to address its taxonomic status.

4.4.4 THE *HYDROPSALIS*- CLADE

The remainder of the South American Clade consists of twelve previously described species (Dickinson *et al.*, 2003) in five genera; *Eleothreptus, Hydropsalis*, *Macropsalis*, *Uropsalis* and "*Caprimulgus"*. The levels of intraspecific diversity vary among the taxa. Some species are monotypic whereas "*Caprimulgus" longirostris* has seven to nine recognized subspecies (Holyoak 2001; Dickinson *et al.*, 2003; Cleere & Nurney,1998; Cleere, 1999, 2010). Relationships within the *Hydropsalis*-clade are somewhat incongruent and unresolved within the individual gene trees (see **Figures 2-5**),

in particular the more basal nodes. The concatenated tree (**Figure 11**) is the best resolved with only two of the basal nodes receiving low bootstrap support.

Han *et al.* (2010) suggested that all species in the SA clade, be given the name *Hydropsalis*, including "*Caprimulgus" longirostris* and the genus *Eleothreptus*. I agree with their recommendation although species of the genera *Lurocalis*, *Nyctidromus* and *Nyctiprogne* do not need to be included in the enlarged *Hydropsalis* as they proposed, as these genera are clearly separate monophyletic units (**Figure 10**). However, all species described in the following section, that includes the genera *Uropsalis, Macropsalis, Eleothreptus,* as well as ten species of "*Caprimulgus*", should be moved into *Hydropsalis*.

The Roraiman Nightjar (*Hydropsalis* ("*Caprimulgus*") *whitelyi*) is the sister-species to the remaining diversity (**Figure 11**). Despite its position receiving high bootstrap support on the best scoring ML tree there is considerable incongruence among the individual gene trees about its placement, especially between the mitochondrial data (**Figures 2-3**) and *RAG-1* (**Figure 4**). *H. whitelyi* is an elusive species that breeds only on the slopes and summits of the tepuis in the south Venezuelan and Guyanan rainforest. Not many specimens have been sampled but they have been found on at least five different tepuis (Holyoak, 2001). There are no subspecies recognized but genetic structure is sometimes seen in tepui-species (i.e. Braun *et al.*, 2005) as gene flow between populations on individual tepuis is apparently limited. Only three individuals were sampled in this study, two from Guyana and one from Venezuela. The *ND2* tree (see **Figure 2**) clearly separates the two Guyanan individuals from the Venezuelan one but the

sequence divergence is still very low (0.3%) and much more sampling is needed to investigate this structure further.

The next node upstream in the *Hydropsalis*-clade on the concatenated tree (**Figure 11**) separates the two species previously placed in the genus *Uropsalis* from the remainder of the clade. The Lyre-tailed Nightjar (*Hydropsalis* (*Uropsalis) lyra*) and the Swallow-tailed Nightjar (*Hydropsalis* (*Uropsalis) segmentata*), were merged by Holyoak (2001) and Cleere (2010) with the monotypic *Macropsalis,* which included the Long-trained Nightjar (*Hydropsalis (Macropsalis) forcipata*). All three species have long tail feathers in which the outermost retrices are greatly elongated. This trait is only seen in males and is a secondary sexual character as members of all three species are polygamous and have lek breeding systems (Holyoak, 2001).

The results here show that the two "*Uropsalis"* species should not be affiliated with *H. forcipata* as they are in separate lineages (**Figure 11),** with *H. forcipata* placed as the sister-taxon to a clade containing *Hydropsalis torquata*, *Hydropsalis climacocerca* and *Hydropsalis ("Caprimulgus") cayennensis*. This latter result is only supported by the *ND2* data, as the two individuals of *forcipata* sampled here were both museum skin specimens. The support values for the placement of *forcipata* are very high however.

Both *lyra* and *segmentata* have very fragmented ranges throughout the high-montane forests of the North and Central Andes, areas known to promote high speciation rates in birds (i.e. Garcia-Moreno & Fjeldså, 2000; Cadena *et al.*, 2007; Weir, 2009; Sedano & Burns, 2010). Thus it is likely that these two species may eventually be split into additional phylogenetic species. This will require considerable new sampling across the range of both species. Unfortunately, they are among the poorest sampled in this

study. *Hydropsalis segmentata* has two distinct subspecies: *segmentata* in the Andes of Colombia and northern Ecuador and *kalinowskii* in the Andes of Peru and Bolivia. Only one individual of each subspecies is sampled here, from Ecuador and Bolivia respectively. *Hydropsalis lyra* has three subspecies: the nominate *lyra* in Colombia, Venezuela and Ecuador; *peruana* in Peru and *argentina* in north-western Argentina (Dickinson *et al.*, 2003). Individuals found in Bolivia have not been placed in a particular subspecies. In this study only two subspecies were sampled, *lyra* and *peruana*.

On the concatenated tree (**Figure 11**) *Hydropsalis segmentata kalinowskii* is the sister taxon to a reciprocally monophyletic *lyra* with *H. s. segmentata* being their sister-group, rendering *segmentata* paraphyletic. Furthermore, within *H. lyra*, the subspecies *lyra* is also paraphyletic as one individual is grouped with the single individual of *H. l. peruana*. Interestingly these two individuals are not from adjacent parts of it range, the *H. l. lyra* individual being from Colombia whereas the *H. l. peruana* individual is from Peru. Their sister taxon, is the *H. l. lyra* individual from Ecuador. More sampling is needed to clarify these relationships. If the different subspecies are representatives of phylotaxa and the relationships seen here hold, this would be an example of a leapfrog-speciation event, which is a phenomenon seen in other avian groups in the Andes (Maijer & Fjeldså, 1997; Johnson, 2002; Cadena *et al.*, 2011).

The position of Little Nightjar (*Hydropsalis ("Caprimulgus") parvulus*) within the *Hydropsalis*-clade is not completely resolved as there is incongruence among the different gene trees (**Figures 2-5**). This is similar to the results of Han *et al.* (2010) where its position is without bootstrap support. On the concatenated tree it is the sister-species

to a well-supported clade of twelve species, but forms a polytomy with the *lyra/segmentata*-clade and *Hydropsalis decussatus* (**Figure 11**).

There are two subspecies of *Hydropsalis parvulus* with allopatric ranges, *heterurus,* found in northern Colombia and Venezuela and the nominate *parvulus,* with a large range south of the Amazon from eastern Peru throughout Bolivia, Paraguay and most of Brazil as well as northern Argentina and Uruguay (Holyoak, 2001; Dickinson *et al.*, 2003). The two subspecies are very similar morphologically, but *heterurus* has more extensive white areas near the tips of the restrices (Holyoak, 2001). Their territorial calls are also considerably different (Davis, 1979; Cleere, 2010). It has been proposed that they are two separate species (Davis, 1979; Hilty, 2003) and Cleere (2010) elevated the two subspecies to species status and names them *Antrostomus parvulus* and *Antrostomus heterurus*, with the latter receiving the common name Todd's Nightjar.

Four individuals of *parvulus* were sampled in this study, but only one belonged to *heterurus* and it was a skin specimen. A nearly complete *ND2* sequence was produced for this individual and it is considerably different (5%) from the *parvulus* individuals (**Figures 2 and 11**). Thus despite the low level of sampling this additional molecular evidence provides strong support for the elevation of *heterurus* to full species status.

The Band-winged Nightjar (*Hydropsalis ("Caprimulgus") longirostris*) is the most taxonomically diverse nightjar species in the New World with seven recognized subspecies (Holyoak, 2001; Dickinson *et al.*, 2003), which are spread over a large distribution range in various habitats as well as being morphologically diverse. No phylogenetic study has previously evaluated the status of these subspecies. In his recent book, Cleere (2010) does elevate two of the subspecies to full species status, *decussatus*

and *roraimae* based on observations on their morphology. This study provides genetic evidence to test these taxonomic changes.

The seven subspecies of *H. longirostris* are: *ruficervix* in the mountains of Colombia, Ecuador and Venezuela; *roraimae* from the tepuis of southern Venezuela; *decussatus* in the arid littoral of northern Chile and Peru; *atripunctatus* in the Andes of Peru and northern Argentina; *bifasciatus* in Chile and western Argentina; *patagonicus* in the Pampas of eastern and southern Argentina south to Patagonia and wintering in northern Argentina and Uruguay; and the nominate *longirostris* in southeastern Brazil (Dickinson *et al.*, 2003). *H. l. bifasciatus* has been split into two subspecies with individuals from southern Chile identified as the subspecies *mochaensis* while individuals from scattered localities in northeastern Brazil have received the name *pedrolimai* (Grantsau, 2008).

There are obvious similarities in the morphology of all the subspecies: the general slender body shape, long beak, and general plumage patterns including a white throat-patch, a brownish collar on the hind-neck, a white band on the four outermost primaries, and broad white tips and bands across the inner margin of their tail feathers. The two northernmost subspecies, *rufiventrix* and *roraimae,* have the darkest plumage with the white markings being less conspicuous. Of the two, *roraimae* is noticeably larger in size than *rufiventrix*, but individuals of *rufiventrix* in Venezuela are intermediate in size between individuals in Ecuador/Colombia and *roraimae*. The morphology suggests close affinities between the two.

Hydropsalis longirostris decussatus is the smallest and palest of all the subspecies, with sandy-light brown being the most prominent color in its plumage, rather

than grey or dark-brown. It is similar to *H. l. atripunctatus*, which is also small in size and with a pale plumage, but *atripunctatu*s has a larger white throat-patch and more prominent reddish-brown and orange patterns in its plumage. It also has the most coarse plumage patterns on its back and coverts, with larger spots of color than seen in other subspecies. The remaining four subspecies from the southern-part of the total distribution (*bifasciatus, longirostris, mochaensis, patagonicus*) are all similar in morphology, and are relatively large nightjars, with fine, intricate plumage patterns in which grey is the predominant color. The subspecies *mochaensis* is slightly darker but otherwise similar to the other three.

The results from the genetic data strongly suggest that some of these subspecies can to be elevated to full phylo-species status (**Figure 11**). The strongest argument is for *decussatus* as it is not even included in an otherwise monophyletic *longirostris* clade. The *ND2*, *CYTB, RAG-1* and the concatenated data sets are congruent in placing *decussatus* well outside a clade that not only contains the remaining *longirostris* individuals but nine other nightjar species (**Figures 2-4,11**). *Hydropsalis longirostris* is therefore paraphyletic. Thus, as suggested by Cleere (2010), *decussatus* should be elevated to full species status.

The remaining subspecies of *Hydropsalis longirostris* are placed in a strongly monophyletic clade (**Figure 11**). The sister-group to this clade contains two species, previously placed in *Eleothreptus* (Cleere, 2010). There is considerable genetic structure within the remaining *longirostris* individuals, which mostly falls along subspecies lines. The two northern subspecies, *ruficervix* and *roraimae* form separate clades that are distinct from one another (3.7 % *ND2* divergence) and from the remaining subspecies

(5% *ND2* divergence). This is supported in particular by the *ND2* data (**Figure 2**), but also by the *ACO1 I9* data (**Figure 5**), and thus is present on the concatenated tree (**Figure 11**). The genetic evidence, the morphology, allopatric ranges, and the little that is known about their vocalizations (Hilty & Brown, 1986) all suggest that both *roraimae* and *ruficervix* should be elevated to species status.

The ACO1 data (**Figures 5**) also suggest that *atripunctatus* is separated from the remaining three subspecies (*bifasciatus*, *longirostris,* and *patagonicus*). This is not supported by the mitochondrial data (**Figures 2-3**) and is thus only weakly supported on the concatenated tree (**Figure 11**). As *atripunctatus* is morphologically distinct from *bifasciatus*, *longirostris* and *patagonicus*, this should be studied further but for now all four are grouped together as a single species, *Hydropsalis longirostris*.

Two species were previously placed in *Eleothreptus*: the Sickle-winged Nightjar (*Hydropsalis (Eleothreptus) anomalus*) and the White-winged Nightjar (*Hydropsalis (Eleothreptus) candicans*). The latter has also previously been placed in the genus "*Caprimulgus"*, but based on his observations of morphology and vocalizations, Cleere (2002) suggested that "*C". candicans* be moved into the genus *Eleothreptus*. This was supported by the results of Larsen *et al.* (2007) in which the *CYTB*-data set supported the sister-relationship of the two species. As mentioned before, I suggest moving both species into the genus *Hydropsalis*. *H. candicans* was not sequenced directly in this study but a partial *CYTB*-sequence from the study of Larsen *et al.* (2007) was incorporated in the concatenated data set along with sequences of all four markers for *H. anomalus*. Both species are monotypic, genetically distinct (4.3% divergence in *CYTB*) and are strongly

supported as the sister-group to the clade containing *Hydropsalis longirostris, H. roraimae* and *H. ruficervix* (**Figure 11**).

The Spot-tailed Nightjar (*Hydropsalis ("Caprimulgus") maculicaudus*) is a widespread and locally common species in grassland that has been found sporadically in many locations throughout South America. The delineation of its breeding range needs improvement as it consists mostly of numerous point localities. The genetic results here confidently place it well within the *Hydropsalis*-clade. It is the sister species to a clade containing *Hydropsalis cayennensis*, *Hydropsalis climacocerca*, *H. torquata H. forcipata* (**Figure 11**).

The Long-trained Nightjar (*Hydropsalis (Macropsalis) forcipata* was discussed above in the section on "*Uropsalis"*. The sister-group to *H. forcipata* contains the original members of the genus *Hydropsalis*; the Ladder-tailed Nightjar (*Hydropsalis climacocerca*) and the Scissor-tailed Nightjar (*Hydropsalis torquata*), along with the White-tailed Nightjar (*Hydropsalis ("Caprimulgus") cayennensis*) (**Figure 11**). The different gene trees are incongruent regarding relationships among these three species. The *ND2* data (**Figure 2**) suggest that *H. torquata* and *H. cayennensis* are sister-taxa but the *CYTB* and *ACO1-I9* gene trees (**Figures 3** and **6**) show *H. climacocerca* and *H. torquata* forming a monophyletic clade, and this is the pattern seen on the concatenated tree with good support (**Figure 11**). Both *H. torquata* and *H. climacocerca* are known for their long tails, which are a secondary sexual character only seen in males.

The Scissor-tailed Nightjar (*Hydropsalis torquata*) has two subspecies, nominate *torquata*, with a large range in Brazil, and *furcifer* in Bolivia, Paraguay, southernmost Brazil, northern Argentina, and Uruguay (Dickinson *et al.*, 2003). The boundary between

the two ranges is unclear and the morphological differences between the two are slight, with the nominate form being slightly smaller and darker in color.

The Ladder-tailed Nightjar (*Hydropsalis climacocerca*) has a large concise, distribution in the Amazon basin and the Guianas. There are five subspecies with the nominate *climacocerca* having by far the largest range covering most of the Amazon basin. *H. c. schomburgki* is found in eastern Venezuela and the Guianas. The remaining three subspecies have very small ranges in the eastern Amazon basin. *H. c. pallidior* and *intercedens* are only known from type-localities in Santarém and Óbidos, Brazil, respectively whereas *canescens* is found in the lower Tapajóz and Santa Rita areas (Holyoak, 2001; Dickinson *et al.*, 2003). Three of the five subspecies were sampled in this study with the two rare ones, *pallidior* and *intercedens* missing. The results indicate that there is little genetic structuring within *H. climacocerca* (**Figure 11**).

The White-tailed Nightjar (*Hydropsalis ("Caprimulgus") cayennensis*) is another grassland species with a distribution limited to the northernmost part of South America from Costa Rica and Ecuador in the west to French Guyana in the east. Despite its relatively small range it is polytypic with six recognized subspecies. The nominal form *cayennensis* has the largest range, breeding in Venezuela and the Guianas; *albicauda* breeds in Costa Rica, Panama and the extreme northern coast of Colombia; *apertus* breeds in western Colombia and northern Ecuador; *insularis* breeds on the Venezuelan coastline and the islands of Margarita, Curacao, Aruba and Bonaire; *leopetes* (or *tobagensis*) breeds in Trinidad and Tobago; and *manati* in Martinique (Holyoak, 2001; Dickinson *et al.*, 2003). In this study, five of the six subspecies were sampled with only

manati missing. Three of these were only available as museum skin specimens and thus only *ND2* sequences were produced for these individuals.

The results from the *ND2* data (**Figure 2**) suggest that there are two clades of *Hydropsalis cayennensis*, split roughly along a west-east axis with the subspecies *albicauda*, *apertus* and *insularis* (an individual from coastal Venezuela) forming a strongly monophyletic clade and *cayennensis* and *leopetes* forming another clade (1.3% divergence in the *ND2* sequences), a pattern retained on the concatenated tree (**Figure 11**). Thus, *Hydropsalis cayennensis* can be split into two phylo-species although better sampling is recommended since there is also an indication from the tree topology that *albicauda* may be a separate species on its own. For now, the subspecies *albicauda*, *apertus* and *insularis* together form the phylo-species *Hydropsalis albicauda*, and *cayennensis* and *tobagensis* remain *Hydropsalis cayennensis*. Morphologically the two phylo-species are nearly identical. One trait that may distinguish between them is that males of *apertus* and *insularis* (less so *albicauda*) have darker, more auburn-colored patterns on the crown, whereas *cayennensis* and *tobagensis* have noticeably more white patterns on the crown. The status of the subspecies *manati* remains unresolved.

There is one nightjar species from South America that was not sampled in this study and it is not clear where it might fall into the phylogeny. This is the Cayenne Nightjar ("*Caprimulgus" maculosus*). It is known from only a single museum specimen collected in 1917 in French Guiana. It is supposedly similar to the sympatric Blackish Nightjar (*Nyctidromus nigrescens*) (Griscom & Greenway, 1937). No other information is available about this species but it is likely that it is related to *N. nigrescens* and thus could be included in the genus *Nyctidromus*.

4.5 THE OLD WORLD CLADE

The last of the four large caprimulgid radiations is a highly diverse clade exclusive to the Old World with the majority of the diversity in Africa and South East Asia, with a few species breeding in Europe, the Middle East and India. As this study focused on the diversity in the New World, this group was heavily under-sampled. Only nine species of the 36 species belonging to the genera *Caprimulgus* and *Macrodipteryx* (Dickinson *et al.*) were sampled (**Figure 7**), all of which are monophyletic. These ten species are: the Bate's Nightjar (*Caprimulgus batesi*), Long-tailed Nightjar (*Caprimulgus climacurus*), European Nightjar (*Caprimulgus europaeus*), Square-tailed Nightjar (*Caprimulgus fossii*), Large-tailed Nightjar (*Caprimulgus macrurus*), Madagascar Nightjar (*Caprimulgus madagascariensis*), Fiery-necked Nightjar (*Caprimulgus pectoralis*), Abyssinian Nightjar (*Caprimulgus poliocephalus*) and Pennant-winged Nightjar (*Macrodipteryx vexillarius*).

A number of other taxa have been placed in this Old World Clade in other studies. Larsen *et al.* (2007) included *Caprimulgus inornatus, Caprimulgus fraenatus* and *Macrodipteryx longipennis* in this clade while Han *et al.* (2010) included *Caprimulgus affinis, Caprimulgus aegyptius, Caprimulgus indicus, Caprimulgus manillensis*, *Caprimulgus nigriscapularis,* and *Caprimulgus rufigena*. Thus when merging the results from all available studies, 18 species of Old World nightjars fall within the Old World Clade. That leaves another 18 species that will need to be sampled to fully understand the phylogeny of this clade. These 18 species are all members of the genus *Caprimulgus* except the two species of the genus *Macrodipteryx* that are also embedded within this clade. So to obtain a strictly monophyletic *Caprimulgus*, the name *Macrodipteryx* must

be changed to *Caprimulgus*. It is possible that some Old World *Caprimulgus* species that have not been included in phylogenetic studies will not fall within the Old World Clade, as was the case with *Gactornis enarratus*. More even, there is the unusual African species *Veles binotatus*, whose placement in the caprimulgid phylogeny is unknown, and unfortunately was not sampled in this study.

There is also considerable intraspecific diversity within a number of Old World nightjar species that needs to be investigated. Based on what this study has demonstrated about the New World diversity, it is likely that Old World species with numerous recognized subspecies may be split into two or more phylo-species. This is especially likely in species with large breeding ranges in tropical areas such as *Caprimulgus aegyptius*, *C. affinis*, *C. climacurus*, *C. fossii*, *C. macrurus*, *C. natalensis*, *C. nubicus, C. pectoralis* and *C. tristigma* (Dickinson *et al.*, 2003). A study similar in scope to this study should be done focusing on the Old World nightjars.

5. TAXONOMIC MODIFICATIONS

Based on the results presented in this study and comparisons with other studies, the following taxonomic modifications are performed for the taxa listed in the following section. There are a number of species where further taxonomic work is needed before suggesting taxonomic changes, thus this list is expected to grow as more information becomes available. A phylogeny presenting all the New World species with their taxonomy modified is depicted in **Figure 13**.

a) The two subfamilies, Chordeilinae and Caprimulginae are no longer used as the results of this study as well as the results of Larsen *et al.* (2007), Barrowclough *et al.* (2006) and Han *et al.* (2010) demonstrate that they are not monophyletic units but polyphyletic assemblages.

b) The genus *Podager* Wagler, 1832 (type species *Podager nacunda* Viellot, 1817), is redefined to include the species *Podager pusillus* Gould, 1861.

c) The genus *Chordeiles* Swainson, 1832 (type species *Chordeiles minor* J. R. Forster, 1771) is redefined to include the species *C. acutipennis* Hermann, 1783; *C. gundlachii* Lawrence, 1856; *C. minor* J. R. Forster, 1771; *C. rupestris* Spix, 1825 and *C. texensis* Lawrence, 1856. The species *C. pusillus* Gould, 1861 and *C. vielliardi* Lencioni-Neto, 1994 are removed

from the genus while the subspecies *C. acutipennis texensis* Lawrence, 1856 is elevated to full species status as *Chordeiles texensis*.

d) The genus *Antrostomus* Bonaparte, 1838 should be used instead of *Caprimulgus* for the species *A. carolinensis* Gmelin, 1789; *A. rufus* Boddaert, 1783; *A. cubanensis* Lawrence, 1860; *A. salvini* Hartert, 1892; *A. badius* Bangs & Peck, 1908; *A. seriocaudatus* Cassin, 1849; *A. ridgwayi* Nelson, 1897; *A. saturatus* Salvin, 1870; *A. vociferus* Wilson, 1812; *A. arizonae* Brewster, 1881 and *A. noctitherus* Wetmore, 1919. The inclusion of *A. ekmani* as suggested by Cleere (2010) is possible but this study does not have data to support its split from *A. cubanensis.*

e) The species traditionally known as *Antrostomus vociferus* Wilson, 1812 is split into two phylo-species. The nominate subspecies *C. v. vociferus* Wilson, 1812 is elevated to full phylo-species status as *Antrostomus vociferus* Wilson, 1812. The subspecies *Antrostomus vociferus arizonae* Brewster, 1881; *A. v. oaxaceae* Nelson, 1900 and *A. v. chiapensis* Nelson, 1900 form a single phylo-species which according to rules of preference takes the name of *A. v. arizonae* and is elevated to full species status as *Antrostomus arizonae* Brewster, 1881. The status of the two subspecies *Antrostomus vociferus setosus* van Rossem, 1934 and *A. v. vermiculatus* Dickey & van Rossem, 1928 remains uncertain but individuals identified as

those subspecies are for now classified as *Antrostomus arizonae* Brewster, 1881.

f) The species known as *Chordeiles vielliardi* Lencioni-Neto, 1994 should be named *Nyctiprogne vielliardi*. All specimens named either *Chordeiles vielliardi* or *Nyctiprogne vielliardi* should be studied and compared to ensure they are indeed the same species.

g) The species *Nyctiprogne leucopyga* Spix, 1825 is split into two phylo-species. The nominate subspecies *N. l. leucopyga* Spix, 1825 is elevated to full phylo-species status under the original species name. That species also includes members of the subspecies *N. l. majuscula* Pinto and Camargo, 1952. The sister taxon to the revised *N. leucopyga* is *Nyctiprogne vielliardi* Lencioni-Neto, 1994. The subspecies of *N. l. latifascia* Friedman, 1945 becomes a new species, *Nyctiprogne latifascia* Friedman, 1945. The positions of *Nyctiprogne leucopyga exigua* Friedman, 1945 and *pallida* (Phelps and Phelps, 1952) are unresolved.

h) The species *Nyctidromus albicollis* Gmelin, 1789, is split into three phylo-species. The nominate subspecies *N. a. albicollis* Gmelin, 1825 is elevated to full phylo-species status under the original species name. The subspecies *N. a. derbyanus* Gould, 1838 is also elevated to full phylo-species status

under the name *Nyctidromus derbyanus* Gould, 1838. Some individuals identified as *N. a. albicollis* may also belong to this phylo-species. Finally, the three subspecies *Nyctidromus albicollis insularis* Nelson, 1898; *N. a. intercedens* Griscom, 1929; *N. a. merrilli* Sennett, 1888 and *N. a. yucatanensis* Nelson, 1901 are members of a new species, *Nyctidromus merrilli* Sennett, 1888.

i) The genus *Nyctidromus* Gould, 1838, should be used instead of *Caprimulgus* for the species *Caprimulgus anthonyi* Chapman, 1923; *Caprimulgus hirundinaceus* Spix, 1825 and *Caprimulgus nigrescens* Cabanis, 1848. Thus there will be six species in the genus *Nyctidromus* Gould, 1838: *Nyctidromus albicollis* Gmelin, 1825; *N. anthonyi* Chapman, 1923; *N. derbyanus* Gould, 1838; *N. hirundinaceus* Spix, 1825; *N. merrilli* Sennett, 1888 and *N. nigrescens* Cabanis, 1848. The rare *Caprimulgus maculosus* is provisionally included in the genus as *Nyctidromus maculosus* based on observations by Cleere (2010) on its morphology.

j) The following taxa take up the genus name *Hydropsalis* instead of *Caprimulgus, Eleothreptus*, *Macropsalis* and *Uropsalis*: *Caprimulgus (Eleothreptus) candicans* (Pelzen, 1866), *C. cayennensis* Gmelin, 1789; *C. longirostris* Bonaparte, 1825; *C. maculicaudus* Lawrence, 1862; *C. parvulus* Gould, 1837; *C. whitelyi* Salvin, 1885; *Eleothreptus anomalus* Gould, 1838; *Macropsalis forcipata* Nitzsch, 1840; *U. lyra* Bonaparte,

1850 and *U. segmentata* Cassin, 1849 thus becoming *Hydropsalis candicans*, *H. cayennensis*, *H. longirostris*, *H. maculicaudus*, *H. parvulus*, *H. whitelyi*, *H. anomalus*, *H. forcipata*, *H. lyra* and *H. segmentata* respectively. The species *Hydropsalis climacocerca* Tschudi, 1844 and *H. torquata* Gmelin, 1789 retain their names. Additionally as described in sections k) to n) the following new species be added to the genus: *Hydropsalis decussatus* Tschudi, 1844; *H. heterurus* Todd, 1915; *H. roraimae* Chapman, 1929; *H. ruficervix* Sclater, 1866 and *H. albicauda* Lawrence, 1875.

k) The subspecies *Caprimulgus parvulus heterurus* Todd, 1915 is elevated to full phylo-species status and becomes *Hydropsalis heterurus* (see recommendations about new genus in section j)). More sampling of individuals and genetic data is recommended.

l) The species *Caprimulgus longirostris* Bonaparte, 1825 is split into four different phylo-species. The subspecies *C. l. decussatus* Tschudi, 1844; *C. l. roraimae* Chapman, 1929 and *C. l. ruficervix* Sclater, 1866 are all elevated to full phylo-species status and become *Hydropsalis decussatus*, *H. roraimae* and *H. ruficervix* respectively (see recommendations about new genus in section k)). Individuals of the other subspecies of *Caprimulgus longirostris* all belong to the species *Hydropsalis longirostris*.

These include *C. l. atripunctatus* Chapman, 1923; *C. l. bifasciatus* Gould, 1837; *C. l. longirostris* Bonaparte, 182) and *C. l. patagonicus* Olrog, 1962. This provisionally also refers to the two subspecies mentioned in Cleere (2010), which he names *Antrostomus longirostris mochaensis* Cleere, 2006 and *A. l. pedrolimai* Grantsau, 2008.

m) The species *Caprimulgus cayennensis* Gmelin, 1789 are split into two different phylo-species according to our results. The subspecies *C. c. albicauda* Lawrence, 1875; *C. c. apertus* Peters, 1940 and *C. c. insularis* Richmond, 1902 together form the new phylo-species *Hydropsalis albicauda* (see recommendations about new genus in section j)). The nominate *C. c. cayennensis* Gmelin, 1789 and *C. c. leopetes* Jardine & Selby, 1830 remain as the original nominate form but with the new name *Hydropsalis cayennensis*. The status of *C. c. manati* Pinchon, 1963 is unresolved at this stage.

n) The two species belonging to the genus *Macrodipteryx* Swainson, 1837; *M. longipennis* Shaw, 1796 and *M. vexillarius* Gould, 1838 are moved to the genus *Caprimulgus.*

6. CONCLUSIONS

The results presented in this study are by far the most extensive phylogenetic work done for the genera and species of Nightjars (Caprimulgidae) found in the New World. The level of taxon sampling is close to three times higher than in the largest study previously completed. Additionally, sampling individuals of nearly all attainable subspecies and on a broad geographic scale for widespread species, has allowed us to identify with high confidence numerous new phylogenetic species, thus greatly altering the current taxonomy of the group, as well as providing preliminary evidence for cases where more such species may be discovered in future studies with better sampling of individuals. This is not only extremely important because it improves and clarifies the taxonomy and classification of the Nightjars in the New World, it also provides a much clearer picture of their evolutionary history with direct implications for further studies on the group.

Sampling densely at the intraspecific level during phylogenetic studies of groups where such diversity is known or suspected is a logical next step in avian systematics where sampling at the genus/biological-species level is already dense in many groups. Knowledge of the true number of phylogenetic species and their relationships with one another is pivotal before using phylogenies as data in larger studies of diversification processes, biogeography, trait evolution, speciation etc.

Finally, this study firmly demonstrates the importance and value of using ancient DNA from museum skin specimens in phylogenetic studies of this kind. With fast developing laboratory methods, amplifying ancient DNA will become simpler, faster and cheaper in the near future. It is a vital source of information that should not be ignored.

7. FIGURES

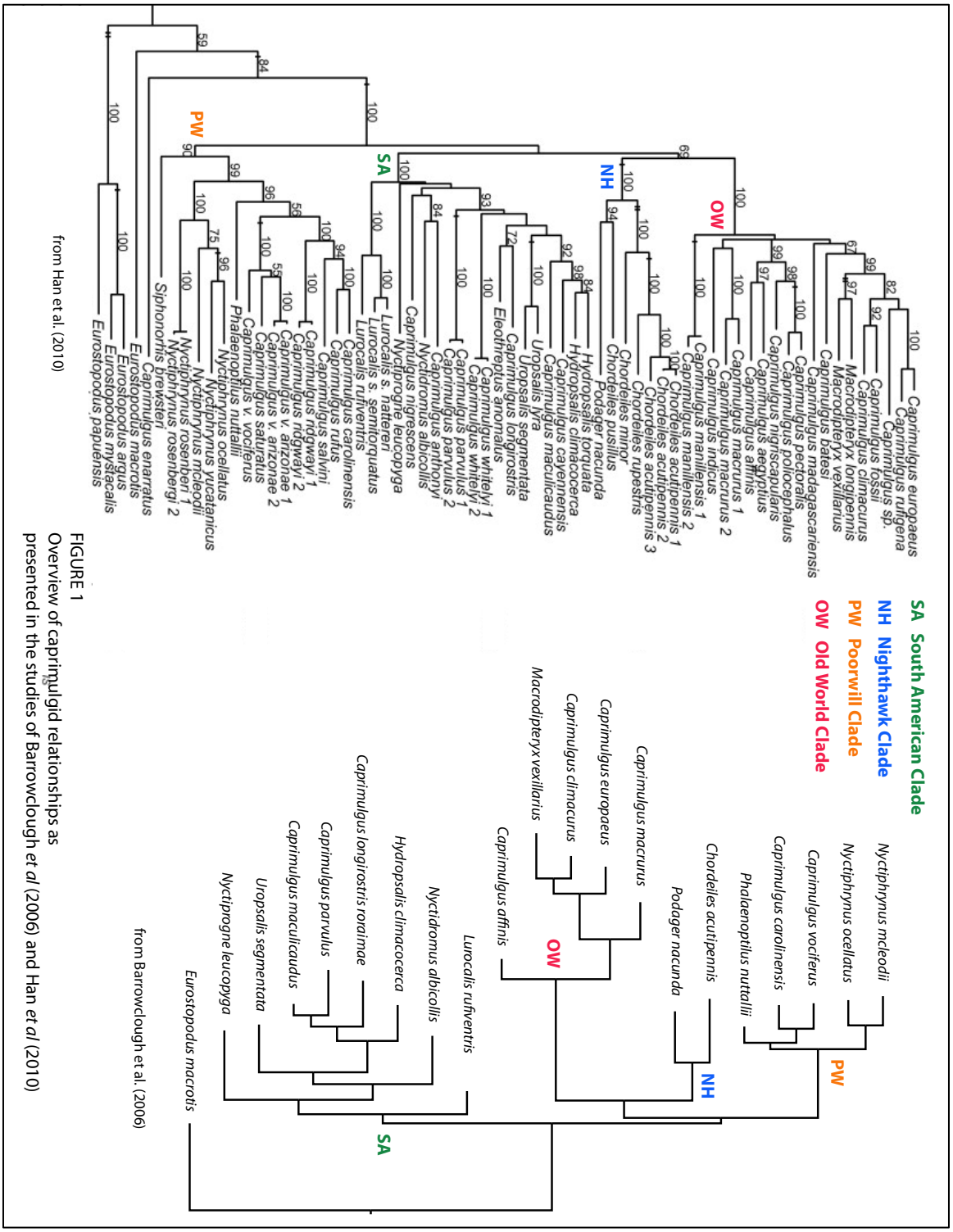


FIGURE 1
Overview of caprimulgid relationships as presented in the studies of Barrowclough *et al* (2006) and Han *et al* (2010)

FIGURE 1

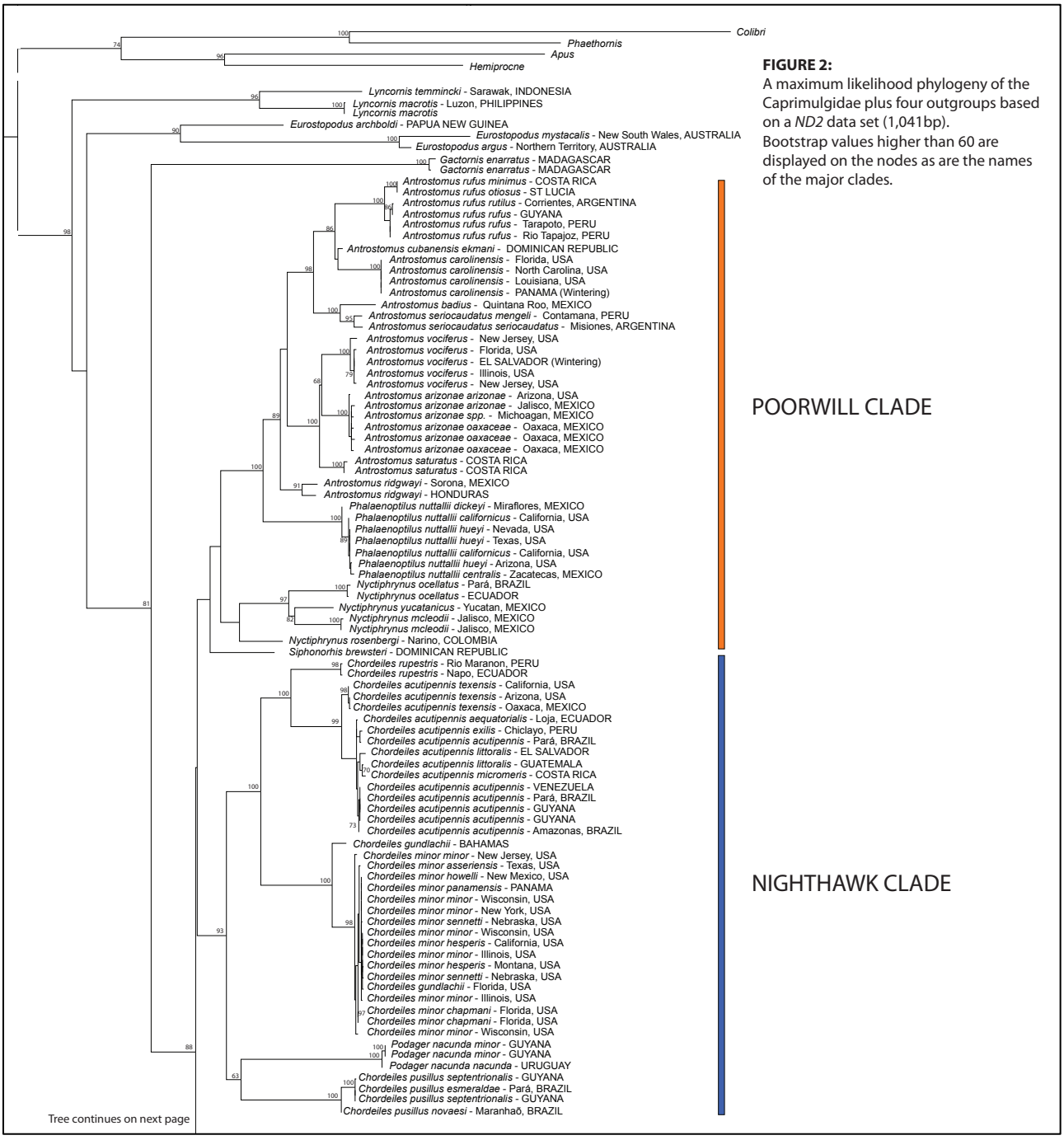


FIGURE 2:
A maximum likelihood phylogeny of the Caprimulgidae plus four outgroups based on a *ND2* data set (1,041bp). Bootstrap values higher than 60 are displayed on the nodes as are the names of the major clades.

FIGURE 2

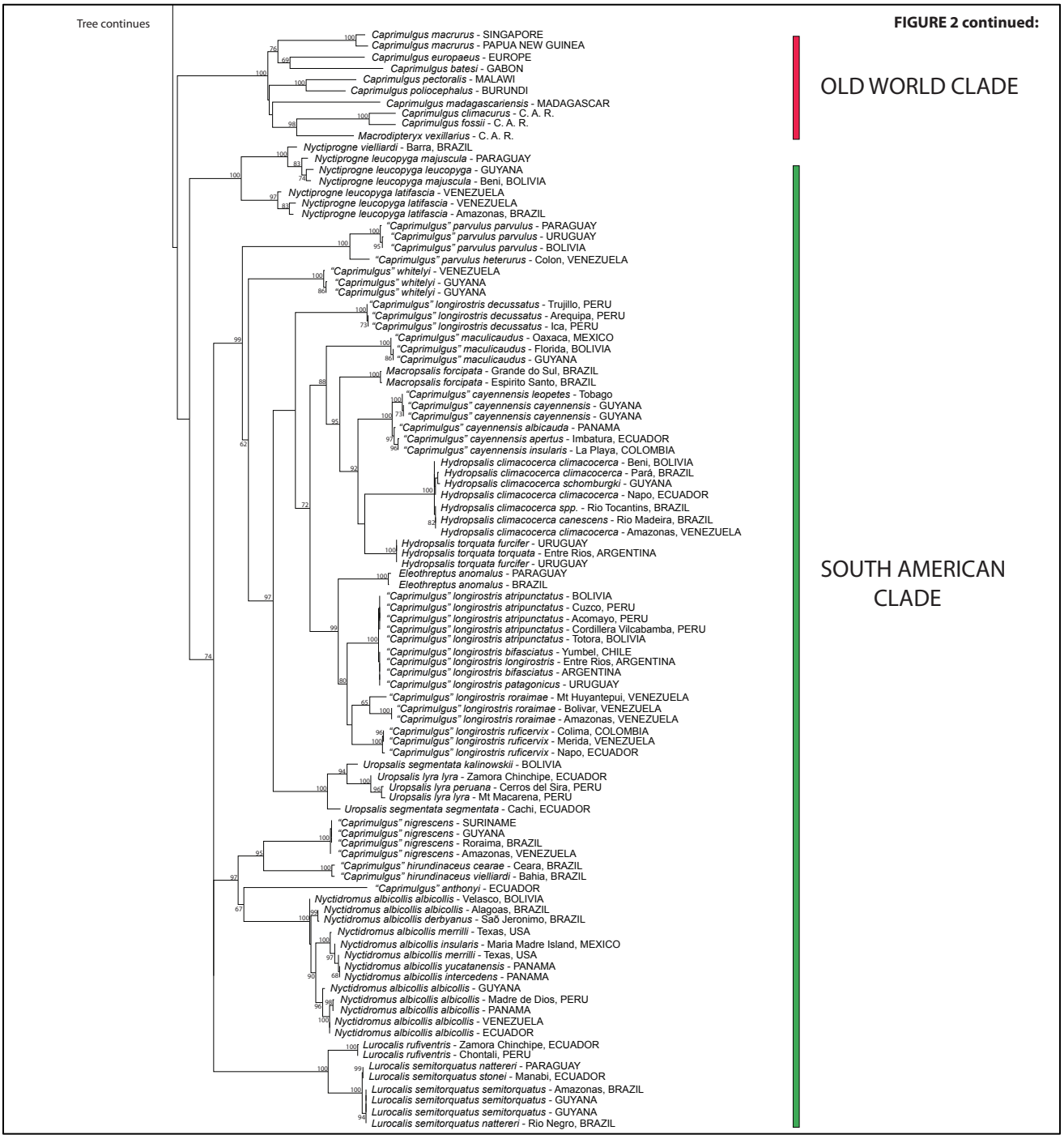


FIGURE 2 continued

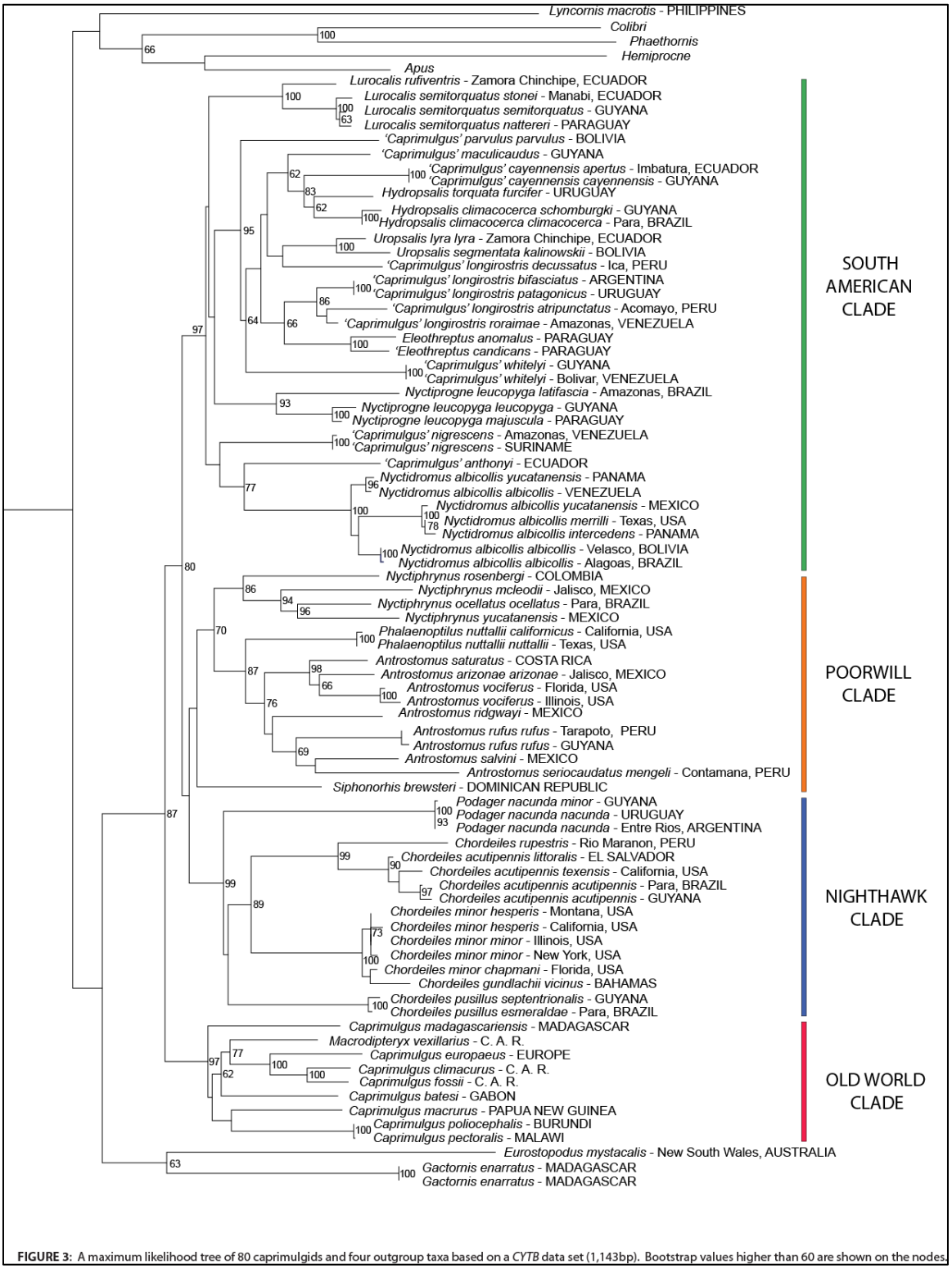


FIGURE 3: A maximum likelihood tree of 80 caprimulgids and four outgroup taxa based on a *CYTB* data set (1,143bp). Bootstrap values higher than 60 are shown on the nodes.

FIGURE 3

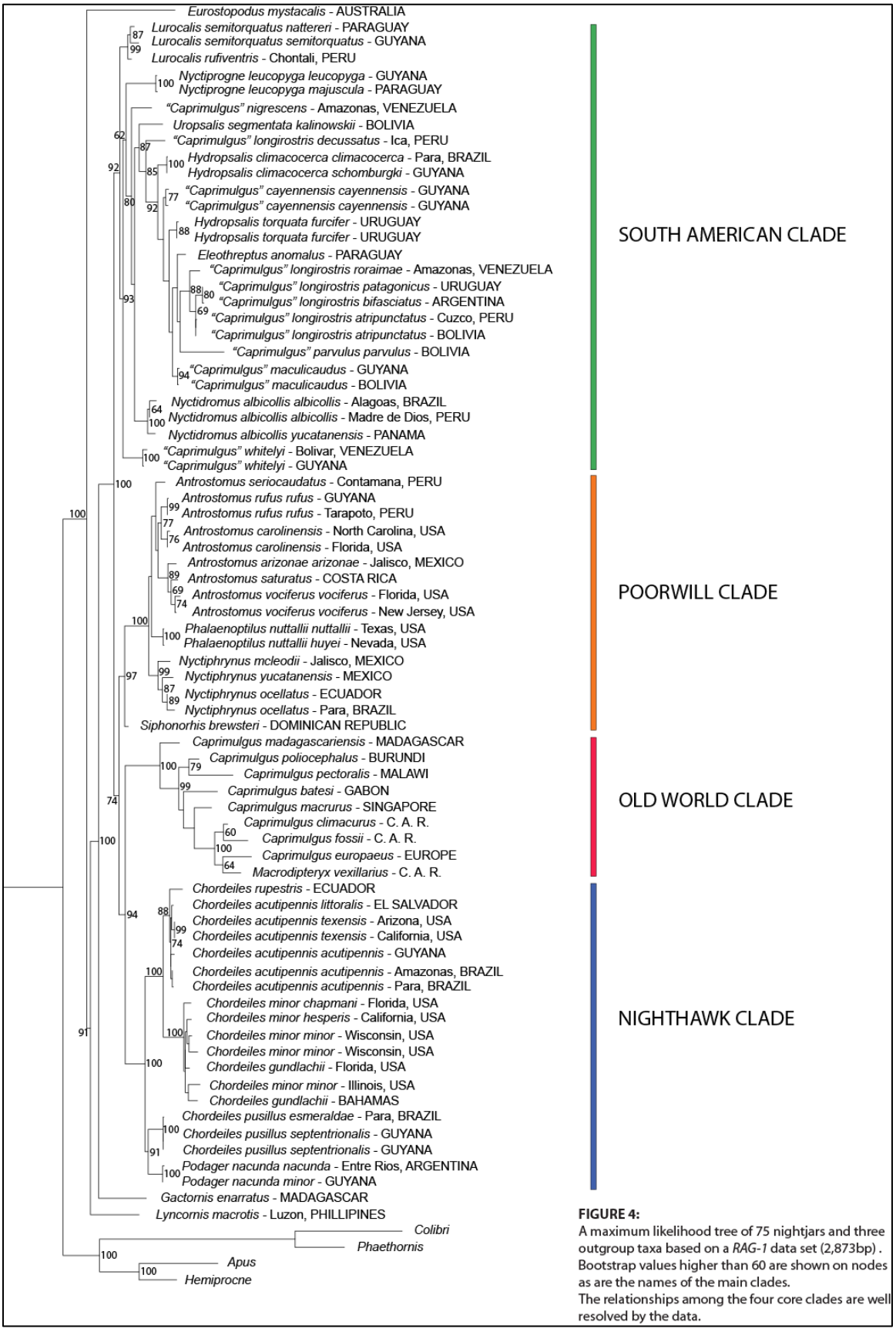


FIGURE 4:
A maximum likelihood tree of 75 nightjars and three outgroup taxa based on a *RAG-1* data set (2,873bp) . Bootstrap values higher than 60 are shown on nodes as are the names of the main clades.
The relationships among the four core clades are well resolved by the data.

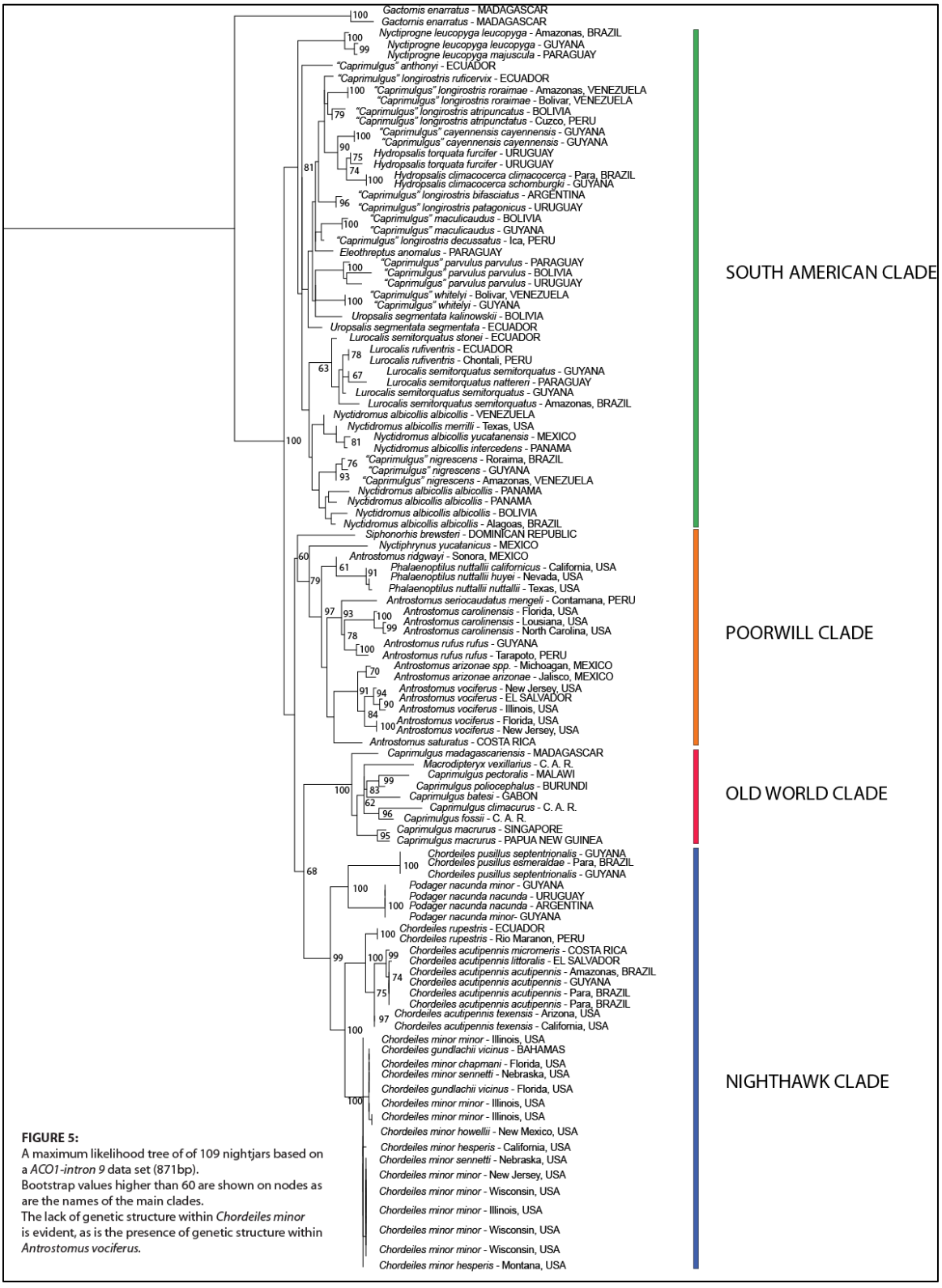


FIGURE 5:
A maximum likelihood tree of of 109 nightjars based on a *ACO1-intron 9* data set (871bp).
Bootstrap values higher than 60 are shown on nodes as are the names of the main clades.
The lack of genetic structure within *Chordeiles minor* is evident, as is the presence of genetic structure within *Antrostomus vociferus*.

FIGURE 5

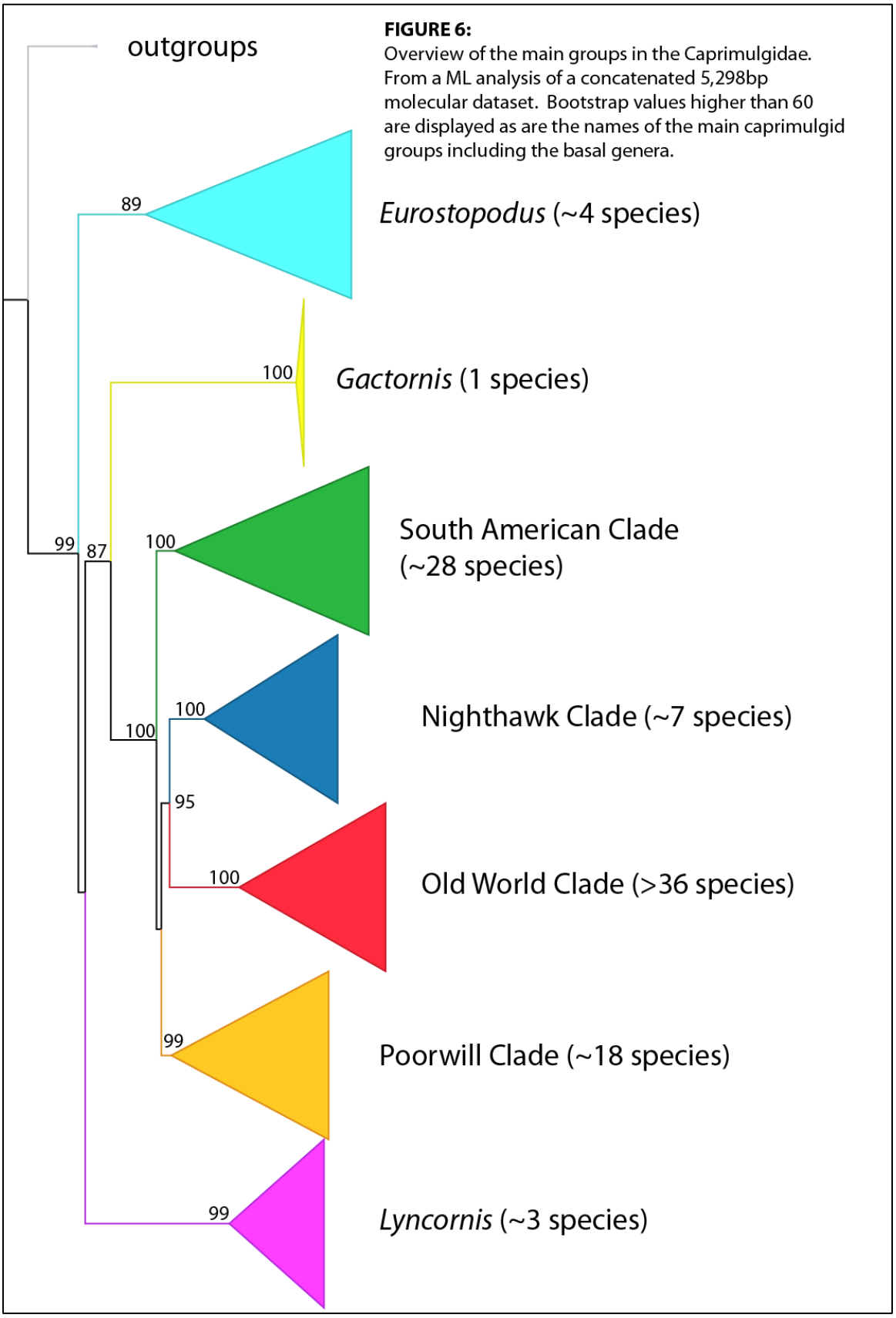


FIGURE 6:
Overview of the main groups in the Caprimulgidae. From a ML analysis of a concatenated 5,298bp molecular dataset. Bootstrap values higher than 60 are displayed as are the names of the main caprimulgid groups including the basal genera.

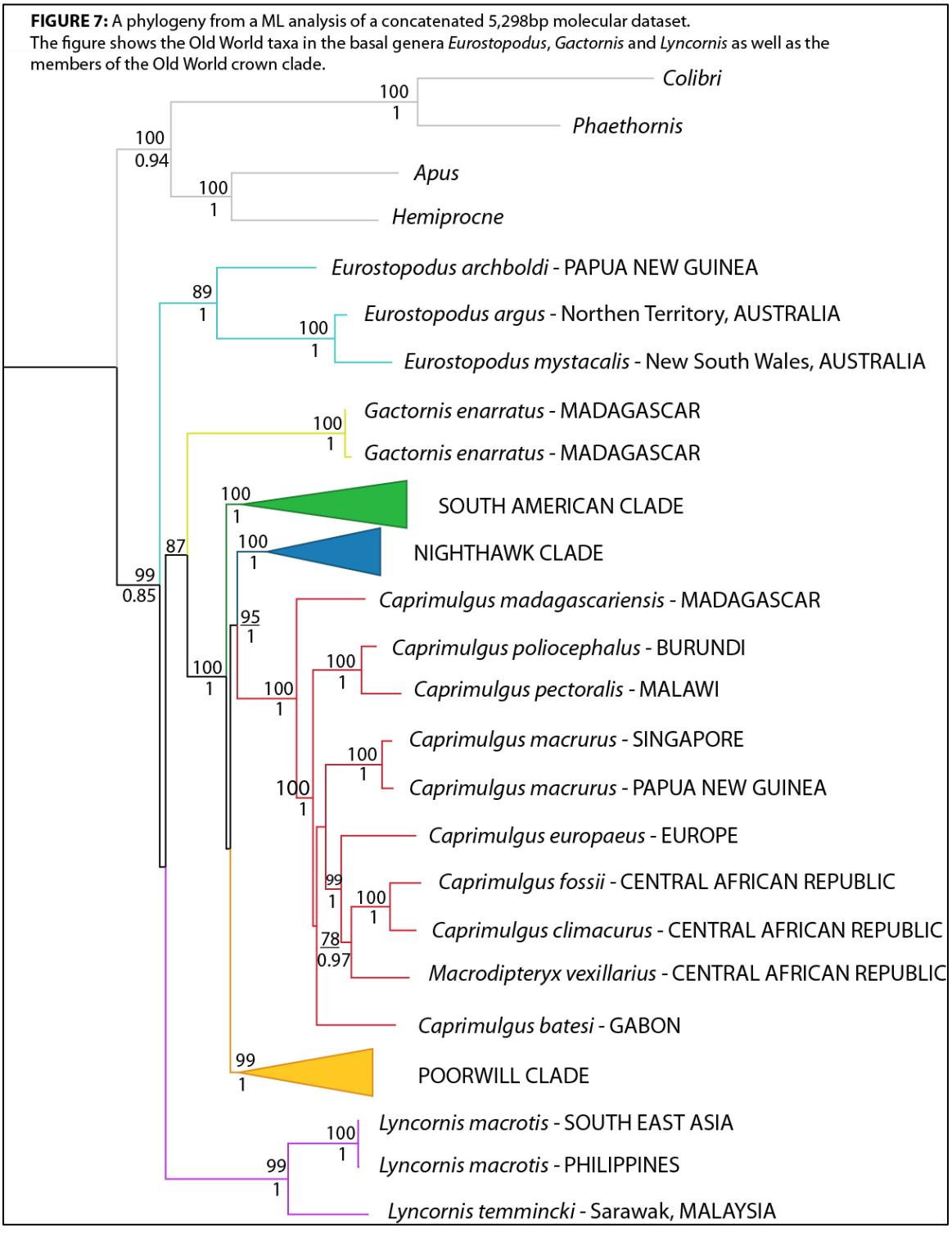


FIGURE 7: A phylogeny from a ML analysis of a concatenated 5,298bp molecular dataset. The figure shows the Old World taxa in the basal genera *Eurostopodus*, *Gactornis* and *Lyncornis* as well as the members of the Old World crown clade.

FIGURE 7

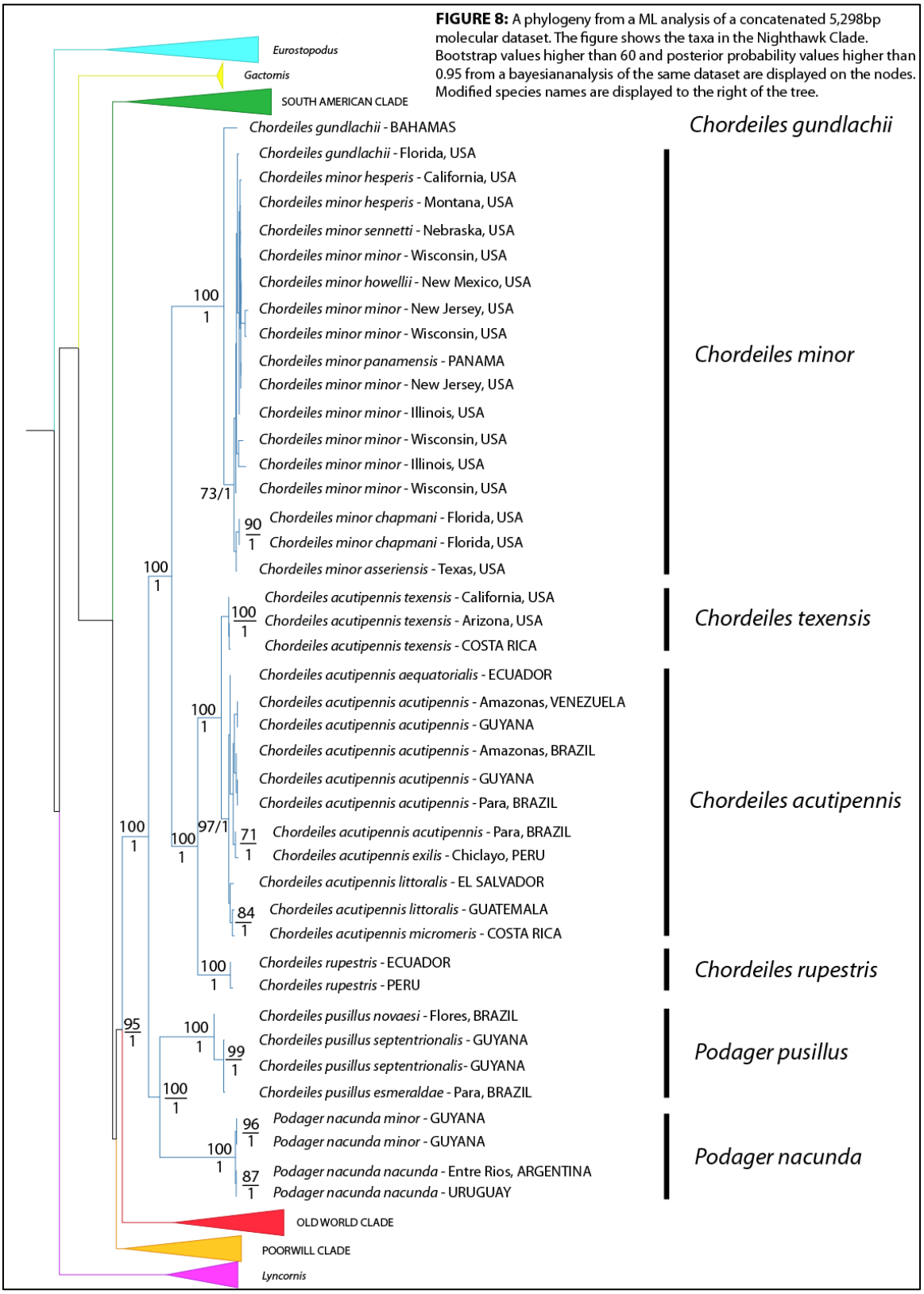


FIGURE 8: A phylogeny from a ML analysis of a concatenated 5,298bp molecular dataset. The figure shows the taxa in the Nighthawk Clade. Bootstrap values higher than 60 and posterior probability values higher than 0.95 from a bayesiananalysis of the same dataset are displayed on the nodes. Modified species names are displayed to the right of the tree.

FIGURE 8

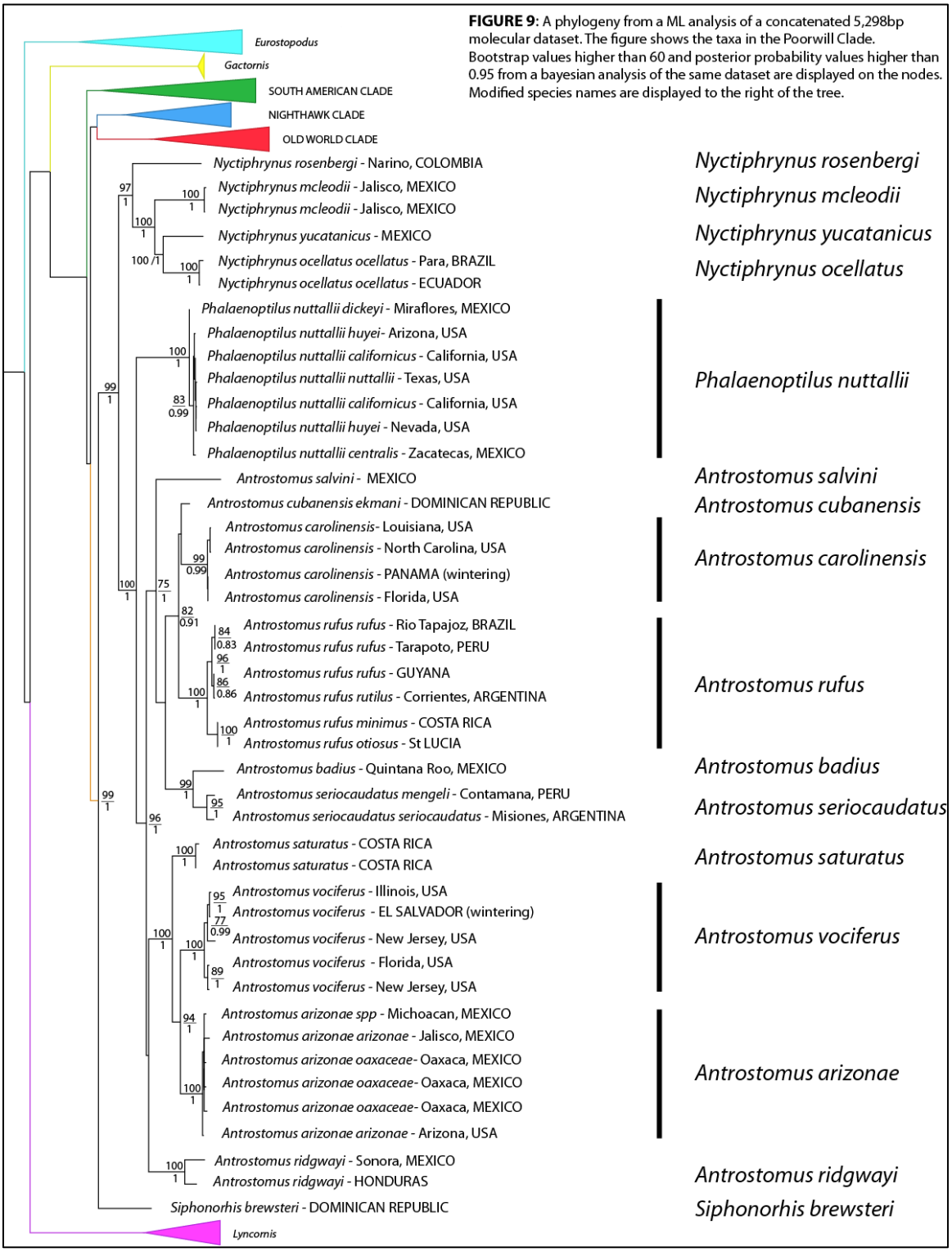


FIGURE 9: A phylogeny from a ML analysis of a concatenated 5,298bp molecular dataset. The figure shows the taxa in the Poorwill Clade. Bootstrap values higher than 60 and posterior probability values higher than 0.95 from a bayesian analysis of the same dataset are displayed on the nodes. Modified species names are displayed to the right of the tree.

FIGURE 9

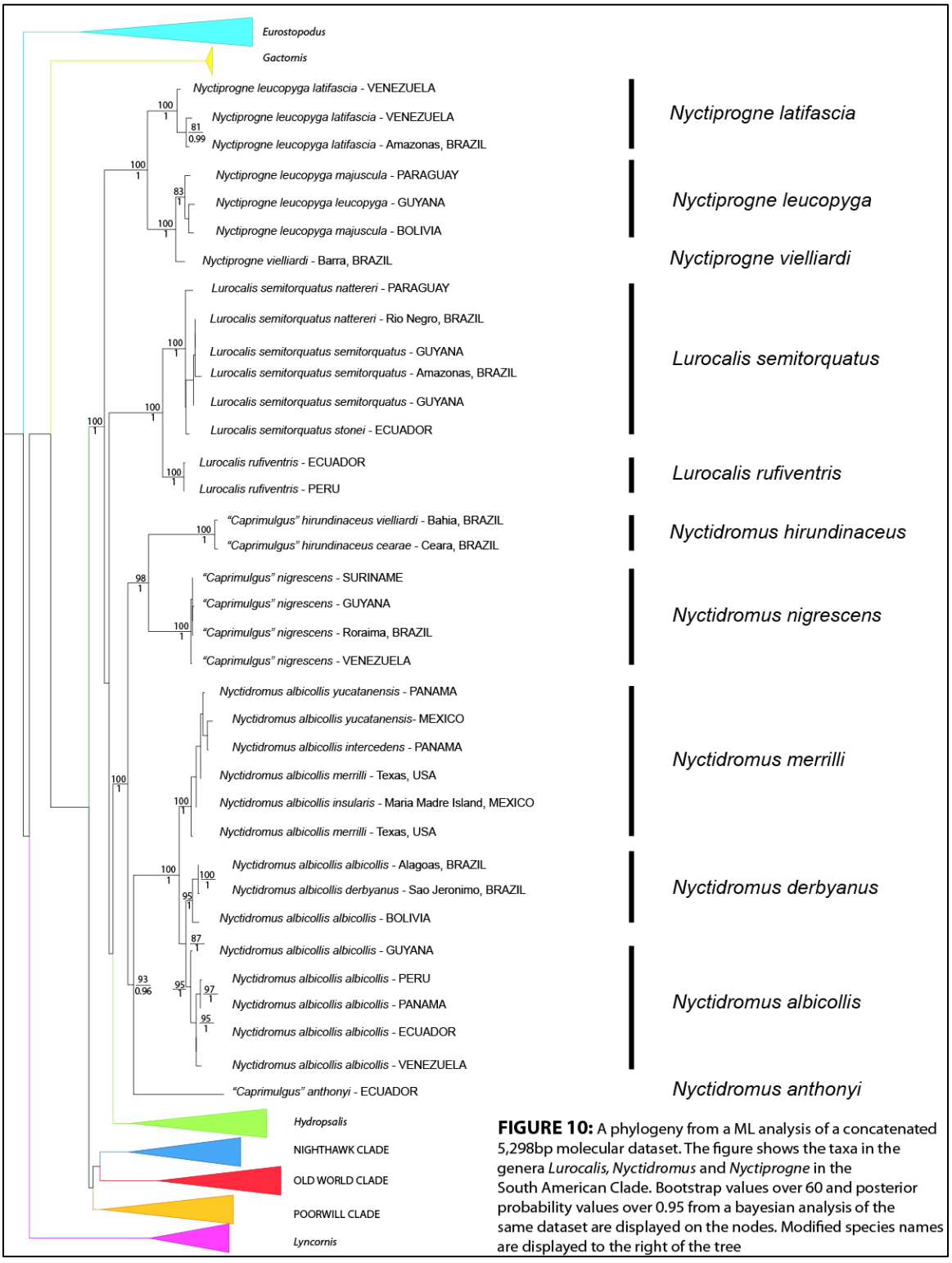


FIGURE 10: A phylogeny from a ML analysis of a concatenated 5,298bp molecular dataset. The figure shows the taxa in the genera *Lurocalis, Nyctidromus* and *Nyctiprogne* in the South American Clade. Bootstrap values over 60 and posterior probability values over 0.95 from a bayesian analysis of the same dataset are displayed on the nodes. Modified species names are displayed to the right of the tree

FIGURE 10

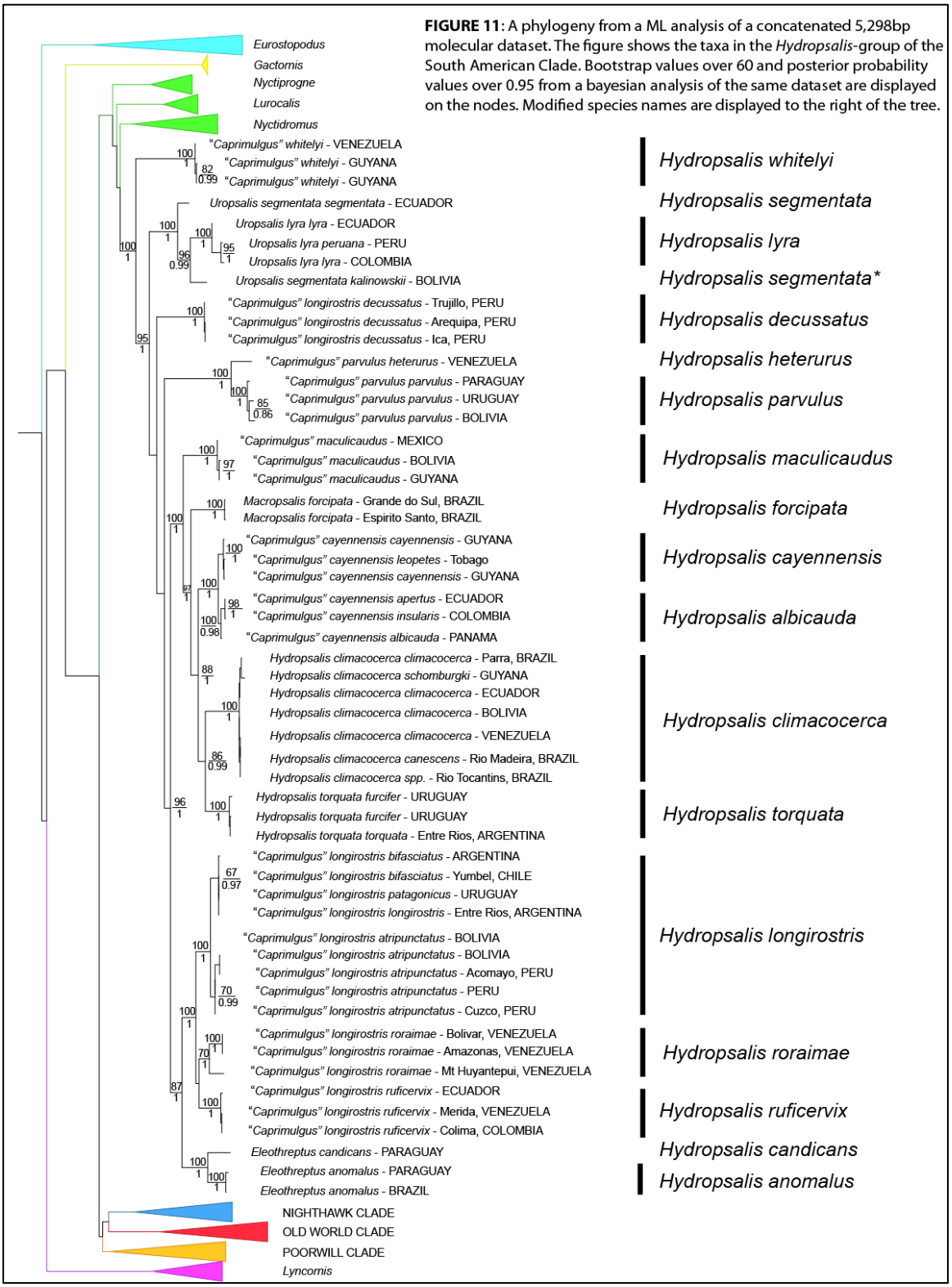


FIGURE 11: A phylogeny from a ML analysis of a concatenated 5,298bp molecular dataset. The figure shows the taxa in the *Hydropsalis*-group of the South American Clade. Bootstrap values over 60 and posterior probability values over 0.95 from a bayesian analysis of the same dataset are displayed on the nodes. Modified species names are displayed to the right of the tree.

FIGURE 11

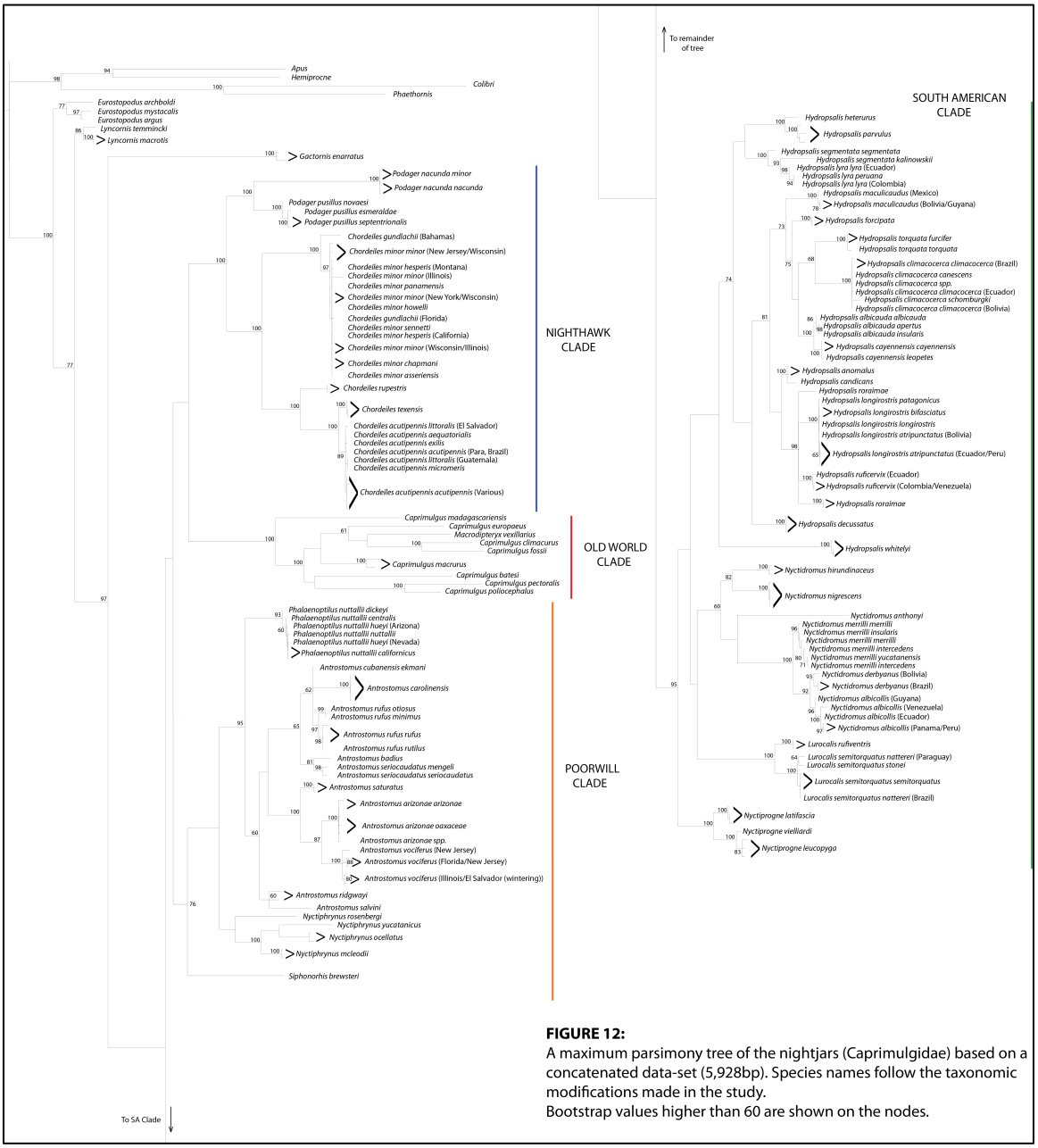


FIGURE 12:
A maximum parsimony tree of the nightjars (Caprimulgidae) based on a concatenated data-set (5,928bp). Species names follow the taxonomic modifications made in the study.
Bootstrap values higher than 60 are shown on the nodes.

FIGURE 12

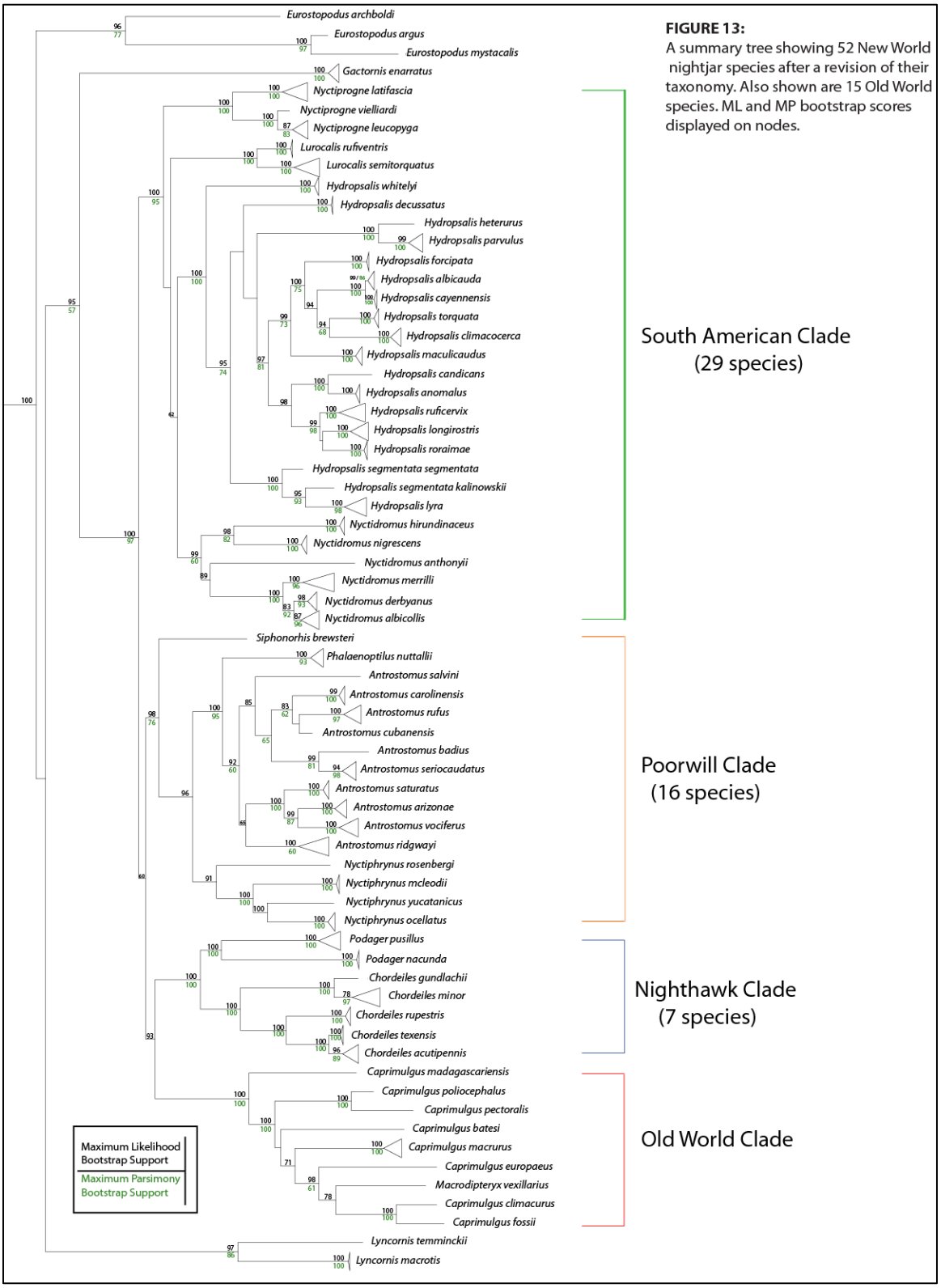


FIGURE 13:
A summary tree showing 52 New World nightjar species after a revision of their taxonomy. Also shown are 15 Old World species. ML and MP bootstrap scores displayed on nodes.

FIGURE 13

8. TABLES

Table 1 – Specimen list

TABLE 1 – PART 1: LIST OF TAXA SAMPLED

Antrostomus badius Bangs & Peck 1908
Antrostomus carolinensis Gmelin 1789
Antrostomus cubanensis ekmani Lönnberg 1929
Antrostomus ridgwayi Nelson 1897
Antrostomus rufus minimus Griscom & Greenway 1937
Antrostomus rufus otiosus Bangs 1911
Antrostomus rufus rufus Boddaert 1783
Antrostomus rufus rutilus Burmeister 1856
Antrostomus salvini Hartert 1892
Antrostomus saturatus Salvin 1870
Antrostomus seriocaudatus mengeli Dickerman 1975
Antrostomus seriocaudatus seriocaudatus Cassin 1849
Antrostomus vociferus arizonae Brewster 1881
Antrostomus vociferus oaxaceae Nelson 1900
Antrostomus vociferus vociferus Wilson 1812
Caprimulgus anthonyi Chapman 1923
Caprimulgus batesi Sharpe 1906
Caprimulgus cayennensis albicauda Lawrence 1875
Caprimulgus cayennensis apertus Peters 1940
Caprimulgus cayennensis cayennensis Gmelin 1789
Caprimulgus cayennensis insularis Richmond 1902
Caprimulgus cayennensis leopetes Jardine & Selby 1830
Caprimulgus climacurus Vielliot 1825
Caprimulgus europaeus Linnaeus 1758
Caprimulgus fossii Hartlaub 1857
Caprimulgus hirundinaceus cearae Cory 1917
Caprimulgus hirundinaceus vielliardi Ribon 1995
Caprimulgus longirostris atripunctatus Chapman 1923
Caprimulgus longirostris bifasciatus Gould 1837
Caprimulgus longirostris decussatus Tschudi 1844
Caprimulgus longirostris longirostris Bonaparte 1825
Caprimulgus longirostris patagonicus Olrog 1962
Caprimulgus longirostris roraimae Chapman 1929
Caprimulgus longirostris ruficervix Sclater 1866
Caprimulgus macrurus Horsfield 1821
Caprimulgus maculicaudus Lawrence 1862
Caprimulgus madagascariensis Sganzin 1840
Caprimulgus nigrescens Cabanis 1848
Caprimulgus parvulus heterurus Todd 1915
Caprimulgus parvulus parvulus Gould 1837
Caprimulgus pectoralis Cuvier 1816

Caprimulgus poliocephalus Ruppell 1835
Caprimulgus whitelyi Salvin 1885
Chordeiles acutipennis acutipennis Hermann 1783
Chordeiles acutipennis aequatorialis Chapman 1923
Chordeiles acutipennis exilis Lesson 1839
Chordeiles acutipennis littoralis Brodkorb 1940
Chordeiles acutipennis micromeris Oberholser 1914
Chordeiles acutipennis texensis Lawrence 1856
Chordeiles gundlachii vicinus Lawrence 1856
Chordeiles minor asseriensis Cherrie 1896
Chordeiles minor chapmani Coues 1888
Chordeiles minor hesperis Grinnell 1905
Chordeiles minor howellii Oberholser 1914
Chordeiles minor minor Forster 1771
Chordeiles minor panamensis Eisenmann 1962
Chordeiles minor sennetti Coues 1888
Chordeiles pusillus esmeraldae Zimmer & Phelps 1947
Chordeiles pusillus novaesi Dickerman 1988
Chordeiles pusillus septentrionalis Hellmayr 1908
Chordeiles rupestris Spix 1825
Eleothreptus anomalus Gould 1838
Eleothreptus candicans Pelzeln 1866
Eurostopodus archboldi Mayr & Rand 1935
Eurostopodus argus Hartert 1892
Eurostopodus mystacalis Temminck 1826
Gactornis enarratus Gray 1871
Hydropsalis torquata furcifer Vielliot 1817
Hydropsalis torquata torquata Gmelin 1789
Hydropsalis climacocerca canescens Griscom & Greenway 1937
Hydropsalis climacocerca climacocerca Tschudi 1844
Hydropsalis climacocerca schomburgki Sclater 1866
Lurocalis rufiventris Taczanowski 1884
Lurocalis semitorquatus nattereri Temminck 1822
Lurocalis semitorquatus semitorquatus Gmelin 1789
Lurocalis semitorquatus stonei Huber 1923
Lyncornis macrotis Vigors 1831
Lyncornis temmincki Gould 1838
Macrodipteryx vexillarius Gould 1838
Macropsalis forcipata Nitzsch 1840
Nyctidromus albicollis albicollis Gmelin 1789
Nyctidromus albicollis derbyanus Gould 1838
Nyctidromus albicollis insularis Nelson 1898
Nyctidromus albicollis intercedens Griscom 1929
Nyctidromus albicollis merrilli Sennett 1888
Nyctidromus albicollis yucatanensis Nelson 1901
Nyctiphrynus mcleodii Brewster 1888

Nyctiphrynus ocellatus ocellatus Tschudi 1844
Nyctiphrynus rosenbergi Hartert 1895
Nyctiphrynus yucatanensis Hartert 1892
Nyctiprogne leucopyga latifascia Friedmann 1945
Nyctiprogne leucopyga leucopyga Spix 1825
Nyctiprogne leucopyga majuscula Pinto & Camargo 1952
Nyctiprogne vielliardi Lencioni-Neto 1994
Phalaenoptilus nuttallii californicus Ridgway 1887
Phalaenoptilus nuttallii centralis Moore 1947
Phalaenoptilus nuttallii dickeyi Grinnell 1928
Phalaenoptilus nuttallii huyei Dickey 1928
Phalaenoptilus nuttallii nuttallii Audobon 1844
Podager nacunda minor Cory 1915
Podager nacunda nacunda Viellot 1817
Siphonorhis brewsteri Chapman 1917
Uropsalis lyra lyra Bonaparte 1850
Uropsalis lyra peruana Berlepsch & Stolzmann 1906
Uropsalis segmentata kalinowskii Berlepsch & Stolzmann 1894
Uropsalis segmentata segmentata Cassin 1849

PART 2: LIST OF SPECIMENS – a) Source, Specimen number, Specimen type

Taxon Name	**Source**	**Specimen number**	**Specimen type**
Antrostomus badius#*	AMNH	#824782	Skin
Antrostomus carolinensis#	AMNH	DOT 13818	Fresh Tissue
Antrostomus carolinensis#	USNM	B16652	Fresh Tissue
Antrostomus carolinensis#	LSUMZ	B-3403	Fresh Tissue
Antrostomus carolinensis#	AMNH	#814800	Skin
Antrostomus cubanensis ekmani#	AMNH	#477312	Skin
Antrostomus ridgwayi#	AMNH	#817016	Skin
Antrostomus ridgwayi#$	AMNH	#326088	Skin
Antrostomus rufus minimus#	AMNH	#389422	Skin
Antrostomus rufus otiosus#	AMNH	#477310	Skin
Antrostomus rufus rufus#	USNM	B04420	Fresh Tissue
Antrostomus rufus rufus#	LSUMZ	B-44579	Fresh Tissue
Antrostomus rufus rufus#	AMNH	#288295	Skin
Antrostomus rufus rutilus#	AMNH	#798850	Skin
Antrostomus salvini#	Sequence from Genbank (Han et al . 2010)		
Antrostomus saturatus#	LSUMZ	B-16198	Fresh Tissue
Antrostomus saturatus#	AMNH	#811270	Skin
Antrostomus seriocaudatus mengeli#	LSUMZ	B-28908	Fresh Tissue
Antrostomus seriocaudatus seriocaudatus#	AMNH	#169760	Skin
Antrostomus vociferus spp. #	FM	394005	Fresh Tissue
Antrostomus vociferus spp. #	FM	433988	Fresh Tissue
Antrostomus vociferus arizonae#	FM	343200	Fresh Tissue
Antrostomus vociferus arizonae#	AMNH	#477247	Skin

All *Antrostomus* specimens were labeled *Caprimulgus*
* Labeled as *Caprimulgus salvini badius*
$ Mislabeled as *Caprimulgus vociferus*

Taxon Name	Source	Specimen number	Specimen type
Antrostomus vociferus oaxaceae#	AMNH	#815275	Skin
Antrostomus vociferus oaxaceae#	AMNH	#815279	Skin
Antrostomus vociferus oaxaceae#	AMNH	#815280	Ski
Antrostomus vociferus vociferus#	AMNH	DOT 7377	Fresh Tissue
Antrostomus vociferus vociferus#$	ANSP	24536	Fresh Tissue
Antrostomus vociferus vociferus#	AMNH	DOT 9310	Fresh Tissue
Antrostomus vociferus vociferus#	FM	444791	Fresh Tissue
Caprimulgus anthonyi	AMNH	DOT 16843	Fresh Tissue
Caprimulgus batesi	USNM	B09936	Fresh Tissue
Caprimulgus cayennensis albicauda	AMNH	#294678	Skin
Caprimulgus cayennensis apertus	ANSP	19607	Fresh Tissue
Caprimulgus cayennensis cayennensis	ANSP	21440	Fresh Tissue
Caprimulgus cayennensis cayennensis	USNM	B04364	Fresh Tissue
Caprimulgus cayennensis insularis	AMNH	#133075	Skin
Caprimulgus cayennensis leopetes	AMNH	#477206	Skin
Caprimulgus climacurus	AMNH	DOT 11123	Fresh Tissue
Caprimulgus europaeus	AMNH	DOT 10905	Fresh Tissue
Caprimulgus fossii	AMNH	DOT 2165	Fresh Tissue
Caprimulgus hirundinaceus cearae	AMNH	#241596	Skin
Caprimulgus hirundinaceus vielliardi	AMNH	#477244	Skin
Caprimulgus longirostris atripunctatus	AMNH	DOT 2733	Fresh Tissue
Caprimulgus longirostris atripunctatus	FM	429897	Fresh Tissue
Caprimulgus longirostris atripunctatus	LSUMZ	B-3571	Fresh Tissue
Caprimulgus longirostris atripunctatus	AMNH	#820494	Skin
Caprimulgus longirostris atripunctatus	AMNH	#823745	Skin
Caprimulgus longirostris bifasciatus	AMNH	DOT 13553	Fresh Tissue

All Antrostomus specimens were labeled *Caprimulgus*
$ Mislabeled as Phalaenoptilus *nuttallii*

Taxon Name	Source	Specimen number	Specimen type
Caprimulgus longirostris bifasciatus	AMNH	#748519	Skin
Caprimulgus longirostris decussatus	LSUMZ	B-5262	Fresh Tissue
Caprimulgus longirostris decussatus	AMNH	#151324	Skin
Caprimulgus longirostris decussatus	AMNH	#329090	Skin
Caprimulgus longirostris longirostris	AMNH	#779169	Skin
Caprimulgus longirostris patagonicus	USNM	B14783	Fresh Tissue
Caprimulgus longirostris roraimae	AMNH	DOT 4729	Fresh Tissue
Caprimulgus longirostris roraimae	LSUMZ	B-4783	Fresh Tissue
Caprimulgus longirostris roraimae	AMNH	#323499	Skin
Caprimulgus longirostris ruficervix	ANSP	27189	Fresh Tissue
Caprimulgus longirostris ruficervix	AMNH	#143565	Skin
Caprimulgus longirostris ruficervix	AMNH	#824761	Skin
Caprimulgus macrurus	AMNH	DOT 9565	Fresh Tissue
Caprimulgus macrurus	USNM	B04000	Fresh Tissue
Caprimulgus maculicaudus	USNM	B14678	Fresh Tissue
Caprimulgus maculicaudus	LSUMZ	B-13935	Fresh Tissue
Caprimulgus maculicaudus	AMNH	#768804	Skin
Caprimulgus madagascariensis	FM	356643	Fresh Tissue
Caprimulgus nigrescens	AMNH	DOT 12694	Fresh Tissue
Caprimulgus nigrescens	FM	389183	Fresh Tissue
Caprimulgus nigrescens	USNM	B04272	Fresh Tissue
Caprimulgus nigrescens	LSUMZ	B-65861	Fresh Tissue
Caprimulgus parvulus heterurus	AMNH	#824104	Skin
Caprimulgus parvulus parvulus	AMNH	DOT 2207	Fresh Tissue
Caprimulgus parvulus parvulus	USNM	B20984	Fresh Tissue
Caprimulgus parvulus parvulus	LSUMZ	B-25754	Fresh Tissue
Caprimulgus pectoralis	FM	444036	Fresh Tissue
Caprimulgus poliocephalus	FM	357948	Fresh Tissue
Caprimulgus whitelyi	AMNH	DOT 11875	Fresh Tissue

Taxon Name	Source	Specimen number	Specimen type
Caprimulgus whitelyi	USNM	B19022	Fresh Tissue
Caprimulgus whitelyi	LSUMZ	B-48367	Fresh Tissue
Chordeiles acutipennis acutipennis	AMNH	DOT 14304	Fresh Tissue
Chordeiles acutipennis acutipennis	ANSP	21428	Fresh Tissue
Chordeiles acutipennis acutipennis	FM	392639	Fresh Tissue
Chordeiles acutipennis acutipennis	USNM	B04145	Fresh Tissue
Chordeiles acutipennis acutipennis	LSUMZ	B-25493	Fresh Tissue
Chordeiles acutipennis acutipennis	AMNH	#816611	Skin
Chordeiles acutipennis aequatorialis	ANSP	18986	Fresh Tissue
Chordeiles acutipennis exilis	AMNH	#824127	Skin
Chordeiles acutipennis littoralis	KU	9367	Fresh Tissue
Chordeiles acutipennis littoralis	AMNH	#813311	Skin
Chordeiles acutipennis micromeris	AMNH	#789456	Skin
Chordeiles acutipennis texensis	AMNH	DOT 4164	Fresh Tissue
Chordeiles acutipennis texensis	LSUMZ	B-18025	Fresh Tissue
Chordeiles acutipennis texensis	AMNH	#476941	Skin
Chordeiles gundlachii vicinus	FM	387662	Fresh Tissue
Chordeiles gundlachii vicinus	LSUMZ	B-48963	Fresh Tissue
Chordeiles minor asseriensis	AMNH	#361249	Skin
Chordeiles minor chapmani	FM	443599	Fresh Tissue
Chordeiles minor chapmani	FM	432665	Fresh Tissue
Chordeiles minor hesperis	AMNH	DOT 7786	Fresh Tissue
Chordeiles minor hesperis	ANSP	22294	Fresh Tissue
Chordeiles minor howellii / sennetti	AMNH	#815662	Skin
Chordeiles minor howellii	AMNH	#827821	Skin
Chordeiles minor minor	AMNH	DOT 10080	Fresh Tissue
Chordeiles minor minor	AMNH	DOT 13811	Fresh Tissue
Chordeiles minor minor	AMNH	DOT 13030	Fresh Tissue
Chordeiles minor minor	FM	395875	Fresh Tissue

Taxon Name	Source	Specimen number	Specimen type
Chordeiles minor minor	FM	428842	Fresh Tissue
Chordeiles minor minor	FM	428933	Fresh Tissue
Chordeiles minor minor	FM	432838	Fresh Tissue
Chordeiles minor minor	FM	456278	Fresh Tissue
Chordeiles minor minor	FM	459722	Fresh Tissue
Chordeiles minor panamensis	AMNH	#766711	Skin
Chordeiles minor *sennetti*	AMNH	#815659	Skin
Chordeiles pusillus esmeraldae	FM	392642	Fresh Tissue
Chordeiles pusillus novaesi	AMNH	#241901	Skin
Chordeiles pusillus septentrionalis	ANSP	21634	Fresh Tissue
Chordeiles pusillus septentrionalis	USNM	B12308	Fresh Tissue
Chordeiles rupestris	ANSP	17721	Fresh Tissue
Chordeiles rupestris	LSUMZ	B-43037	Fresh Tissue
Eleothreptus anomalus	KU	3275	Fresh Tissue
Eleothreptus anomalus	AMNH	#477064	Skin
Eleothreptus candicans	Sequence from Genbank (Larsen et al. 2006)		
Eurostopodus archboldi	AMNH	#816464	Skin
Eurostopodus argus	AMNH	#803858	Skin
Eurostopodus mystacalis	AMNH	DOT 2401	Fresh Tissue
Gactornis enarratus#	FM	352811	Fresh Tissue
Gactornis enarratus#	FM	431158	Fresh Tissue
*Hydropsalis torquata furcifer**	ANSP	22420	Fresh Tissue
*Hydropsalis torquata furcifer**	USNM	B06315	Fresh Tissue
Hydropsalis torquata torquata	AMNH	#449183	Skin
Hydropsalis climacocerca canescens	AMNH	#281556	Skin
Hydropsalis climacocerca climacocerca	ANSP	19378	Fresh Tissue

Labeled as *Caprimulgus enarratus*
* Labeled as *Hydropsalis brasiliana*

Taxon Name	Source	Specimen number	Specimen type
Hydropsalis climacocerca climacocerca	USNM	B06949	Fresh Tissue
Hydropsalis climacocerca climacocerca	AMNH	#791814	Skin
Hydropsalis climacocerca climacocerca	AMNH	#816610	Skin
Hydropsalis climacocerca schomburgki	ANSP	21533	Fresh Tissue
Hydropsalis climacocerca ssp.	AMNH	#430379	Skin
Lurocalis rufiventris	ANSP	19588	Fresh Tissue
Lurocalis rufiventris	LSUMZ	B-32761	Fresh Tissue
Lurocalis semitorquatus nattereri	KU	277	Fresh Tissue
Lurocalis semitorquatus nattereri	AMNH	#272590	Skin
Lurocalis semitorquatus semitorquatus	AMNH	DOT 14155	Fresh Tissue
Lurocalis semitorquatus semitorquatus	ANSP	20825	Fresh Tissue
Lurocalis semitorquatus semitorquatus	USNM	B11905	Fresh Tissue
Lurocalis semitorquatus stonei	ANSP	18451	Fresh Tissue
*Lyncornis macrotis**	USNM	B03732	Fresh Tissue
*Lyncornis macrotis**	Sequence from Genbank (Brown et al. 2008 as *Eurostopodus* macrotis)		
*Lyncornis temminckii**	AMNH	#648315	Skin
Macrodipteryx vexillarius	AMNH	DOT 10638	Fresh Tissue
Macropsalis forcipata	AMNH	#317317	Skin
Macropsalis forcipata	AMNH	#314025	Skin
Nyctidromus albicollis albicollis	AMNH	DOT 8787	Fresh Tissue
Nyctidromus albicollis albicollis	ANSP	16491	Fresh Tissue
Nyctidromus albicollis albicollis	FM	399123	Fresh Tissue
Nyctidromus albicollis albicollis	FM	433071	Fresh Tissue
Nyctidromus albicollis albicollis	USNM	B00440	Fresh Tissue
Nyctidromus albicollis albicollis	USNM	B11635	Fresh Tissue
Nyctidromus albicollis albicollis	LSUMZ	B-12198	Fresh Tissue
Nyctidromus albicollis derbyanus	AMNH	#393364	Skin

*Labeled as *Eurostopodus*

Taxon Name	Source	Specimen number	Specimen type
Nyctidromus albicollis insularis	AMNH	#477162	Skin
Nyctidromus albicollis intercedens	LSUMZ	B-27017	Fresh Tissue
Nyctidromus albicollis merrilli	LSUMZ	B-37032	Fresh Tissue
Nyctidromus albicollis merrilli	AMNH	#361109	Skin
Nyctidromus albicollis yucatanensis	ANSP	27121	Fresh Tissue
Nyctidromus albicollis yucatanensis	LSUMZ	B-19253	Fresh Tissue
Nyctiphrynus mcleodii#	FM	343199	Fresh Tissue
Nyctiphrynus mcleodii#	AMNH	#702848	Skin
Nyctiphrynus ocellatus ocellatus	ANSP	19987	Fresh Tissue
Nyctiphrynus ocellatus ocellatus	USNM	B07024	Fresh Tissue
Nyctiphrynus rosenbergi	AMNH	#117635	Skin
Nyctiphrynus yucatanicus	KU	2110	Fresh Tissue
Nyctiprogne leucopyga latifascia	AMNH	#431874	Skin
Nyctiprogne leucopyga latifascia	AMNH	#245957	Skin
Nyctiprogne leucopyga latifascia	AMNH	DOT 14305	Fresh Tissue
Nyctiprogne leucopyga leucopyga	USNM	B19380	Fresh Tissue
Nyctiprogne leucopyga majuscula	KU	3144	Fresh Tissue
Nyctiprogne leucopyga majuscula	AMNH	#791797	Skin
Nyctiprogne vielliardi	AMNH	#291910	Skin
Phalaenoptilus nuttallii californicus	AMNH	DOT 9848	Fresh Tissue
Phalaenoptilus nuttallii californicus	AMNH	#754341	Skin
Phalaenoptilus nuttallii centralis	AMNH	#783838	Skin
Phalaenoptilus nuttallii dickeyi	AMNH	#131568	Skin
Phalaenoptilus nuttallii hueyi	LSUMZ	B-40919	Fresh Tissue
Phalaenoptilus nuttallii hueyi	AMNH	#754348	Skin
Phalaenoptilus nuttallii nuttallii	LSUMZ	B-21804	Fresh Tissue

Labeled as *Otophanes mcleodii*

Taxon Name	Source	Specimen number	Specimen type
Podager nacunda minor	ANSP	21646	Fresh Tissue
Podager nacunda minor	USNM	B12379	Fresh Tissue
Podager nacunda nacunda	USNM	B20909	Fresh Tissue
Podager nacunda nacunda	USNM	B02768	Fresh Tissue
Siphonorhis brewsteri	KU	8149	Fresh Tissue
Uropsalis lyra lyra	ANSP	19587	Fresh Tissue
Uropsalis lyra lyra	AMNH	#460138	Skin
Uropsalis lyra peruana	AMNH	#820936	Skin
Uropsalis segmentata kalinowskii	AMNH	DOT 2877	Fresh Tissue
Uropsalis segmentata segmentata	ANSP	15766	Fresh Tissue

PART 2: LIST OF SPECIMENS – b) Geographic location, sequenced obtained

Taxon name	Geographic location	Sequences in data matrix
*Antrostomus badius**#	Quintana Roo, Mexico	ND2
Antrostomus carolinensis#	North Carolina, USA	ND2, ACO1 I-9 & RAG-1
Antrostomus carolinensis#	Florida, USA	ND2, ACO1 I-9 & RAG-1
Antrostomus carolinensis#	Louisiana, USA	ND2 & ACO1 I-9
Antrostomus carolinensis#	Panama (on wintering grounds)	ND2
Antrostomus cubanensis ekmani#	San Domingo, Dominican Republic	ND2 (partial)
Antrostomus ridgwayi	Sonora, Mexico	ND2, cytB, ACO1 I9 (partial)
*Antrostomus ridgwayi**	La Flor, Honduras	ND2
Antrostomus rufus minimus	Costa Rica	ND2
Antrostomus rufus otiosus	St. Lucia	ND2
Antrostomus rufus rufus	Berbice, Guyana	ND2, cytB, ACO1 I9 & RAG-1
Antrostomus rufus rufus	Tarapoto, Peru	ND2, cytB, ACO1 I9 & RAG-1
Antrostomus rufus rufus	Rio Tapajoz, Brazil	ND2
Antrostomus rufus rutilus	Corrientes, Argentina	ND2
Antrostomus salvini	Mexico	cytB
Antrostomus saturatus	San Jose, Costa Rica	ND2, cytB, ACO1 I9 & RAG-1
Antrostomus saturatus	Talamanca Cordillera, Costa Rica	ND2
Antrostomus seriocaudatus mengeli	Contamana, Peru	ND2, cytB, ACO1 I9 & RAG-1
Antrostomus seriocaudatus seriocaudatus	Misiones, Argentina	ND2
Antrostomus vociferus spp.	Michoagan, Mexico	ND2, ACO1 I9 & RAG-1
Antrostomus vociferus spp.	El Salvador	ND2, ACO1 I9
Antrostomus vociferus arizonae	Jalisco, Mexico	ND2, cytB & ACO1 I9 (partial)
Antrostomus vociferus arizonae	Huachuca Mts, Arizona, USA	ND2

All *Antrostomus* specimens were labeled *Caprimulgus*
* Labeled as *Caprimulgus salvini badius*
$ Mislabeled as *Caprimulgus vociferus*

Taxon name	Geographic location	Sequences in data matrix
Antrostomus vociferus oaxaceae	Oaxaca, Mexico	ND2
Antrostomus vociferus oaxaceae	Oaxaca, Mexico	ND2
Antrostomus vociferus oaxaceae	Oaxaca, Mexico	ND2
Antrostomus vociferus vociferus	Florida, USA	ND2, cytB, ACO1 I9 & RAG-1
Antrostomus vociferus vociferus#	New Jersey, USA	ND2 & ACO1 I9
Antrostomus vociferus vociferus	New Jersey, USA	ND2, ACO1 I9 & RAG-1 (partial)
Antrostomus vociferus vociferus	Illinois, USA	ND2, cytB & ACO1 I9
Caprimulgus anthonyi	El Oro Province, Ecuador	ND2, cytB, ACO1 I-9
Caprimulgus batesi	Gabon	ND2, cytB, ACO1 I-9 & RAG-1
Caprimulgus cayennensis albicauda	Panama	ND2
Caprimulgus cayennensis apertus	Imbatura Province, Ecuador	ND2 & cytB
Caprimulgus cayennensis cayennensis	Guyana	ND2, cytB, ACO1 I-9 & RAG-1
Caprimulgus cayennensis cayennensis	Berbice, Guyana	ND2, ACO1 I-9 & RAG-1
Caprimulgus cayennensis insularis	Norte De Santander, Colombia	ND2
Caprimulgus cayennensis leopetes	Tobago, Trinidad and Tobago	ND2
Caprimulgus climacurus	Central African Republic	ND2, cytB, ACO1 I-9 & RAG-1
Caprimulgus europaeus	North Sea	ND2, cytB & RAG-1
Caprimulgus fossii	Central African Republic	ND2, cytB, ACO1 I-9 & RAG-1
Caprimulgus hirundinaceus cearae	Ceara, Brazil	ND2
Caprimulgus hirundinaceus vielliardi	Bahia, Brazil	ND2
Caprimulgus longirostris atripunctatus	Bolivia	ND2, ACO1 I-9 & RAG-1
Caprimulgus longirostris atripunctatus	Cuzco, Peru	ND2, ACO1 I-9 & RAG-1
Caprimulgus longirostris atripunctatus	Acomayo, Peru	ND2 & cytB
Caprimulgus longirostris atripunctatus	Cordillera de Vilcabamba, Peru	ND2
Caprimulgus longirostris atripunctatus	Cochabamba, Bolivia	ND2
Caprimulgus longirostris bifasciatus	Argentina	ND2, cytB, ACO1 I9 & RAG-1

All *Antrostomus* specimens were labeled *Caprimulgus*
$ Mislabeled as *Phalaenoptilus nuttallii*

Taxon name	Geographic location	Sequences in data matrix
Caprimulgus longirostris decussatus	Ica, Peru	ND2, cytB, ACO1 I9 & RAG-1
Caprimulgus longirostris decussatus	Trujillo, Peru	ND2
Caprimulgus longirostris decussatus	Arequipa, Peru	ND2
Caprimulgus longirostris longirostris	Entre Rios, Argentina	ND2
Caprimulgus longirostris patagonicus	Tacuarembo, Uruguay	ND2, cytB, ACO1 I9 & RAG-1
Caprimulgus longirostris roraimae	Bolivar, Venezuela	ND2, cytB (partial) & ACO1 I9
Caprimulgus longirostris roraimae	Amazonas, Venezuela	ND2, cytB, ACO1 I9 & RAG-1
Caprimulgus longirostris roraimae	Mt Huyantepui, Venezuela	ND2
Caprimulgus longirostris ruficervix	Napo, Ecuador	ND2 & ACO1 I9
Caprimulgus longirostris ruficervix	Colima, Colombia	ND2
Caprimulgus longirostris ruficervix	Merida, Venezuela	ND2
Caprimulgus macrurus	Singapore	ND2, ACO1 I9 & RAG-1
Caprimulgus macrurus	New Ireland, Papua New Guinea	ND2 & cytB
Caprimulgus maculicaudus	Guyana	ND2, cytB, ACO1 I9 & RAG-1
Caprimulgus maculicaudus	Florida, Bolivia	ND2 & ACO1 I9
Caprimulgus maculicaudus	Oaxaca, Mexico	ND2
Caprimulgus madagascariensis	Antananarivo, Madagascar	ND2, cytB, ACO1 I9 & RAG-1
Caprimulgus nigrescens	Amazonas, Venezuela	ND2, cytB, ACO1 I9 & RAG-1
Caprimulgus nigrescens	Roraima, Brazil	ND2 & ACO1 I9
Caprimulgus nigrescens	Berbice, Guyana	ND2 & ACO1 I9
Caprimulgus nigrescens	Suriname	ND2 & cytB
Caprimulgus parvulus heterurus	Colon, Venezuela	ND2 (partial)
Caprimulgus parvulus parvulus	Bolivia	ND2, cytB, ACO1 I9 & RAG-1
Caprimulgus parvulus parvulus	Artigas, Uruguay	ND2 & ACO1 I9
Caprimulgus parvulus parvulus	Paraguay	ND2 & ACO1 I9
Caprimulgus pectoralis	Malawi	ND2, cytB, ACO1 I9 & RAG-1
Caprimulgus poliocephalus	Burundi	ND2, cytB, ACO1 I9 & RAG-1
Caprimulgus whitelyi	Bolivar, Venezuela	ND2, cytB, ACO1 I9 & RAG-1

Taxon name	Geographic location	Sequences in data matrix
Caprimulgus whitelyi	Guyana	ND2 & ACO1 I9
Caprimulgus whitelyi	Kopinang, Guyana	ND2, cytB & RAG-1
Chordeiles acutipennis acutipennis	Amazonas, Brazil	ND2, ACO1 I9 & RAG-1
Chordeiles acutipennis acutipennis	Upper Takutu, Guyana	ND2, cytB & ACO1 I9
Chordeiles acutipennis acutipennis	Para, Brazil	ND2, cytB, ACO1 I9 & RAG-1
Chordeiles acutipennis acutipennis	Berbice, Guyana	ND2 & RAG-1
Chordeiles acutipennis acutipennis	Para, Brazil	ND2 & ACO1 I9
Chordeiles acutipennis acutipennis	Amazonas, Venezuela	ND2
Chordeiles acutipennis aequatorialis	Loja, Ecuador	ND2
Chordeiles acutipennis exilis	Chiclayo, Peru	ND2
Chordeiles acutipennis littoralis	El Salvador	ND2, cytB, ACO1 I9 & RAG-1
Chordeiles acutipennis littoralis	Guatemala	ND2
Chordeiles acutipennis micromeris	Costa Rica	ND2 & ACO1 I9
Chordeiles acutipennis texensis	Arizona, USA	ND2, ACO1 I9 & RAG-1
Chordeiles acutipennis texensis	Chocolate Mts, California, USA	ND2, cytB, ACO1 I9 & RAG-1
Chordeiles acutipennis texensis	Costa Rica	ND2
Chordeiles gundlachii vicinus	Florida, USA	ND2, ACO1 I9 & RAG-1 (partial)
Chordeiles gundlachii vicinus	Bahamas	ND2, cytB, ACO1 I9 & RAG-1
Chordeiles minor asseriensis	Tivoli, Texas, USA	ND2
Chordeiles minor chapmani	Florida, USA	ND2, cytB, ACO1 I9 & RAG-1
Chordeiles minor chapmani	Florida, USA	ND2
Chordeiles minor hesperis	California, USA	ND2, cytB, ACO1 I9 & RAG-1
Chordeiles minor hesperis	Montana, USA	ND2, cytB & ACO1 I9
Chordeiles minor howellii / *sennetti*	Nebraska, USA	ND2 & ACO1 I9
Chordeiles minor howellii	New Mexico, USA	ND2 & ACO1 I9
Chordeiles minor minor	New York, USA	ND2 & cytB
Chordeiles minor minor	New Jersey, USA	ND2
Chordeiles minor minor	New York, USA	ND2
Chordeiles minor minor	Wisconsin, USA	ND2, ACO1 I9 & RAG-1

Taxon name	Geographic location	Sequences in data matrix
Chordeiles minor minor	Wisconsin, USA	ND2, ACO1 I9 & RAG-1
Chordeiles minor minor	Wisconsin, USA	ND2 & ACO1 I9
Chordeiles minor minor	Wisconsin, USA	ND2 & ACO1 I9
Chordeiles minor minor	Illinois, USA	ND2, ACO1 I9 & RAG-1
Chordeiles minor minor	Illinois, USA	ND2 & ACO1 I9
Chordeiles minor panamensis	Panama	ND2
Chordeiles minor *sennetti*	Nebraska, USA	ND2 & ACO1 I9
Chordeiles pusillus esmeraldae	Para, Brazil	ND2, cytB, ACO1 I9 & RAG-1
Chordeiles pusillus novaesi	Flores, Brazil	ND2 (partial)
Chordeiles pusillus septentrionalis	Guyana	ND2, cytB, ACO1 I9 & RAG-1
Chordeiles pusillus septentrionalis	Guyana	ND2, ACO1 I9 & RAG-1
Chordeiles rupestris	Napo, Ecuador	ND2, ACO1 I9 & RAG-1
Chordeiles rupestris	Rio Maranon, Peru	ND2, cytB & ACO1 I9
Eleothreptus anomalus	Paraguay	ND2, cytB, ACO1 I9 & RAG-1
Eleothreptus anomalus	Brazil	ND2
Eleothreptus candicans	Paraguay	cytB
Eurostopodus archboldi	Mt Albert Edward, New Guinea	ND2 (partial)
Eurostopodus argus	Northern Territory, Australia	ND2 (partial)
Eurostopodus mystacalis	New South Wales, Australia	ND2, cytB, ACO1 I9 & RAG-1
Gactornis enarratus#	Toliara, Madagascar	ND2, cytB, ACO1 I-9 & RAG-1
Gactornis enarratus#	Antsiranana, Madagascar	ND2, cytB & ACO1 I-9
*Hydropsalis torquata furcifer**	Uruguay	ND2, cytB, ACO1 I9 & RAG-1
*Hydropsalis torquata furcifer**	Tacuarembo, Uruguay	ND2, ACO1 I9 & RAG-1
Hydropsalis torquata torquata	Entre Rios, Argentina	ND2
Hydropsalis climacocerca canescens	Rio Madeira, Brazil	ND2
Hydropsalis climacocerca climacocerca	Napo, Ecuador	ND2

Labeled as *Caprimulgus enarratus*
* Labeled as *Hydropsalis brasiliana*

Taxon name	Geographic location	Sequences in data matrix
Hydropsalis climacocerca climacocerca	Para, Brazil	ND2, cytB, ACO1 I9 & RAG-1
Hydropsalis climacocerca climacocerca	Beni, Bolivia	ND2
Hydropsalis climacocerca climacocerca	Amazonas, Venezuela	ND2
Hydropsalis climacocerca schomburgki	Guyana	ND2, cytB, ACO1 I9 & RAG-1
Hydropsalis climacocerca ssp.	Rio Tocantins, Brazil	ND2
Lurocalis rufiventris	Zamora Chinchipe, Ecuador	ND2, cytB & ACO1 I9
Lurocalis rufiventris	Chontali, Peru	ND2, ACO1 I9 & RAG-1
Lurocalis semitorquatus nattereri	Paraguay	ND2, cytB, ACO1 I9 & RAG-1
Lurocalis semitorquatus nattereri	Rio Negro, Brazil	ND2 (partial)
Lurocalis semitorquatus semitorquatus	Amazonas, Brazil	ND2 & ACO1 I9
Lurocalis semitorquatus semitorquatus	Potaro-Siparuni, Guyana	ND2 & ACO1 I9
Lurocalis semitorquatus semitorquatus	Guyana	ND2, cytB, ACO1 I9 & RAG-1
Lurocalis semitorquatus stonei	Manabi, Ecuador	ND2, cytB & ACO1 I9
*Lyncornis macrotis**	Luzon, Phillipines	ND2, cytB & RAG-1
*Lyncornis macrotis**	Unknown	ND2
*Lyncornis temminckii**	Sarawak	ND2 (partial)
Macrodipteryx vexillarius	Central African Republic	ND2, cytB, ACO1 I9 & RAG-1
Macropsalis forcipata	Espirito Santo, Brazil	ND2
Macropsalis forcipata	Grande do Sul, Brazil	ND2
Nyctidromus albicollis albicollis	Venezuela	ND2, cytB & ACO1 I9
Nyctidromus albicollis albicollis	Morona-Santiago, Ecuador	ND2
Nyctidromus albicollis albicollis	Alagoas, Brazil	ND2, cytB, ACO1 I9 & RAG-1
Nyctidromus albicollis albicollis	Madre de Dios, Peru	ND2, ACO1 I9 & RAG-1
Nyctidromus albicollis albicollis	Bocas del Toro, Panama	ND2, ACO1 I9 & RAG-1
Nyctidromus albicollis albicollis	Guyana	ND2
Nyctidromus albicollis albicollis	Velasco, Bolivia	ND2, cytB & ACO1 I9
Nyctidromus albicollis derbyanus	Sao Jeronimo, Brazil	ND2

* Labeled as *Eurostopodus*

Taxon name	Geographic location	Sequences in data matrix
Nyctidromus albicollis insularis	Maria Madre Island, Mexico	ND2
Nyctidromus albicollis intercedens	Panama	ND2, cytB & ACO1 I9
Nyctidromus albicollis merrilli	Webb County, Texas, USA	ND2, cytB & ACO1 I9
Nyctidromus albicollis merrilli	Cameron County, Texas, USA	ND2
Nyctidromus albicollis yucatanensis	Panama	ND2 & cytB
Nyctidromus albicollis yucatanensis	Mexico	cytB & ACO1 I9
Nyctiphrynus mcleodii#	Jalisco, Mexico	ND2, cytB & RAG-1
Nyctiphrynus mcleodii#	Jalisco, Mexico	ND2
Nyctiphrynus ocellatus ocellatus	Sucumbios, Ecuador	ND2 & RAG-1 (partial)
Nyctiphrynus ocellatus ocellatus	Para, Brazil	ND2, cytB & RAG-1
Nyctiphrynus rosenbergi	Narino, Colombia	ND2 (partial) & cytB
Nyctiphrynus yucatanicus	Mexico	ND2, cytB, ACO1 I9 & RAG-1
Nyctiprogne leucopyga latifascia	Rio Cassiquaire, Venezuela	ND2 (partial)
Nyctiprogne leucopyga latifascia	Rio Cassiquaire, Venezuela	ND2 (partial)
Nyctiprogne leucopyga latifascia	Amazonas, Brazil	ND2, cytB(partial) & ACO1 I9
Nyctiprogne leucopyga leucopyga	Upper Takutu, Guyana	ND2, cytB, ACO1 I9 & RAG-1
Nyctiprogne leucopyga majuscula	Paraguay	ND2, cytB, ACO1 I9 & RAG-1
Nyctiprogne leucopyga majuscula	Beni, Bolivia	ND2 (partial)
Nyctiprogne vielliardi	Barra, Brazil	ND2
Phalaenoptilus nuttallii californicus	Shasta, California, USA	ND2, cytB & ACO1 I9
Phalaenoptilus nuttallii californicus	San Diego, California, USA	ND2
Phalaenoptilus nuttallii centralis	Zacatecas, Mexico	ND2
Phalaenoptilus nuttallii dickeyi	Miraflores, Mexico	ND2
Phalaenoptilus nuttallii hueyi	Clark County, Nevada, USA	ND2, ACO1 I9 & RAG-1
Phalaenoptilus nuttallii hueyi	Arizona, USA	ND2
Phalaenoptilus nuttallii nuttallii	Jeff Davis County, Texas, USA	ND2, cytB, ACO1 I9 & RAG-1
Podager nacunda minor	Upper Takutu, Guyana	ND2 & ACO1 I9

Labeled as *Otophanes mcleodii*

Taxon name	Geographic location	Sequences in data matrix
Podager nacunda minor	Guyana	ND2, cytB, ACO1 I9 & RAG-1
Podager nacunda nacunda	Artigas, Uruguay	ND2, cytB & ACO1 I9
Podager nacunda nacunda	Entre Rios, Argentina	cytB, ACO1 I9 & RAG-1
Siphonorhis brewsteri	Dominican Republic	ND2, cytB, ACO1 I9 & RAG-1
Uropsalis lyra lyra	Zamora Chinchipe, Ecuador	ND2 & cytB
Uropsalis lyra lyra	Mt Macarena, Colombia	ND2 (partial)
Uropsalis lyra peruana	Cerros del Sira, Peru	ND2 (partial)
Uropsalis segmentata kalinowskii	Bolivia	ND2, cytB, ACO1 I9 & RAG-1
Uropsalis segmentata segmentata	Carchi, Ecuador	ND2 & ACO1 I9

Table 2 - Primers used for amplification and sequencing

a) General all-purpose primers

See attached table

b) Specifically designed primers for amplification of degraded DNA from toe-pad extractions

ND2

Eleven sets of primers were designed using reference sequences from the following taxa:

Chordeiles minor and its congeners (CM)
Caprimulgus longirostris and close relatives (CL)
Antrostomus rufus and close relatives (RUF)
Antrostomus vociferus and close relatives (AV)
Eurostopodus macrotis (MA)
Eurostopodus mystacalis (MY)
The genus *Lurocali*s (L)
Nyctidromus albicollis and close relatives (NA)
The genus *Nyctiphrynus* (NPHR)
The genus *Nyctiprogne* (NP)
Phalaenoptilus nuttallii (PN)
The genus *Siphonorhis* (SIPH)

Each primer set includes taxon-specific primers ranging from a single primer aimed to amplify a particular gene region to nine or ten primer pairs that together capture the whole gene. On occasions primers from different primer sets were paired up to amplify problematic regions. The length of fragments amplified and sequenced using various primer pairs ranged from around 80bp to up to 200bp. Primers which names include numbers (1-9) are always leading primers while primers which names are followed by a letter (A-I) are reverse primers. The external primers designed using *Chordeiles minor* reference sequences were also successfully used for most other taxa.

Primer name	Sequence 5' to 3'
CM FW (External primer)	GCTATCGGGCCCATACCCCGAA
CM REV (External primer)	CAGGTTAATATCTTGCGGGTCT
CM 1	CACTGGGCAATAGCTTGAACC
CM 2	ATCAAATACTTCCTAGTGCAGGCA
CM 3	TGGCTCCTACTGACAACAGCAATTG

CM 4	ACCGGCCTCCTTCTATCGACA
CM5	ATCATGGCCATTATCTCAGCAG
CM 6	ACTAACCCTCATAACATTCTACC
CM 7	ACCTCATGAACAAAGGTCCCAACAC
CM 8	CAATGGCACATCTACAGCTCAACA
CM 9	CAATGGCACATCTACAGCTCAACA
CM A	ATACTTCCTAGTACAGGCAGCA
CM B	GAGACATCACCCAGCTAACACA
CM C	AACTTGGACTAGTACCATTCC
CM D	ATCACTATCCTCCTTCTCACATCC
CM E	CTAGCTTTCTCATCCCTCGCACACT
CM F	ACCGCCACCATCTTCCTCACTCTA
CM G	GCTTCCTGCCAAAATGACTTATAC
CM H	CGTCTCGCATACTATTCAACA
CM I	CATAATCCTAACAACCATCTAGA
CL 1	ACAATCTCAAGCAACCATTGA
CL 2	TTCCTAGTACAAGCAACTGC
CL 3	ATAAACGCATGATTCACCGGA
CL 4	CAGAAGTACTTCAGGGCACCTC
CL 5	GCTTCAGCAGCCCTAGGGGG
CL 6	ATCATAACAGCCACCGTAT
CL 7	TAGCTGGACTTCCCCCA
CL 8	TCGCATACTACTCAACAATTAC
CL A	GAGCAGTAGAAGCCGCAATC
CL B	ATAAAACTAGGCCTAGTCCCATT
CL C	CTCCTACTATCAACAATAAT
CL D	CAAATCCGAAAAATCCTAGC
CL E	CCTAAATGCAACACTCAT
CL F	ACAAGAAATAACCACAGCAGC
CL G	TCCTCAATATCGGCCTTACT
RUF 1	GACTAGAAATTAACACTCTA
RUF 2	TCTGATTCCCAGAAGTCCTTCA
RUF 3	ACTAATAACCACTATAGCTA
RUF 4	CATAACTACTACCATCTTC
RUF 5	CATATTATCACTACTTGGACTA
RUF A	ATTGCCTCAGCCGCCCTAGGA
RUF B	TACTACCATCTTCCTTA
RUF C	ACTGCAACAGCCACAATCAT
AV 1	GCCTCCTCCTAGGAACAACCATTA
AV 2	GCCATTCTCCTATTCTCCAGC
AV 3	ACCATTCCACTTCTGATTCCCA
AV 4	TCACTCAACCCAACACTAAT
AV 5	AGCCTTCTCATCCATCTCCCAC
AV 6	ACTCTCAACCATAATAAC
AV 7	ACAAGAAATAACCACAGCAGC
AV 8	ACACAAAACAATGGCATA

AV A	CCTCATCTCAAAATCCCAC
AV B	CTCCAGCACAATAAACGCATGA
AV C	TGATTCCCAGAAGTCCTTCAAG
AV D	AACCAAACACAAATCCGA
AV E	AAACTCACCCTCATAACATTC
AV F	AATGCAACCCTCATACTAA
AV G	TTACCTCCGTCTCGCATA
AV H	ATCTCCCCTATAATCCTTACC
MA 3	TGATTACCATGGCCATTGCAT
MA 5	TCAACAATAATAACCTCATG
MA 7	TCAACAATCACCCTTTCAC
MA A	TACATCCAACTCACTCAACC
MA C	ATAACCGCTACCATCTTC
MA E	ACCTTCGTCTTGCGTACCA
MY 2	GAAGTACTCCAAGGCTCA
MY 4	ATCATCCTATACAGCCCAA
MY A	ATTCCCTCCAATTACTATTC
MY C	ATAACCTCCTCTATCTTC
L 2	ACATCCTCCCTTCTGCTAACA
L 3	ATCACCATTCTCTTCCTAAC
L 5	CCATCTTTCTTACCCTCAACA
L 6	TGGCTGCTGGGGTTATTTCT
L B	AGCCCTAGGAGGCTGAAT
L C	CTAAGCTTACCCTCATAAC
L E	AGAAATAACCCCAGCAGCCA
L F	TGCCATTCTCACCTCAATAT
NA 1	CACTGAGCAACAGCCTGAACC
NA 2	ACTTTCTAGTACAAGCAAC
NA 3	ATTCCCCGAAGTCCTCCAAG
NA 4	ACTATAGCCATCGCCTCAGCAG
NA 5	ACTCACCCTAATAACATTCTACC
NA 6	ACCTCGTGAACAAAAATCCCGA
NA 7	ATAACCACAGCAGCCACAATT
NA 8	ACCCTCAAATTGCCATTTTCAC
NA A	TACTTTCTAGTACAAGCAACT
NA B	TGCCTCCTACTAACAACAGC
NA C	ATCACCATTCTCCTTCTCACATCA
NA D	GCCTTCTCGTCCATCTCTCA
NA E	ATCTTCTTTACCCTCAACAC
NA F	CCAAAATGACTCATCATCCA
NA G	CGCCTCGCATACTACTCAACA
NPHR 4	CACTAATAACCACTATAGCC
NPHR 5	AGCCTTTTCATCCATCTCCCAC
NPHR 6	TCCTCACCCTAAACACAACCA
NPHR 7	CCCAACACTCAATGCAAC
NPHR A	ACCCAACACTAATAACCACTAT

NPHR B	AACTCACCCTCATAACATTC
NPHR C	ACACTCAATGCAACCCTCAT
NPHR D	CAGCAGCCACCATCATCGC
NP 1	TGAGCAACAGCCTGAGCTGGGCT
NP 2	TAACTCACCCAACATCCTGC
NP 3	CAACCACCATCCTCTTCCTTA
NP 4	TCCTAGCCTTCTCATCCAT
NP 5	CACTATCTTCTTCACTCT
NP 6	CACTAACAGGCTTCCTGCCAA
NP 7	TCGCATACTACTCAACAATC
NP A	TCTGATTCCCAGAAGTACTTCAA
NP B	TAATAACCACCATAGCCCT
NP C	TCACCCTCATAACATTCTAC
NP D	ACGCAACCCTCATACTAAC
NP E	CATATTATCACTACTAGGA
NP F	TCGCCATCCTCACCTCAAT
PN 1	TAGAAATCAACACCCTAGCCA
PN 2	TAGGCCTCAACCAAACACA
PN 3	TCATACTAACCTTACTATC
PN A	CAGCATAATAAACGCATGATT
PN B	ATGCAGCCCTCATACTAAC
SIPH 8	CACAACAGCCACAATCATCG

Table 3 – PCR settings

1. Step-down PCR for amplification of ND2, RAG-1 and ACO1 I-9 from fresh tissues.

Initialization at 94°C for 2 min, followed by 1 cycle of 94°C for 15 seconds (denaturation), 58°C for 15 seconds (annealing) and 70°C for one min (extension), then 1 cycle of 94°C for 15 seconds, 56°C for 15 seconds and 70°C for one min, 1 cycle of 94°C for 15 seconds, 54°C for 15 seconds and 70°C for one min and finally 29 cycles of 94°C for 15 seconds, 52°C for 15 seconds and 70°C for one min, with a final extension of 70°C for 5 min.

2. Step-down PCR for amplification of CYTB from fresh tissues.

Initialization at 94°C for 5 min, followed by 10 cycles of 94°C for 15 seconds, 54°C for 15 seconds and 72°C for 1 min, then 10 cycles of 94°C for 15 seconds, 52°C for 15 seconds and 72°C for 1 min, then 20 cycles of 94°C for 15 seconds, 50°C for 15 seconds and 72°C for 1 min, with a final extension of 72°C for 5 minutes.

3. General setup for amplification of short ND2 fragments from toe-pad specimens.

The general set-up for PCR amplification of short *ND2* fragments was a three or four-stage step-down with various sets of annealing temperatures (ranging from 60°C as the highest temperature in a given step-down reaction to 46°C as the lowest temperature in a given reaction). In a four-stage step-down procedure, there would generally be 10 cycles of 94°C for 15 seconds, highest annealing temperature for 10 seconds and 72°C extension for 30 seconds, followed by 10 cycles of 94°C for 15 seconds, the second-highest temperature for 10 seconds and 72°C extension for 30 seconds, then 10 cycles of 94°C for 15 seconds, the second-lowest temperature for 10 seconds and 72°C extension for 30 seconds and finally 20 cycles of 94°C for 15 seconds, the lowest temperature for 10 seconds and 72°C extension for 30 seconds. In a three-stage step-down procedure there are 30 cycles of the lowest annealing temperature reactions instead of 20.

4. Cycle-sequencing reaction setup.

15 cycles of 96°C for 1 minute, 50°C for 5 second and 60°C for 1 minute 15 seconds, followed by 5 cycles of 96°C for 10 seconds, 50°C for 5 seconds and 60°C for 1 minute 30 seconds and finally 5 cycles of 96°C for 10 seconds, 50°C for 5 minutes and 60°C for 2 minutes.

CHAPTER 4

THE HISTORICAL BIOGEOGRAPHY AND ECOLOGICAL DIVERSIFICATION OF THREE RADIATIONS OF NEW WORLD NIGHTJARS (CAPRIMULGIDAE)

1. INTRODUCTION

The nightjars (Caprimulgidae) are an interesting group for studies in avian biogeography as they represent an old lineage that has gradually attained a cosmopolitan distribution through the Cenozoic and have successfully colonized numerous habitat types. The nightjars belong to the order Caprimulgiformes, a collective of ancient lineages leading back to the origin of the Neoaves. The biogeography of the caprimulgiforms is complex with the families having disjunct distributions on a global scale. Some are restricted to the Neotropics (Nyctibiidae, Steatornithidae and Trochilidae), others to South East Asia and/or Australia (Aegothelidae, Hemiprocnidae and Podargidae), and both the nightjars and the swifts (Apodidae) are cosmopolitan. The biogeographic history of the group has received considerable attention lately (Cracraft, 2001; Mayr, 2011; Nesbitt *et al.*, 2011) and a Gondwanan origin has been hypothesized for the whole group (Cracraft, 2001). Uncertainties regarding the estimation of the age of the group (Brown *et al.*, 2008; Nesbitt *et al.*, 2011; Pacheco *et al.*, 2011), as well as the discovery of Paleogene fossil taxa in areas of the world where their extant relatives are not found, have added complexity to this hypothesis. Stem-members of the current families Nyctibiidae, Podargidae, Steatornithidae, and Trochilidae have been found in fossil sites in Europe and North America (Olson, 1987; Karhu, 1999; Mayr, 1999, 2003, 2004; Bochencskí & Bochenskí, 2008; Nesbitt *et al.*, 2011) and provide strong evidence for a larger distribution of those families early in their evolutionary history.

Interestingly, the fossil record of the nightjars (Caprimulgidae) is nearly non-existent with only fragmental material found from Eocene sites in Europe (Mourer-Chauviré, 1989). The extant diversity of the family spans all continents except Antarctica

with Africa, South America and Central America being the most species-rich areas. In the absence of fossil information, phylogenies are an important tool in inferring their historical biogeography. Numerous studies have shown that the species found in the New World all belong to one of three radiations (Barrowclough *et al.*, 2006; Han *et al.*, 2010; this thesis) whereas the Old World diversity either belongs to basal lineages within the family (in particular the genera *Eurostopodus* and *Lyncornis*) or a large crown-radiation distributed in Africa, Asia, and Europe (del Hoyo *et al.*, 1999). Evidence from molecular systematics suggests that portions of the large Old World crown-radiation are embedded within multiple New World lineages. Thus, the three New World radiations are not a single monophyletic assemblage (Barrowclough *et al.*, 2006; Han *et al.*, 2010; this thesis).

In a recent study (this thesis), I produced a phylogeny of these three New World radiations, in which all but three traditionally recognized species of New World nightjars were sampled (the three missing being very rare). Additionally, hidden diversity was investigated by sampling intensively subspecies of polytypic biospecies, which are numerous in the family. This deep intraspecific sampling resulted in a number of subspecies being elevated to full phylogenetic species status, increasing the total diversity of the family from 89 to 99 species. The importance of using phylogenies that are thoroughly sampling at the phylogenetic species level cannot be overstated. Completeness of phylogenies used in studies of diversification and biogeography is crucial for fully understanding the true degree and origin of diversity, not only of individual groups but also avian communities and biotas of particular areas.

The avifauna of the New World has long captured the interest of biogeographers (i.e., Haffer, 1974, 1985; Cracraft, 1985; Cracraft & Prum, 1988; Blackburn & Gaston, 1996; Hawkins *et al.*, 2006) as it is exceptionally diverse on a global scale, with the Neotropics in particular constituting a diversity hotspot with high levels of species richness and endemism. The latitudinal layout of the New World has greatly impacted the history of its biotas, with North and South America being connected by he relatively narrow landmass of Central America, which has served as a key area of biotic interchange between the two continents (Weir *et al.*, 2009; Smith *et al.*, 2010, 2012a).

Within the two continents themselves, the diversification of avian biotas into a diverse array of areas and habitats has been influenced by a variety of processes including the rise of mountain chains such as the Andes (Cracraft & Prum, 1988; Garcia-Moreno & Fjeldså, 2000; Fjeldså & Rahbek, 2006; Sedano *et al.*, 2010), riverine dynamics such as the Amazon River system (Pereira & Baker, 2004; Aleixo & Rosetti, 2007; Ribas *et al.*, 2012), sea-level changes (Brumfield & Capparella, 1996; Nores, 1999; Nores, 2004; Hernández *et al.,* 2005), climate change-induced expansion and fragmentation of habitats such as grasslands and dry forests (Cardoso Da Silva & Bates, 2002; Porzecanski & Cracraft, 2005; Werneck, 2011) and in North America, in particular, recent periods of glaciation isolating biotas in separate refugias (Bermingham *et al.*, 1992; Avise & Walker, 1998; Klicka & Zink, 1999; Johnson & Cicero, 2007). The timing of many of these events has been estimated, which allows for the testing of hypotheses regarding the role of specific events impacting the evolutionary histories of certain taxa.

The nightjars (Caprimulgidae) are a key avian group to use in studies of biogeography and ecological diversification in the New World for a variety of reasons: 1) they are relatively species-rich for a non-passerine group (Dickinson *et al.,* 2003); 2) they are widely distributed throughout the New World including numerous islands of the Caribbean (Holyoak, 2001); 3) they show large variation in range sizes (Holyoak, 2001); 4) they represent an old extant avian lineage with a suspected presence in the New World extending back to the Paleogene (i.e. Ericson *et al.*, 2006); 5) they are morphologically conservative with overall body-shape, including beak and wing morphology similar among species with a few exceptions related to sexual dimorphism (Cleere, 1999; Holyoak, 2001); 6) their unique nocturnal/crepuscular lifestyle has led to a relatively non-diverse diet and foraging behavior. Yet, they inhabit a great variety of habitats, including different forest types, various grassland habitats, in lowlands and montane areas and in both areas of high aridity and high rainfall (Cleere, 1999; Holyoak, 2001); 7) and finally they are also diverse in their movement habits, with species ranging from being completely sedentary to long-distance seasonal migrants (Cleere & Nurney, 1999; Holyoak, 2001).

In this study I investigate the temporal, spatial and ecological history of the New World nightjars, using the new phylogenetic-species level phylogeny. The three independent radiations will be compared and contrasted using time-calibrated phylogenies, biogeography analyses, and ecological trait ancestral state reconstructions with the goal of elucidating general patterns of diversification in this group, what processes were fundamental in creating those patterns, and how the broad geographic scale of the New World nightjars came to be. The calibrated phylogenies generated in

this study will provide a platform to test whether the three different radiations are temporally concordant with respect to their origin, patterns of cladogenesis, rates of diversification, and rate dynamics. Biogeographic analyses provide information about the spatial aspect of their diversification history and ancestral-area reconstructions display scenarios about source areas for certain lineages but also about spatial pathways of diversification in the form of historical vicariance events, gradual range expansion, or long-distance dispersal. Combined, the calibrated phylogenies and the ancestral-area reconstructions provide opportunities to test area-specific hypotheses about the role of well-known geographic or geological events and processes that may have impacted the history of whole radiations, lineages within those radiations, as well as individual species.

The ecological trait reconstructions provide information about the frequency and topological/temporal order of transitions between habitats within the family. Shifts from one kind of habitat to another are likely to be related to the availability of habitat type at a given time and thus to changes in the distribution of these habitats. Taxa that are characterized by a genetic predisposition for habitat choice conservatism may not react to changes in habitat availability by shifting from their older habitat to a newer one. It has been suggested that habitat choice conservatism may be particularly prevalent in humid, tropical regions since many groups that are diverse in those areas have not dispersed into areas characterized by different kinds of habitats, whereas the opposite pattern of temperate groups dispersing into tropical areas is quite common (Wiens & Donoghue, 2004; Hawkins *et al.*, 2006). Thus, it might be expected that more cases of habitat shifts of taxa moving into more tropical habitat types such as tropical rainforests from an ancestral temperate habitat would be found, than the other way around.

Another ecological trait of interest for birds is the prevalence of migratory behavior. Various degrees of migratory behavior are present among the New World nightjars, from localized nomadic movements within breeding ranges (particularly in the lowland tropics) to long-distance migration particularly between North and South America (Holyoak, 2001). The evolutionary history of migration within bird groups is extremely complex due to the known plasticity of the trait (Berthold, 1999; Zink, 2002, 2011; Helbig, 2003; Pulido, 2007; Salewski & Bruderer, 2007), and in most cases in which migratory behavior has been mapped on phylogenies it seems to have evolved multiple times within the same group (Joseph *et al.*, 1999; Outlaw *et al.* 2003, Outlaw & Voelker, 2006; Winker & Pruett, 2006; Kondo & Omland, 2007) with some exceptions (Winger *et al.*, 2012). Prevalence of migratory behavior may affect dispersal propensity. Thus, higher numbers of long-distance dispersal events may be expected in groups with more migratory species.

Combined, these analyses are designed to provide an overview of the diversification history of the three radiations of New World caprimulgids. Thus, as this analysis includes nearly all taxa of a diverse family in the New World that spans much of the Tertiary and was exposed to multiple historical events across the two continents, it should yield insight into the identification and description of general large-scale patterns that characterize the evolutionary history of the New World avifauna as well as the processes that have generated those patterns.

2. METHODS

2.1 PHYLOGENETIC ANALYSES

To establish a robust framework for estimating divergence dates at various levels of the phylogeny, different kinds of molecular markers are required. Above the genus level, and most certainly at the family level, nuclear markers with a low saturation rate are needed, but at the species level mitochondrial markers may be more useful (Wilson *et al.*, 1985; Harrison, 1989; Barker *et al.*, 2002; Paton *et al.*, 2003). Thus, two main data sets were assembled: A dataset consisting of sequences of the nuclear gene *RAG-1,* and a mitochondrial 2-locus dataset (*ND2* and *CYTB)*.

For the *RAG-1* dataset, taxon sampling was not dense at the species level within Caprimulgidae, and instead included representatives of all the different genera and major lineages recognized (Han *et al.,* 2010; this thesis). A total of 59 individuals representing 48 species were sampled (**Table 1a**). The sampling of outgroup taxa was also dense, including representatives of all other caprimulgiform families, numerous other neoavian taxa as well as basal galloanseran and palaeognath taxa leading to a total number of 92 individuals.

A representative of all but three phylogenetic species from the three New World radiations was sampled for the mitochondrial dataset, based on previous results (this thesis). Additionally, the Old World lineages within the family were sampled, as well as a number of species belonging to the genus *Caprimulgus*, a monophyletic Old World crown assemblage. A total of 53 New World species were included and seven Old world species (**Table 1b)**. All phylogenetic species sampled have a complete or nearly complete

ND2 sequence (1041bp) with the exception of *Antrostomus cubanensis* and *Eurostopodus archboldi*, which have less than 600bp of the sequence and *Antrostomus salvini* and *Hydropsalis candicans* in which only *CYTB* is available. For *CYTB*, a total of 48 species were sampled, most with complete (1144bp) or nearly complete sequences.

All phylogenies were reconstructed using two approaches: maximum likelihood as implemented in RaxML (Stamatakis *et al.*, 2008) and Bayesian inference as implemented in Beast v1.6.2 (Drummond and Rambaut, 2007). Maximum Likelihood analyses were performed on the whole data set (210 individuals) as well as the individual partitions in RAxML (Stamatakis *et al.*, 2008) on the open RAxML BlackBox cluster server (http://phylobench.vital-it.ch/raxml-bb/). RAxML incorporates bootstrap analyses for support in their tree-search analyses, using rapid bootstrap (RBS) heuristics. Bootstrap inferences were conducted under the GTR+CAT model of rate heterogeneity, however the final trees were scored under GTR+Γ, which is the standard RAxML tree-search algorithm. To ensure that these default settings modeled the data accurately, PHYML as implemented in jModelTest (Posada, 2008) was administered on all individual locus data-sets to calculate which models of substitution were most suitable for each data-set, with the Aikake Information Criterion chosen to rank the models. Bayesian phylogenetic analyses were performed in Beast v1.6.2 (Drummond and Rambaut, 2007) using the highest scoring tree from the RaxML analysis as a starting tree. A GTR+Γ base substitution model was chosen for both the *RAG-1* and mitochondrial datasets, with third codon positions partitioned separately. Phylogeny and dates of divergence (see next section) were inferred simultaneously. The analysis of the *RAG-1* dataset was run for 30 million generations, whereas the mitochondrial dataset was run for 15 million

generations. In both analyses, tree samples were taken every 1000 generations and stationarity was evaluated in TRACER v1.3 (Rambaut & Drummond, 2007) with the first 20% of trees discarded as burn-in.

2.2 MOLECULAR DATING ANALYSES

RAG-1 data were employed to obtain estimates for the divergence times of the Caprimulgidae and other family-level taxa within the Caprimulgiformes, major Old and New World lineages within the Caprimulgidae, and divergences of sub-lineages within the three major New World radiations. The slowly evolving *RAG-1* gene is a much-used exonic marker in avian systematics (i.e. Groth & Barrowclough, 1999; Barker *et al.*, 2004; Johansson *et al.*, 2002; Paton *et al.*, 2003; Griffiths *et al.*, 2004; Barrowclough *et al.*, 2006) as it exhibits virtually no saturation back to the base of birds (Groth & Barrowclough, 1999), rendering it particularly useful for molecular dating at higher taxonomic levels (Barker *et al.*, 2004; Baker *et al.*, 2007; Hugall *et al.*, 2007).

The mitochondrial data were employed to estimate divergence dates of species and species groups of the caprimulgids only. For divergence points deeper in time there is a risk of the signal in the mitochondrial data to be lost due to saturation. A common result of this is that the branches leading to the more basal nodes become disproportionally longer and the estimated dates of divergence for those nodes are therefore older than expected (Pereira & Baker, 2006). To address this issue, and because no indubitable Paleogene fossil caprimulgids are known, the timetree based on the *RAG-1* data was utilized to calibrate basal nodes during molecular dating analyses of the mitochondrial data.

Divergence dates were estimated in Beast v1.6.2 (Drummond and Rambaut, 2007) in all analyses. An uncorrelated lognormal clock model was chosen, with a Yule speciation rate tree prior. Ages of chosen nodes were constrained using calibrations. As the two datasets were assembled to produce estimates of the origin of the Caprimulgidae and of key divergence events within the family, respectively, different dating strategies were applied that were relevant for each dataset, as described in the next two sections. Because phylogeny was inferred simultaneously in analyses of both datasets, other settings in Beast v1.6.2 are the same as previously described.

2.2.1 DATING OF DEEPER CAPRIMULGID LINEAGES

In the dating analysis of the *RAG-1* dataset, fossils were used as calibrations. The Caprimulgiformes are known for their relatively well-documented fossil record (summarized in Mayr, 2009). As the nightjars themselves lack robust fossil data, it is necessary to include fossil representatives from the other caprimulgiform families to calibrate molecular dating analyses that rely on a relaxed molecular clock. As the two main datasets were assembled to produce estimates of the origin of the Caprimulgidae and of key divergence events within the family respectively, different dating strategies were applied that were relevant for each dataset.

The ages of seven fossil taxa were chosen to calibrate the divergence dates for seven clades on the phylogeny. Two of the fossils are caprimulgiforms, four are from other neoavian lineages and one is a galloanseran. The fossils all belong to the stem of the modern lineages represented on the phylogenetic tree, so the ages of the fossils were utilized as a lower limit for the age of the basal nodes of those lineages. An exponential

distribution prior was chosen, with the mean parameter set between 1.2 and 2. The precise placement of stem fossils is not always known with certainty, but fossils that are thought to be closely related to the crown-taxa are likely to be closer in age to the crown than to the base of the stem (depending on the length of the branch). When knowledge about the fossil taxon suggested this was the case, a higher mean value for the exponential prior was chosen than when the age of the fossil was suspected to be closer to the age of the node being calibrated than to the age of the crown-taxa.

The fossil calibrations were the following:

1. The stem-fossil *Vegavis* (66-68 MYA) (Clarke *et al.*, 2005) was used as a lower bound for the divergence between the Anseriformes (*Anser* and *Anseranas*) and Galliformes (*Gallus*). The exponential calibration prior was set at 68 MYA with a mean of 1.6.
2. The fossil *Eocypselus vincenti* (52-53 MYA) (Harrison, 1984), a stem-apodioid (Mayr, 2009) was used as a lower bound for the divergence between Aegothelidae (*Aegotheles*) and the Apodi (*Apus*, *Colibri*, *Hemiprocne* and *Phaethornis*). The exponential calibration prior was set at 53 MYA with a mean of 1.7.
3. The fossil *Scaniacypselus szarskii* (47-50 MYA) (Peters, 1985), a stem-swift (Mayr, 2009) was used as a lower bound for the divergence between Trochilidae (*Colibri* and *Phaethornis*) and the clade containing Apodidae (*Apus*) and Hemiprocnidae (*Hemiprocne*). The exponential calibration prior was set at 50 MYA with a mean of 1.3.

4. The fossil *Hydrotherikornis oregonus* (38-40 MYA) (Miller, 1931, a stem-alcid (Chandler & Parmey, 2003; Mayr, 2009), was used as a lower bound for the divergence between Charadrii (*Charadrius*) and Lari (*Larus*). The exponential calibration prior was set at 40 MYA with a mean of 1.8.
5. The fossil *Palaeotodus escampsiensis* (~38 MYA), a stem-todid (Mourer-Chauvire, 1985), was used as a lower bound for the divergence between Todidae (*Todus*) and Alcedinidae (*Alcedo*). The calibration prior was set at 40 MYA with a mean of 1.6.
6. The fossil genus *Limnofregata* (~48 MYA), a stem-fregatid (Olson, 1977; Olson & Matsuoka, 2005), was used as a lower bound for the divergence between Sulidae (*Sula*) and Fregatidae (*Fregata).* The calibration was set at 50 MYA with a mean of 1.2.
7. The fossil *Lithoptila* (55-57 MYA), a stem phaethontid (Bourdon *et a*l., 2005), was used as a lower bound for the divergence between Phaethontidae (*Phaethon*) and the lineage leading to *Eurypyga* and *Rhynochetos*. The calibration was set at 58 MYA with a mean of 1.8.

No calibration or temporal constraint was set on the root, which represents the node separating the Neognathae and Palaeognathae. A number of clades were also constrained to be monophyletic, without a calibration being placed on them. This includes core radiations within the Caprimulgidae such as the nighthawks (*Chordeiles* and *Podager*), the clade containing *Antrostomus* and its closest relatives, and the large South American clade that contains the genera *Hydropsalis, Nyctidromus, Lurocalis* and *Nyctiprogne.*

2.2.2 DATING OF SHALLOWER CAPRIMULGID LINEAGES

Estimated divergences within the family from the analysis of the *RAG-1* data were employed as priors for the dating analysis of the mitochondrial dataset. Instead of using exponential priors, a normal distributed prior was set as the true age of the nodes could be either older or younger than the calibration derived from *RAG-1*.

The calibrated nodes for the analysis of the mitochondrial data set were:

1. For the family Caprimulgidae, the normal-distributed calibration prior was set at 55 MYA with a standard deviation of 1.5
2. For the clade containing the four core radiations – the Old World *Caprimulgus* radiation, the New World nighthawk radiation (*Chordeiles, Podager*) the New World poorwill radiation (*Antrostomus, Nyctiphrynus, Phalaenoptilus, Siphonorhis*) and the large South American radiation (*Hydropsalis, Lurocalis, Nyctidromus, Nyctiprogne*) the normal-distributed calibration prior was set at 42 MYA with a standard deviation of 1.3
3. For the clade containing the New World nighthawk radiation (*Chordeiles, Podager*) the calibration was set at 23 MYA with a standard deviation of 1.3.
4. For the clade containing the New World poorwill radiation (*Antrostomus, Nyctiphrynus, Phalaenoptilus, Siphonorhis*) the calibration was set at 31 MYA with a standard deviation of 1.3.

5. For the clade containing the South American radiation (*Hydropsalis, Lurocalis, Nyctidromus, Nyctiprogne*), the calibration was set at 35 MYA with a standard deviation of 1.3.
6. For the clade containing the genus *Nyctidromus*, the calibration was set at 17 MYA with a standard deviation of 1.0.

2.3 BIOGEOGRAPHIC ANALYSES

To investigate the spatial patterns of nightjar diversification in the New World, ancient area relationships were inferred from the phylogenies using the software RASP (Yu *et al*., 2010, 2011). RASP (Reconstruct Ancestral State in Phylogenies) provides two main tools for inferring ancestral states; a parsimony tool that is an updated version of S-DIVA (Statistical dispersal-vicariance analysis, Yu *et al.,* 2010) which assumes vicariance and assigns costs to dispersal and extinction events, and a more recently developed statistical procedure called Bayesian Binary MCMC (BBM) (Yu *et al.*, 2011) that uses a full hierarchical Bayesian inference approach that does not fix relative rates of change among character states but specifies prior probability distributions on them instead. The ancestral states are then inferred by weighting each value for a given state according to its probability given the data.

Four separate analyses were performed, with different taxon sampling:

1. The caprimulgiform clade from the RAG-1 phylogeny including 48 caprimulgid species. This is the only analysis that infers ancestral areas within the nighthawk radiation.

2. The mitochondrial phylogeny of the poorwill clade including 16 poorwill species.
3. The mitochondrial phylogeny of the South American clade including 28 nightjar species.
4. The mitochondrial phylogeny of the nighthawk clade including 7 nighthawk species.

The major sub-clades were analyzed separately to allow for a more varied and thus more precise choice of areas in each analysis without increasing the total number of areas too much, which inhibits the efficiency of the analysis.

Only five main areas were included in the analysis of the RAG-1 phylogeny, in order to map major shifts in biogeographic distribution on an inter-continental scale. The areas were North America, Central America (including most of Mexico), the Caribbean, South America, and the Old World. Maximum of four areas were allowed in area combinations for the reconstructed ancestral states.

The focus of the analysis of the poorwill phylogeny is on patterns within North- and Central America and the Caribbean while South America plays a smaller role. Seven areas were defined: Eastern North America, Western North America, coastal and lowland areas of Mexico, Mexican highlands, Central America south of the isthmus of Tehuantepec, the Caribbean, and finally South America as a single unit.

The analysis of the South American clade specifically addressed patterns within the South American continent. Ten areas were defined: the Northern Andes (Colombia to Ecuador), Central Andes (Peru and Bolivia), Pacific lowlands (from the Tumbesian area of endemism in Ecuador to the arid coastlands of southern Peru and northern Chile), the

lowlands of northern Colombia and Venezuela (including the Chocó, Guajira and Llanos areas of endemism), the Northern Amazon area (including the Guianan shield and the Tepui highlands), the Southern Amazon area (from Inambari in the west to Pará in the east), the central grassland areas (Cerrado, Caatinga, Chaco), the Atlantic Forest, and finally the southern most temperate belt (Pampas, Patagonia etc.). This area categorization is only a simplified viewpoint of biogeographic zones in South America but represents the combination of well-known areas of endemism (Cracraft, 1985; Haffer, 1985) into larger composite areas. A number of species are widespread and inhabit multiple areas, but most species are confined to one or two areas. To boost the efficiency of the analysis, the maximum number of areas allowed in area combinations for the reconstructed ancestral states, was maintained at four.

The analysis of the nighthawk phylogeny includes areas on both continents, but slightly more coarsely defined than in the analyses of the other two clades, as the distributions of the nighthawks tend to be larger and cover multiple smaller areas. Seven areas were defined: North America, Mexico (north of the Ishtmus of Tehuantepec), Central America (between the Isthmus of Panama and the Isthmus of Tehuantepec), the Caribbean Islands, lowland areas of Colombia, Venezuela, Ecuador and Peru (including Chocó, Guajira, Llanos and Tumbesian areas of endemism), the Amazon Basin and the central grassland area (Cerrado, Caatinga, Chaco). The different area classification schemes for each analysis and distribution of the phylo-species are shown in **Table 2.**

Both S-Diva and BBM analyses were performed on all four phylogenies. In the BBM analyses, the default settings of fixed state frequencies, equal among-site rate variation, and 50000 cycles of 10 chains were used. The output from each analysis is a

phylogeny with the inferred reconstructed ancestral areas on all internodes as charts that display the distribution of probabilities of each inferred area or area combination.

2.4 ANCESTRAL TRAIT RECONSTRUCTION ANALYSES

2.4.1 HABITAT CHOICE

Traits related to habitat choice were optimized on the phylogenetic species tree using two approaches, a maximum likelihood approach as implemented in the Bayes Multistate method in the software BayesTraits (Pagel & Meade, 2006) and a parsimony trait reconstruction as implemented in the phangorn package in the software R (Schliep, 2011). The Bayes Multistate method in BayesTraits is useful for traits that adopt two or more discrete traits. It uses maximum likelihood methods to "derive point estimates of the values of traits at ancestral nodes of phylogenies" (Pagel & Meade, 2006) and can be utilized with single phylogenetic trees or samples of trees.

The mitochondrial caprimulgid phylogeny was split into two phylogenies that were analyzed separately using BayesTraits. The nighthawks, poorwills and Old World lineages were together in one phylogeny, whereas the South American radiation was analyzed separately. Two simplified habitat "characters" were chosen each with three "traits":

- Habitat type: 1) Present in open habitats such as grasslands, savannah, deserts, farmlands etc., 2) present in forests and other woodlands, temperate or tropical, and 3) present in both open habitats and forests.
- Habitat altitude: 1) Present in lowlands, 2) present in montane areas and other highland habitats, and 3) present in both lowland and highland habitats.

The South American radiation has the highest diversity of habitats of the three nightjar radiations. Thus, a more complex ancestral trait reconstruction for habitat choice was performed on the phylogeny of the South American radiation, using the maximum parsimony ancestral reconstruction command ancestral.pars that is implemented in the phangorn package in R. Habitat types were chosen based on the classification of Stotz (1996) which takes vegetation type, prevalence of precipitation/aridity, as well as altitude into consideration, but was further simplified with some of his categories pooled together. The total number of habitat types in the analysis was seven, and they are described in **Table 3**. Information on habitat choice was obtained from specialized guidebooks on nightjars and their relatives such as Holyoak (2001) and Cleere (2010) as well as from Stotz *et al.* (1996

2.4.2 MIGRATION

Migratory behavior is known in a number of nightjar species. To evaluate the evolution of this trait in the three New World radiations, the trait was optimized on the mitochondrial phylogeny. Migration is considered a labile character trait in birds but in some studies there is evidence of a phylogenetic signal, as discussed earlier. Ancestral traits were reconstructed using a parsimony trait reconstruction in Mesquite v. 2.75 (Maddison & Maddison, 2011). The migratory trait had three character states in the analysis:

1. Long-distance migratory species in non-breeding season
2. Partial migratory or nomadic species.
3. Sedentary species

3. RESULTS

3.1 PHYLOGENETIC ANALYSES

3.1.1 RAG-1 PHYLOGENY

The phylogeny from the Bayesian analysis of the *RAG-1* dataset performed in Beast v1.6.2 is shown in **Figure 1**. The topology is congruent with the maximum likelihood analysis performed in RAxML. The *RAG-1* data strongly support a monophyletic Caprimulgiformes but multiple relationships within that clade are not strongly supported, especially basally. The Apodioidea (Apodi and Aegothelidae) are well supported, and *Podargidae* and *Caprimulgidae* are sister-taxa, which is a pattern only seen in phylogenies based on RAG-1 (Barrowclough *et al.,* 2006) and other sources of evidence do not support (Hackett *et al.,* 2008; Mayr, 2010; Nesbitt *et al.,* 2011; this thesis). As the lineages at the base of Caprimulgiformes all diverged from one another very rapidly (68-62 MYA), this is not likely to affect the estimation of dates within Caprimulgidae.

Within the Caprimulgidae, *Eurostopodus mystacalis* and *Lyncornis macrotis* are placed basally, whereas *Gactornis enarratus* is the sister-taxon to a large core-nightjar clade, which contains the four major radiations recognized in numerous previous studies (Barrowclough *et al.*, 2006; Han *et al.*, 2010: own study). *RAG-1* resolves the relationships of these four clades with high confidence, placing the large South American clade that contains the genera *Hydropsalis, Lurocalis, Nyctidromus* and *Nyctiprogne* as the sister-group to a clade containing the three other radiations: the poorwills and its relatives (the genera *Antrostomus, Nyctiphrynus*, *Phalaenoptilus* and *Siphonorhis*) and

the nighthawks (*Chordeiles* and *Podager*) as the sister-group to the Old World radiation (predominantly the genus *Caprimulgus*).

3.1.2 MITOCHONDRIAL PHYLOGENY

The phylogenetic tree from the Bayesian analysis of the mtDNA tree (combined matrix of *ND2* and *CYTB* sequences) is shown in **Figure 2**. There are some fundamental differences between the topologies of the *RAG-1* and the mtDNA trees. The most glaring one is that the Old World radiation of the genus *Caprimulgus* is not embedded among the New World radiations but is their sister-group. Thus all the New World taxa are present in one monophyletic lineage. This topology receives considerable support on the Bayesian tree (**Figure 2**) and was identical to the topology on the mitochondrial tree, although a number of nodes that had high posterior probability scores only had moderate bootstrap support on the mitochondrial tree.

3.2 MOLECULAR DATING ANALYSES

3.2.1 RAG-1 ANALYSIS

The dated chronogram resulting from the Beast analysis of the *RAG-1* data set using eight fossil calibrations is shown in both **Figures 3a** and **3b**. In **Figure 3a** major clades within the Caprimulgidae are collapsed. The lineages within Caprimulgidae and their estimated ages of divergence are depicted in **Figure 3b**. The analysis only places 95% confidence limits on nodes that received posterior probability score of 0.5 or higher. Ages of all nodes that were estimated in the analysis and their confidence limits are displayed in **Table 4**. The age of the root, which was unconstrained in the analysis, is estimated at 103.0 MYA with a broad confidence limit (85.4-151.2 MYA). The split

between Galloanserae and Neoaves is estimated at 90.5 MYA and the root of the neoavian radiation is at 75.0 MYA.

The majority of the neoavian lineages (**Figure 3a**) date near to the time period surrounding the K-Pg boundary (65 MYA). This includes the lineage leading to the modern caprimulgiforms, estimated at 68.1 MYA near the end of the Cretaceous. The basal lineages within this clade are not well resolved on this chronogram, but the lineages leading to four of the extant families (Caprimulgidae, Nyctibiidae, Podargidae, Steatornithidae) and the one leading to the Apodioidea all date back to between 62 and 67 MYA.

The age of the lineage leading to the nightjars (Caprimulgidae) is 62.2 MYA (**Figure 3a**), with the first split within the family (between *Eurostopodus* and the remainder) estimated to be about 55 MYA. The root of the core crown clade containing the four main radiations of modern nightjars is estimated at 42 MYA. The South American radiation, which is the sister-group to the other four core clades, diverges at 35.4 MYA. The separation of the poorwill clade from the Old World *Caprimulgus* radiation and the nighthawk clade is estimated at 39 MYA and finally, the split between the nighthawk clade and the *Caprimulgus* radiation is estimated at 36 MYA. Ages of other lineage divergences within the four core clades are shown in **Figure 3b** and listed in **Table 4**.

3.2.1 MITOCHONDRIAL ANALYSIS

The results from the dating analysis of the mtDNA data using calibrations from chosen nodes estimated from the *RAG-1* chronogram are shown for the nighthawk clade

in **Figure 4a**, the poorwill clade in **Figure 4b** and the South American clade in **Figure 4c**. When comparing the same nodes in the two analyses, there is a tendency in the analysis for the mtDNA data to estimate an older age than the *RAG-1* results suggest (**Figure 3b**). This is particularly prevalent within the nighthawk and poorwill clades, but much less so in the South American clade. Also, closer to the tips of the chronogram, this effect becomes less obvious

3.3 BIOGEOGRAPHIC ANALYSES

The results from the Bayesian Binary MCMC analysis in RASP are displayed in **Figures 5-7**. The pie charts displayed on all the internodes represent the inferred reconstructed ancestral areas for the clades in question. Each color represents either a single area or combinations of areas as explained in the legend.

3.3.1. RAG-1 PHYLOGENY

The area reconstructions on the *RAG-1* phylogeny are depicted in **Figure 5**. Only the nodes of the Caprimulgiformes are displayed in the figure. An Old World origin is clearly reconstructed for the nightjars. This is unsurprising as the three basal lineages within Caprimulgidae (the genera *Eurostopodus, Gactornis* and *Lyncornis*) are all restricted to the Old World. The analysis is not successful at reconstructing ancestral areas for the nodes that separate the four core lineages. Only the node at the base of the clade that contains the nighthawk clade and the Old World clade is resolved but the area suggested as ancestral for that clade is a composite area that includes both South America and the Old World, which is not an informative result. Thus, it cannot be stated with confidence where the four core-clade radiation originated.

The analysis is more successful in reconstructing ancestral areas for the four clades individually. A South American origin is suggested for the nighthawk clade (**Figure 5**) with *Podager* restricted to South America, whereas *Chordeiles* is predicted to have dispersed out of South America on at least two occasions. One was the ancestor of *C. texensis,* which dispersed into Central America, whereas the other is the ancestor of *C. gundlachii* and *C. minor*, with the two species colonizing the Great Antilles and mainland North America, respectively.

Within the poorwill clade the results in **Figure 5** suggest an origin for the bulk of the diversity in Central America with six independent dispersal events occurring, both into North America (lineages leading to *Phalaenoptilus nuttallii, A. vociferus,* and the ancestor of *Antrostomus carolinensis* and *A. cubanensis*) and into South America (lineages leading to *Antrostomus seriocaudatus*, *Nyctiphrynus rosenbergi,* and the ancestor of *A. otiosus* and *A. rufus*). Important taxa like *Antrostomus cubanensis, A. badius* and *Nyctiphrynus yucatanicus* are missing in this analysis.

3.3.2 MITOCHONDRIAL PHYLOGENY

The results of a RASP analysis of the mitochondrial poorwill dataset includes these missing taxa and is based on a more complex area definition (**Figure 6**) with seven areas defined including three areas within Mesoamerica (Mexican lowlands, Mexican highlands and Central America). The area reconstruction on the basal nodes is not well resolved with multiple areas, or area combinations, more or less equally represented. The relatively high score for the Caribbean at the root node is because of the restricted modern range of the basal *Siphonorhis*, which is only found on Hispaniola and Jamaica.

Mexico, and in particular the Mexican lowlands, are reconstructed as an important source area for the remainder of the radiation.

In **Figure 5**, the entirety of South America is combined into a single area. The root of the SA clade and a large majority of its respective internodes are reconstructed as originating strictly within the continent. A number of taxa have dispersed into Central America or to islands in the Caribbean. **Figure 7** depicts the RASP analysis for the SA clade with South America split into nine areas. It provides a much more detailed reconstruction of the biogeographic history of this radiation. At first sight the results demonstrate a highly complex history that is characterized by multiple colonization events of numerous areas with basically all well-established areas of endemism inhabited by at least one species. A closer look reveals some patterns.

The core area of origin for the whole radiation is the northern part of South America, in particular the lowland tropics of the Amazon basin which is depicted in light blue (**Figure 7**) consists of the tropical rainforest areas of endemism north of the Amazon River including the Guianan shield, Imerí, Napo and the Tepuis in Venezuela. This composite area is repeatedly the most prominent area in the ancestral reconstructions of the basal nodes within the SA clade, including the nodes that separate the genera *Lurocalis, Nyctiprogne, Nyctidromus* and *Hydropsalis* from one another as well as the basal splits within those four genera (in particular *Hydropsalis* and *Nyctiprogne*).

Within *Lurocalis*, an early split between a highland northern Andean lineage (leading to *L. rufiventris*) and a more general Northern South American lowland lineage (leading to *L. semitorquatus*) is the most prominent event, whereas the Amazon River is apparently an important barrier in the early diversification of *Nyctiprogne*.

Nyctidromus originated in northern South America (**Figure 7**), but the four main lineages within the clade have very different spatial histories. Two of the species are restricted to small areas of endemism, *N. hirundinaceus* in the Caatinga dry forests in eastern Brazil, whereas its closest relative *N. nigrescens* is found throughout the Amazon basin on both sides of the river, and *N. anthonyi* in the Tumbesian area of endemism in Ecuador. The results in Chapter 2 suggest that the traditionally recognized *N. albicollis* is in fact three phylogenetic species: *N. merrilli* in Central America, and its two sister-species *N. derbyanus,* with a large range in central and south Brazil, and *N. albicollis* with an even larger range in northern South America that extends into southern Central America.

The most diverse genus within the SA Clade, *Hydropsalis* also has the most complex history of spatial diversification, with taxa present all over the South American continent. A number of species are restricted to areas of endemism but others are widespread. The reconstruction in the RASP analysis shows that the basal lineages originated in the tropical forest areas north of the Amazon River, but the current distributions of the basal *Hydropsalis* species are varied, with species found in the Andes (*H. lyra/H. segmentata*), the Tepuis (*H. whitelyi*), and on the arid Peruvian coast (*H. decussatus*).

The two crown-clades within the *Hydropsalis* radiation have different biogeographic histories (**Figure 7**). One is proposed to have originated in the corridor of open habitats in Central Brazil - the Cerrado, Chaco and Caatinga (combined here in one area) that separate the Atlantic Forest from the tropical forests in the Amazon Basin and the Eastern Andean slopes. Two species are endemic to these grassland habitats (*H.*

anomalus and *H. candicans*). The species complex that formally belonged to a single species (*Caprimulgus longirostris*) has two major subgroups, one in montane tropical forest areas in the north of the continent (with *H. ruficervix* in the Northern Andes and *H. roraimae* in the tepuis of Venezuela), and the other in the more temperate grassland areas of the south (*H. longirostris* in the Pampas, Patagonia, Southern Andes of Chile and Argentina and northeast to the Cerrado and Chaco and *H. l. atripunctatus*, a potential phylo-species, in the paramo highlands of the Central Andes).

The other *Hydropsalis*-clade has a very complex biogeographic history with a number of widespread species (*H. maculicaudus* and *H. torquata*), an Atlantic Forest endemic (*H. forcipata*), an Amazon rainforest species (*H. climacocerca*), and a northern species-complex (*H. cayennensis* & *H. albicauda*) with scattered populations in Central America, the Chocó, the grasslands of Venezuela and on a few islands in the Lower Antilles. This complex collective of distributions in a relatively small clade affects the RASP analysis such that no particular area is predicted as ancestral for the group.

The ancestral-area reconstruction analysis for the nighthawk clade is shown in **Figure 8**. Seven areas were defined, spanning both continents. The ancestral states at the basal nodes within the clade are not well resolved in the analysis with both northern South America and Mesoamerica suggested as ancestral areas for the whole radiation, but of the two the former is considered more likely.

Podager is restricted to South America and a large ancestral area in northern part of the continent, that includes the Amazon Basin and the lowlands in the north and northwest, is suggested for the genus. The ancestral area for *Chordeiles* is less clear although an origin in South America is not predicted, with Mexico, Central America and

North America the three areas that score highest as potential primitive areas. The results are similarly unresolved for key divergence nodes within the genus, although Central America is reconstructed as the ancestral area of the lineage containing *C. acutipennis* and *C. texensis*.

3.4 ANCESTRAL TRAIT ANALYSES

3.4.1 HABITAT TYPE

The optimization of habitat type from the Bayes Traits analysis of the mitochondrial phylogeny is shown in **Figures 9** (nighthawks, poorwills and Old World taxa) and **10** (South American clade). While the ancestral trait reconstructions are not well resolved on the most basal nodes, there are clear differences among the main nightjar radiations. The nighthawks are predominantly open-habitat species with nearly all phylo-species preferring grasslands, savannah or desert habitats (**Figure 9**). The only exception is *Chordeiles rupestris*, which inhabits the Amazon rainforest, although it is mostly found on sandy banks along rivers and avoids dense forest. An open-habitat or generalist ancestor is predicted for the nighthawk clade.

Members of the poorwill clade (**Figure 9**) are predominantly found in a diverse array of forested habitats including temperate and tropical, dry and humid. A few species are generalists, often occupying forest borders, scrublands and farmlands. *Phalaenoptilus nuttallii* is the only species that is an open-habitat specialist, inhabiting arid montane areas in Southwestern North America and northern Mexico. A forested habitat is predicted for the ancestor of the poorwill clade.

In the South American clade the patterns are more complex than in the other radiations, with the three habitat types evenly represented in the clade with eleven phylo-species inhabiting open habitats, nine in forests, and 10 being generalists in mixed and marginal areas (**Figure 10)**. These three habitat types are spread over the phylogeny suggesting numerous habitat shifts within the group. Because of this, ancestral reconstructions of habitat choice on many internodes are poorly resolved.

3.4.2 HABITAT ALTITUDE

The optimizations of habitat altitude (highland habitats, lowland habitats, both) are shown for nighthawks and poorwills in **Figure 11** and for the South American clade in **Figure 12**. Within the nighthawk clade there are no strict highland taxa, but one species, *Chordeiles texensis,* is predominantly distributed in lowlands but extends into highlands as well. In the poorwill clade there is evidence for two independent shifts from lowlands to highlands in the clade (within *Nyctiphrynus* and *Antrostomus*), with one reversal into lowland habitats (*A. vociferus*). Additionally the species *Phalaenoptilus nuttallii* and *Antrostomus ridgwayi* extend their ranges over both highland and lowland habitats (**Figure 11**).

Within the SA Clade most of the species are strictly lowland-dwellers (**Figure 12**). A shift into highland-dwelling is optimized as occurring four times, in the lineages leading to *Lurocalis rufiventris*, *Hydropsalis whitelyi,* and in two groups in which more than one species is restricted to highlands: the *Hydropsalis lyra/segmentata* species complex and within the *longirostris*-complex. In the latter, the taxa *H. ruficervix*, *H. roraimae* and *H. longirostris atripunctatus* are all restricted to highland habitats whereas *H. l. bifasciatus* and *H. l. longirostris* can be found at different altitudes.

3.4.3 HABITAT CHOICE IN THE SOUTH AMERICAN RADIATION

The results from the parsimony trait reconstruction in R depict a more detailed picture of habitat choice among the species of the South American radiation (**Figure 13**). There are seven habitat categories that incorporate both habitat type and altitude. The reconstruction reconstructs lowland, tropical evergreen forests to be the primitive habitat for the whole South American radiation. The same habitat remained important in the early diversification history of the genera *Lurocalis*, *Nyctidromus* and *Nyctiprogne*. There are a number of habitat shifts within those three genera, most associated with individual species. These include three independent shifts into dry habitats: two into the Caatinga dry scrubland of eastern Brazil (*Nyctidromus hirundinaceus* and *Nyctiprogne vielliardi*) and one into the Tumbesian arid scrubland of Ecuador (*Nyctidromus anthonyi*). There is a single shift in the *Nyctidromus albicollis* species-complex in which all three species inhabit the broadly defined habitat of second growth forests as well as scrublands, plantations, and farmlands. *Lurocalis rufiventris* is the only non-*Hydropsalis* species inhabiting the high montane forests of the Northern Andes.

Within *Hydropsalis*, the reconstructed primitive habitat type is highland forest in particular montane evergreen and elfin forests. The analysis suggests that these highland habitats remained important throughout the diversification history of this genus. There are numerous shifts into other habitats, and most lead to only one or two species with the exception of the clade containing the species *albicauda, cayennensis, climacocerca* and *torquata* in which three out of four species inhabit lowland, seasonally-wet grasslands. Many of the other habitat shifts within *Hydropsalis* are into dry habitats, predominantly

campo grasslands but also lowland dry forests (*H. heterurus*) and arid scrublands (*H. decussatus*).

3.4.4 MIGRATORY BEHAVIOR

The optimization of migratory behavior as analyzed using a parsimony optimality criterion in Mesquite is shown in **Figure 14**. The results clearly demonstrate that migratory behavior evolved at least six times within the Caprimulgidae and in all four of the major core clades. Within the three New World clades, it is most prominent in the nighthawk and the poorwill clades. Of the six phylogenetic nighthawk species, only two are sedentary, *Podager pusillus* and *Chordeiles acutipennis. Chordeiles texensis* and the sister-species *Chordeiles gundlachii* and *Chordeiles minor* are all long-distance migrants that winter far away from their breeding grounds. *Chordeiles rupestris* and the one subspecies of *Podager nacunda* show partial migratory behavior with local movements within their range having been documented (Holyoak, 2001). The Mesquite analysis indicates that the ancestor of the *Chordeiles*-clade may have been migratory but the ancestor of the nighthawk clade itself was not.

Three poorwill species are long-distance migrants (**Figure 14**) which breed in North America and migrate south to Central and/or South America. These are *Antrostomus carolinensis*, *A. vociferus,* and *Phalaenoptilus nuttallii*, although the southernmost populations of *P. nuttallii* are probably sedentary in the arid areas of Mexico (Oberholser, 1925). Additionally, *Antrostomus arizonae*, *A. ridgwayi,* and *A. rufus* are partial migrants, exhibiting seasonal movements within their breeding ranges. The remaining six species are all sedentary, although information about their migratory behavior is scarce (Holyoak, 2001), and their breeding ranges small and restricted to

tropical areas in Central and South America. A migratory or partially migratory origin is predicted for the ancestor of *Antrostomus* and *Phalaenoptilus*, whereas a sedentary lifestyle is predicted for the ancestor of the whole poorwill clade, however.

Within the South American clade there is only one example of a long-distance migrant, *Antrostomus longirostris patagonicus*, which is an austral migrant and migrates from its breeding range in Patagonia north to Northern Argentina and Uruguay (Holyoak, 2001). Another subspecies, *A. l. bifasciatus,* is known to show local movements within its breeding range in Chile. All other subspecies of *A. longirostris* and its closest relatives are sedentary. Six other species, distributed in all four genera (*Hydropsalis, Lurocalis, Nyctidromus* and *Nyctiprogne*), show partial migratory or nomadic behavior, they are. The ancestral trait reconstruction suggests that this behavior evolved independently in all these lineages, and that all ancestral species within the clade were most likely non-migratory (**Figure 14**).

4. DISCUSSION

4.1 THE TEMPORAL AND GEOGRAPHICAL ORIGIN OF THE CAPRIMULGIDAE

This study provides the first published chronogram that includes all caprimulgiform families and the major caprimulgid lineages (**Figure 3a**). The Caprimulgiformes are a part of the large neoavian radiation and though the relationships among the neoavian lineages are poorly resolved, the results suggest that the majority of the early neoavian lineages diverged from one another at the very end of the Cretaceous or in the early Paleogene, close to the K/Pg boundary. These dates are somewhat intermediate with dates from analyses using other nuclear markers that postdate the K/Pg boundary (Ericson *et al.*, 2006), and dates from analyses using mitochondrial markers, that fall well within the Cretaceous (Pereira & Baker, 2006; Brown *et al*., 2008; Pacheco *et al.*, 2011). The results of Figure 3a suggest that caprimulgiforms are among the older neoavian groups and date back to the end of the Cretaceous (68 MYA) but the confidence limits for the age estimate do span across the K/Pg boundary (61-77 MYA). These results differ slightly from the results of Ericson *et al.* (2006), in which the caprimulgiforms originate after the K/Pg boundary and are not among the oldest neoavian groups. In studies using mitochondrial markers, the caprimulgiform taxa are either poorly sampled (Pacheco *et al.*, 2011) or non-monophyletic (Brown *et al.*, 2008), but individual lineages tend to originate in the Cretaceous.

The first divergences between lineages within Caprimulgidae took place in the Eocene between 55 and 42 MYA (**Figure 3a**). There are no known fossil caprimulgids,

but fossil members of other extant caprimulgiform families such as Nyctibiidae and Podargidae are known from Eocene (33-55 MYA) fossil sites in Europe and North America (summarized in Mayr, 2009), so early diversification of the caprimulgids in the Eocene is not a surprising result. The origin of the crown-Caprimulgidae clade, which contains the four main extant radiations, is estimated at around 42.0 MYA in the late Eocene. The four core clades separated from one another relatively quickly, apparentlt within a five million year period. Further diversification within those clades is not temporally concurrent, given the extant diversity. Diversification within the large South American radiation that contains the genera *Hydropsalis, Lurocalis, Nyctidromus* and *Nyctiprogne* commences at the end of the Eocene. The earliest splits within the poorwill radiation (*Antrostomus, Nyctiphrynus, Phalaenoptilus* and *Siphonorhis*) is slightly younger (mid-Oligocene), whereas the basal split between the genera *Chordeiles* and *Podager* in the nighthawk radiation only dates back to 23.4 MYA or to the Oligocene/Miocene boundary (**Figure 3b**).

An Old World origin is likely for the Caprimulgidae, as *Eurostopodus* and *Lyncornis*, whichare the first genera to diverge from the remainder in the caprimulgid phylogeny (**Figure 1**), are distributed in Southeast Asia and Australia. The genus *Gactornis* is found in Madagascar and is the sister-taxon to the remaining nightjar diversity that is split into four radiations, three in the New World and one in the Old World. The ancestral-area analyses fail to resolve the ancestral area of these four groups (**Figure 5**) so the exact geographic origin of the total radiation (all four groups) is ambigious.

It has been suggested that the current distribution of the caprimulgiform families, including Caprimulgidae, can be explained by the breakup of Gondwana (Cracraft, 2001). This breakup was at its latter stages in the Eocene when the basal lineages of the caprimulgids diverged from one another. The split between the terrestrial biotas of Antarctica and Australia was around 60 MYA, as a result of a marine transgression separating the two landmasses (Woodburn & Case, 1996) However, the two continents were only separated by narrow seaways until the mid Paleogene (35-40 MYA) (Royer & Rollet, 1997), so dispersal of some volant taxa until that time cannot be ignored. The complete separation between Antarctica and South America occurred even later with the formation of the Scotia Sea between 40 and 20 MYA (Lawver *et al.*, 1992; Barker, 2001; Eagles, 2010). It is possible that these vicariance events in the Southern Hemisphere impacted early caprimulgid diversification, including possible movement of taxa between South America, Antarctica and Australia in either direction, which could explain the extant distribution of multiple lineages in these areas. It is possible that all four core radiations had separated from one another, before the three New World groups became isolated from the Old World nightjar diversity.

The situation of *Gactornis* is problematic. It separated from its sister-taxon around 47 MYA (**Figure 3a**), with the only extant representative found on Madagascar. Madagascar has been isolated from Africa since the early Cretaceous (Krause *et al.*, 1997), although connections to Antarctica are thought to have existed into the late Cretaceous (80 MYA) (Krause *et al.*, 1997; Buckley *et al.*, 2000). The origin of *Gactornis* is much younger than those connections, and as has been suggested for other Malagasy faunal groups (Yoder & Nowak, 2006), vicariance is perhaps an unlikely

explanation for the current distribution of *Gactornis,* and a long-distance dispersal event may be more likely.

4.2 BIOGEOGRAPHY OF THE THREE NEW WORLD NIGHTJAR RADIATIONS

The spatial history of nightjar diversification in the New World is complex, and the three radiations differ considerably in their biogeography. The caprimulgids have been successful in colonizing both continents, with most areas currently inhabited by nightjar species. But, there is a clear continental separation between the two largest radiations (**Maps 1-2**). The members of the poorwill radiation are predominantly found in Central, North America and the Caribbean, with four species breeding in South America (**Map 1**), whereas the South American radiation is nearly restricted to South America, with only a few species extending their range into Central America (**Map 2**). The nighthawk radiation, despite having the fewest species, has the largest total distribution covering the majority of both continents (**Map 3**). Range sizes of individual species also differ among the three radiations. The majority of nighthawk species have large ranges, but most poorwill species have rather small ranges. The South American clade has the most species, is the oldest (**Figure 3b**), and has a mixture of species with small ranges, which often are restricted to a particular area of endemism, as well as widespread species. Range overlap is generally low, particularly within each major clade, with many areas only inhabited by a single nightjar species. This is most extreme in the poorwills in which sympatry is almost nonexistent. In the South American radiation, widespread species account for most cases of sympatry, especially in lowland areas (Stotz, 1996).

A South American origin is hypothesized for both the nighthawk and the South American clades, but the geographic origin of the poorwill clade is more unclear (**Figure**

5). The tropical northern part of South America, in particular the Amazon basin and the Guianan Shield, is predicted to be the area of origin for the South American radiation (**Figure 7**). This area is inhabited by species in all four genera (*Hydropsalis, Lurocalis, Nyctiprogne* & *Nyctidromus*). The nighthawk radiation may have originated in a similar area, as both species in the genus *Podager* and two species of the genus *Chordeiles* inhabit this area (**Figure 8**). The early lineage divergence events within the genera *Podager* and *Chordeiles* are temporally congruent with similar events within *Nyctidromus* and *Nyctiprogne*, occurring between 21 and 14 MYA, whereas the early diversification of *Hydropsalis* dates back to the late Oligocene (24 MYA) (**Figures 4a** and **4c**). Thus, tropical northern South America may have served as a crucial center of diversification for numerous nightjar lineages, particularly in the Miocene.

4.2.1 BIOGEOGRAPHY OF NIGHTJARS IN SOUTH AMERICA

Spatial diversification within the South American clade (SA clade) has been a highly complex, gradual process with taxa diversifying across South America, resulting in a continent-wide distribution with extant diversity distributed in multiple areas of endemism (**Figure 7**) (Cracraft, 1985; Haffer, 1985; Stotz, 1996). Because some areas are combined into a single area in the RASP analysis, the pattern is even more complex than depicted. For example, the three species that inhabit lowland areas of the Pacific Coast, which is a single area in the analysis (**Figure 7**), are not sympatric. *Nyctidromus anthonyi* is the only species inhabiting the Tumbesian area of endemism in Ecuador (**Map 4**), *Hydropsalis decussatus* is found in the arid coastal areas of Peru (**Map 5**), and *H. longirostris patagonicus* is distributed in Chile. Both *N. anthonyi* and *H. decussatus* are sister to taxa that are either widespread species or groups of species with varied

ranges (**Maps 4-5**). Thus, their origins appear to represent a vicariant, possibly trans-Andean split. The temporal origin of the lineages leading to these two species is similar, between 17 and 15 MYA during the early to mid Miocene (**Figure 4c**). The Central Andes had already reached a considerable altitude in the late Miocene after numerous episodes of uplift in the Oligocene and Miocene (Gubbels *et al*., 1993; Kennan *et al*., 1997; Hartley, 2003; Nestor *et al*., 2006). The uplift of the Andes was a long, complex process and how it induced allopatric speciation across different avian groups is not completely understood (Ribas *et al.,* 2007), but the timing of the divergence events that isolated these three nightjar lineages in coastal areas may be at least partially explained by active tectonics in the Central and Northern Andes during the Miocene (Guerrero, 1997; Barke & Lamb, 2006). These lineages are now only represented by a single species each, perhaps further diversification was halted by the rather extreme aridification of these areas in the Pliocene (Hartley, 2003; Rech *et al*., 2009).

4.2.1.1. Diversification in the Andes.

A noticable pattern in the diversification of the South American clade is that areas renowned for their high avian diversity, such as the Andes (Cracraft & Prum, 1988; García-Moreno *et al*., 2000; Fjeldså *et al*., 2006; Sedano *et al*., 2010) and parts of the Amazon basin (Remsen & Parker III, 1983; Haffer, 1990; Nores, 1999), are not areas of spectacular nightjar diversity, despite a long history for some nightjar lineages in these areas (**Figure 7**). Five species arose in the highland areas of the Andes. *Lurocalis rufiventris* is found in both the North and Central Andes, and its sister-species *L. semitorquatus* has a large distribution in mostly lowland areas east of the Andes (**Map 6**). *Hydropsalis ruficervix* inhabits the montane forests of the Northern Andes whereas its

sister-species, *H. roraimae,* is endemic to the Pantepui highlands in Venezuela. These two species are closely related to *Hydropsalis longirostris,* which has a large distribution in southern South America, and one of its subspecies, *atripunctatus,* is found in the paramo of the Central Andes (**Map 7**). It is possible that the whole group was montane in origin (**Figure 13**) but the Andes are not reconstruced as their ancestral area (**Figure 7**). The final Andean group is the *Hydropsalis lyra/segmentata* species-complex. These two species (formerly belonging to *Uropsalis*) both inhabit the high altitude forests of the Northern and Central Andes (**Map 8).** The phylogenetic results indicate that *H. segmentata* is paraphyletic, with the northern Andean *H. s. segmentata* being the sister to a clade containing the central Andean *H. s. kalinowskii* and *H.lyra* which is found in both Andean regions. *H. lyra* is further divided into three subspecies, with clear geographic boundaries (Holyoak, 2001; Dickinson *et al*., 2003), but information about their phylogenetic relationships is scarce. *Hydropsalis lyra* and *H. segmentata* are apparently the only nightjars that have diversified further after colonizing the Andes.

There is temporal congruence in the history of these three Andean groups. The separation of *Lurocalis rufiventris* from its sister-species, the separation of the clade containing *Hydropsalis ruficervix* and *H. roraimae* from the clade containing *H. longirostris,* and the beginning of lineage divergence within the *H. lyra/H. segmentata* complex all occured between 8 and 6 MYA in the late Miocene (**Figure 4c**). This was a time when orogenesis in the Northern Andes was reaching its climax and diversification of other groups of birds and other organisms in the region was at its peak (Fjeldså, 1994; Kattan *et al.,* 2004; Pereira & Baker, 2004; Lim, 2008; Santos *et al.,* 2009; Sedano & Burns, 2009). Any of these taxa, in particular the *H.lyra/H. segmentata* complex, would

be good study groups for investigation of local speciation and biogeography processes occurring in the Northern and Central Andes.

The sister-relationship between *Hydropsalis roraimae* and *H. ruficervix* points to a historical connection between the Northern Andes and the Pantepui highlands in Venezuela. The split between the two species is estimated at 3.8 MYA (**Figure 4c**), which is slighthly younger than similar Andes-Tepui divergence events in other avian groups (Brumfield & Edwards, 2007; Mauck & Burns, 2009), and well after the formation of the sandstone tepuis had reached its climax during the Miocene (Maguire, 1970). Different causal events may have caused the separation between the two species, such as the rapid final uplift of the Colombian Cordilleras (Gregory-Wodzicki, 2000), marine transgressions (Nores *et al.,* 2004) or climate changes in the early Pliocene connected to changes in ocean currents (Billups, 2002).

The origin of another Pantepui endemic, *Hydropsalis whitelyi*, is even more problematic. Its topological position at the base of *Hydropsalis* is not well resolved (**Figure 2**) and its sister-group is not known with confidence. The lineage leading to *H. whitelyi* is old, dating back to the early Miocene at 22 MYA (**Figure 4c**), but when it arose in the highlands is difficult to guess. It is found on numerous tepuis but no information exists about potential inter-population genetic diversity.

4.2.1.2. Diversification in the Amazon Basin.

The only nightjar species that are restricted to the Amazon Basin are *Nyctidromus nigrescens, Nyctiprogne latifascia, Hydropsalis climacocerca* (except one subspecies in the Guianas), and the nighthawk *Chordeiles rupestris*. Of these three, only *N. latifascia* is a true forest-dwelling species, whereas *N. nigrescens* inhabits forest edges and clearings

and both *H. climacocerca* and *C. rupestris* prefer river banks, sandbars and rocky outcrops (Holyoak, 2001). The sister-taxa of *H. climacocerca* and *C. rupestris* are found on both sides of the Amazon basin (*H. cayennensis*-species complex (**Map 9**) and *C. acutipennis*-species complex (**Map 10**)). Both *H. climacocerca* and *C. rupestris* diverged from their sister-taxa around 7-10 MYA in the middle to late Miocene (**Figures 4a** and **4c**), a period when the current eastwards drainage system of the Amazon River was in formation (Hoorn *et al*., 1995). Occupancy of these new river bank habitats by ancestral populations of these two species, and separation from their savannah-dwelling relatives might have been a concurrent event. The situation of *Nyctidromus nigrescens* is different, as its sister-species, *N. hirundinaceus*, is an endemic in the xeric Caatinga forests in northeastern Brazil (**Map 11**), and the split between the two species pre-dates the origin of the other Amazonian species (**Figure 4c**).

Nyctiprogne latifascia, on the other hand, has a small range near the headwaters of the Rio Negro as well as the Rio Casiquaire which drains into the Orinoco system (**Map 12**). It represents an ancient lineage that split from its more widespread sister-taxon, which today consists of *N. leucopyga* and *N. vielliardi*. (**Figure 4c).** Two subspecies of *N. leucopyga*, *exigua* and *pallida*, are distributed north of *N. latifascia* in Venezuela (**Map 12**). They are morphologically more similar to other *N. leucopyga* subspecies further south in the Amazon Basin, although genetic information about their systematic taxus is missing (this thesis).

In addition to these four species, numerous widespread nightjar species that have large ranges throughout the lowland areas of South America inhabit the Amazon area.

The majority of these species live in open or semi-open habitats, including savannahs, farmlands, plantations, and forest edges. The evidence suggests that the Amazon River has been a barrier for the distribution of some of these widespread taxa and induced allopatric speciation numerous times. The most common pattern is a North/South divergence across the Solimões and Amazon Rivers. This is a well-known barrier in birds and other organisms (ie. Cortés-Ortiz *et al*., 2003; Pereira & Baker, 2004; Aleixo & Rosetti, 2007; Lim, 2007; Pereira & Wajntal, 2008; Ribas *et al*., 2012).

This pattern is seen in at least four nightjar taxa, and during different times after the formation of the Amazon River. The oldest example is the split of *H. torquata* from its sister-taxa *H. climacocerca/H.cayennensis*-complex around 8.4 MYA (**Figure 4c**). *H. cayennensis* and *H. albicauda* inhabit savannah and semi-open woodlands in Panama, Colombia, Venezuela and the Guianas, *H. torquata* lives in similar habitats south of the Amazon River, and *H. climacocerca* is a riverbank specialist in the Amazon Basin (**Map 9**) as previously described. The relationships between the three species are not completely resolved (this thesis), the mitochondrial phylogeny (**Figure 2**) supports *H. climacocerca* and *H. cayennensi*s-species complex as sister-taxa while previous studies (Han *et al.,* 2010) suggest that *H. climacocerca* and *H. torquata* are sister-species. Nevertheless, early divergence among all three species coincides with the formation of the Amazon River.

The divergence between *Hydropsalis heterurus* and *H. parvulus* is another example of an allopatric speciation involving the Amazon Basin as a barrier. *H. heterurus* is endemic to the Llanos grasslands in Venezuela and *H. parvulus* has a large distribution in grasslands south of the Amazon River (**Map 13**). Their divergence dates back to 4.8

MYA. A similar pattern is seen in *Nyctidromus* in which *Nyctidromus albicollis* and *N. derbyanus* diverged from one another 2.8 MYA (**Figure 4c**) within Amazonia. The split seems to be along the Amazon River drainage (**Map 14**), although the geographic boundaries have not been precisely delinated (this thesis). There is evidence for splits between subspecies of *Lurocalis semitorquatus* (**Map 6**) (this thesis), that may be less than 1 MYA old (**Figures 4a** and **4c**) or even older (according to *RAG-1* data – **Figure 3b**), but those require better study. These more recent events post-date the establishment of the current shape and size of the Amazon riverine system (Lundberg *et al.,* 1988; Figueiredo *et al*., 2009).

4.2.1.3. Diversification in the Caatinga, Cerrado and Chaco.

An important area for nightjar diversity in South America is the central Brazilian Plateau that today is mostly covered by dry forests, grasslands and agricultural areas and includes well established areas of endemism such as the Caatinga, Cerrado and Chaco. This composite area has a well-documented common history (Cole, 1960; Porzecanski & Cracraft, 2004; Colli *et al.,* 2005; Werneck, 2011) and today is home to 16 nightjar species. Some are widespread throughout the region as well as in other adjacent areas. These species include *Lurocalis semitorquatus, Nyctiprogne leucopyga, Hydropsalis longirostris, H. maculicaudus, H. parvulus, H. torquata, Nyctidromus albicollis, N. derbyanus* in the South American radiation, the poorwill *Antrostomus rufus,* and the nighthawks *Chordeiles acutipennis, Podager nacunda* and *P. pusillus.* This type of distribution evolved independently multiple times in the family, and there are examples of both old and young extant species in this group (**Figures 4a, 4b**, and **4c**).

Other species that inhabit the area are restricted to specific areas of endemism, and therefore have small ranges. These are also representatives of different genera, and include both old and new taxa. *Nyctidromus hirundinaceus* and *Nyctiprogne viellardi* are both endemic to the Caatinga (**Maps 11** and **12**), but *N. hirundinaceus* represents an old lineage (13 MYA) whereas *N. vielliardi* is much younger (3 MYA) (**Figure 4c**). Despite the age difference, both species have a sister-taxon that inhabits the Amazon Basin (*Nyctidromus nigrescens* and *Nyctiprogne leucopyga* respectively), suggesting that a connection between these two areas has been present in some form over a long period of time. The origin of the lineage leading to *N. hirundinaceus* coincides with mid-Miocene marine transgressions, which may have isolated parts of the Caatinga from the Amazon Basin (Hernández *et al.,* 2006).

Further south, the sister-species *Hydropsalis anomalus* and *H. candicans* inhabit the wet grasslands and swamps of the Chaco area of endemism, and dry pockets of Cerrado grassland, respectively (**Map 7**). They diverged from one another around 4.8 MYA (**Figure 4c**). As information about the extant distribution of the rare *H. candicans* is scarce, little inference can be made about the biogeographic history of these two species but a Chaco or Cerrado origin is most likely (**Figure 7**).

The results of the ancestral-area analysis for the South American radiation (**Figure 7**) suggest that this composite open habitat/dry forest area which includes the Cerrado, Chaco and Caatinga, was the ancestral area of an 11-species radiation within *Hydropsalis* (**Figure 7**). Only five of these species inhabit the area today, with the remainder found in other areas, including adjacent areas such as the Atlantic Forest (*H. forcipata*) or the Amazon Basin (*H. climacocerca*), but other areas are more distant such

as the Northern Andes (*H. ruficervix*) or the grasslands of Colombia and Venezuela (*H. albicauda* and *H. cayennensis*). The origin of this clade dates back to 15 MYA (**Figure 4c**) in the mid-Miocene. During this time a large lake, Lake Pebas, was present in western Amazonia (Wesselingh *et al.,* 2002) and high sea-levels resulted in marine incursions covering vast areas in South America, including the Chaco area in the Paraná Basin (Hernández *et al*., 2006). The Cerrado is hypothesized to be one of the older and more stable areas in South America, dating back to at least the Eocene (Romero, 1993) and as it is largely confined to the central Brazilian Plateau it was not affected as greatly by these marine incursions as the Chaco (Hernández *et al.,* 2006). It is possible that these marine incursions might have impacted early diversification within this group but how exactly is difficult to reconstruct as the presence of species with widespread distributions causes lack of resolution in the ancestral-area analysis at numerous nodes within the clade (**Figure 7**).

4.2.2 BIOGEOGRAPHY OF NIGHTJARS IN NORTH AND CENTRAL AMERICA AND THE CARIBBEAN

North of the Isthmus of Panama, the story of nightjar diversification predominantly involves the other two radiations, the poorwill and the nighthawks. Of the two the poorwill radiation is the more diverse and has an older history in the New World, dating back to about 33 MYA in the mid-Oligocene (**Figure 3b**). A total of thirteen poorwill species species inhabit North and Central America, the Caribbean, with five species breeding in South America (**Map 1**). In the nighthawk radiation, four species are

distributed in the area (**Map 3**). One species, *Chordeiles acutipennis* spans both continents by extending its range into southern Mesomaerica (**Map 10**).

4.2.2.1. Diversification in Mesoamerica.

Central America and Mexico has the highest diversity of nightjars outside of South America in the New World, with eight poorwills and three nighthawks found in the region. This was an important core area of diversification for the poorwill clade (**Figure 6**), in particular within the genus *Antrostomus,* but two *Nyctiphrynus* species and *Phalaenoptilus nuttallii* also inhabit the area. There is a mixture of species with small, well-defined ranges such as *Antrostomus saturatus* in the humid cloudforests of Costa Rica, *A. salvini* in the lowland woodlands of the Mexican Gulf area of Mexico, *A. badius* and *Nyctiphrynus yucatanicus* in the Yucatan Peninsula, and *N. mcleodii* in the oak and pine-oak woodlands in the highlands of Western Mexico. At the same time, some polytypic species are more widespread, like *Antrostomus ridgwayi* which inhabits open woodlands at various altitudes from Northern Mexico south to Nicaragua, *A. arizonae* with five subspecies from the highlands of Mexico including Chiapas, south to Honduras, and *Phalaenoptilus nuttallii*, which extends its distribution from the highlands of Mexico north to western North America (delHoyo *et al.,* 1999; Holyoak, 2001).

The distributions of the highland species (*Antrostomus arizonae, A. saturatus, Nyctiphrynus mcleodii*) correspond well with recognized areas of endemism in Mesoamerica (Halffter, 1987; Liebherr, 1994; Marshall & Liebherr, 2001; Morrone, 2006). The impact of geographic barriers that separate these Mesoamerican areas of endemism and are known for inducing vicariant speciation in many taxa including birds (i.e. Humphries, 1982; Marshall & Liebherr, 2001; García-Moreno *et al.,* 2006; Morrone,

2006; León-Paniagua *et al.,* 2007; Castoe *et al.,* 2008; McCormack *et al., 2008*) is not as evident as might be expected in the poorwill phylogeny mostly because interspersed through the phylogeny are species found outside of Mesoamerica, in both North and South America and the Caribbean. The only strong example of within-Mesoamerica vicariant speciation is the separation of *Antrostomus saturatus* in the northern Talamancan Cordillera in Costa Rica from its sister-taxon, the clade of *A. arizonae* and *A. vociferus* which has a large range in southern North America, and northern Mesoamerica extending as far south as the Chiapan Guatemalan Highlands and Honduras (**Map 15**). As *A. saturatus* and *A. arizonae* are both highland-dwelling taxa, the most likely barrier is the Nicaraguan Depression which is known to have been inundated by marine transgressions until the Pliocene (Halffter, 1987; Coates, 1997), but the divergence of these two taxa dates back 8 MYA in the late Miocene when these areas were presumably separated.

4.2.2.2. Disjunct distributions of sister-taxa in the poorwill radiation.

As stated above, the diversification patterns within both *Antrostomus* and *Nyctiphrynus* are characterized by repeated cases of sister-taxa having wideley-separated disjunct distibutions. As the bulk of the poorwill diversity is predicted to have originated in Mesoamerica (**Figure 6**), these patterns indicate dramatic distributional shifts from one distribution in Mesoamerica to distant localities in North America, the Caribbean and South America. Within *Antrostomus* there are two such scenarios. The sister-species to *A. arizonae* is *A. vociferus* which breeds in the eastern part of North America. The two species were previously considered to be conspecifics, but the results show that they split from one another almost 7 MYA in the late Miocene (**Figure 4b**). *A. vociferus* is

migratory, and winters in Eastern Mexico and Central America (Holyoak, 2001) where it is likely to be sympatric with *A. arizonae* (**Map 15**), but the genetic divergence suggests that the two species are highly distinct and it is not known if they hybridize at all. The old age of the split supports a vicariance hypothesis. Similar geographical patterns in which species in eastern or southeastern North America have a Mexican origin are seen in other North American birds such as *Melanerpes* woodpeckers (García-Trejo *et al*., 2009), *Toxostoma* trashers (Zink *et al*., 1999) and *Aimophila* sparrows (DaCosta *et al*., 2009), but it is not known whether they are temporally congruent with the *Antrostomus arizonae/vociferus* split.

A more extreme case of distributional disjunction between related taxa is the case of *Antrostomus seriocaudatus*. It is closely related to *A. salvini* and *A. badius,* of which both have small ranges in the lowlands of eastern Mexico, but *A. seriocaudatus* breeds in central South America, including southern Brazil, Bolivia and Paraguay (see **Map 16**). It split from the other two species between 5 and 10 MYA (**Figure 4b**), but the relationships among the three species are not fully resolved (this thesis) (**Figure 2**). Either the ancestral ranges of one or more of the species were much greater, their common ancestor had a large distribution that became severely fragmented, or the extant distibution of *A. seriocaudatus* is the result of a long-distance dispersal event. The occurrence of migratory behavior within the genus may add weight to the dispersal hypothesis.

The patterns within *Nyctiphrynus* are similarly confusing (see **Map 17**). Two of the species (*N. ocellatus* and *N. rosenbergi*) breed in South America, whereas the other two (*N. yucatanensis* and *N. mcleodii*) breed in Mexico. The two Mexican species are not

most closely related, however, as *N. yucatanensis* and *N. ocellatus* are sister-species. Unlike *Antrostomus*, a South American origin is predicted for the genus (**Figure 6**). Migration or other seasonal movement patterns are not known for species in this genus so long-distance dispersal is perhaps a less likely explanation for the disjunct distributional ranges than in *Antrostomus*. Thus, a gradual episode of vicariance from an original widespread distribution may have taken place, with *N. rosenbergi* becoming isolated in the Chóco region more than 21 MYA in the early Miocene. *N. mcleodi* in the highlands of the Sierra Madres of western Mexico separated from *N. ocellatus* and *N. yucatanicus* 12. 6 MYA, perhaps with the Isthmus of Tehuantepec serving as a barrier, although it predates similar divergences in other groups by more than 9 MYA (Hasbún *et al.,* 2005; Castoe *et al.,* 2008). Another explanation for the isolation of *N. mcleodii* may be active volcanism in the Sierra Madres in the Miocene (Ferrari *et al.,* 1999; Nieto-Samaniego *et al.,* 2006). The final divergence between *N. ocellatus* and *N. yucatanicus* may have taken place in Central America, because despite the bulk of the range of *N. ocellatus* being south of the Amazon Basin and east of the Andes in South America, one of its two subspecies, *N. o. lautus*, has been found in Nicaragua and Costa Rica (**Map 17**). This subspecies has not been included in molecular phylogenies, so a closer look at the relationships of these taxa is required to fully understand the biogeography.

Long-distance dispersal is more probable as the cause of a yet another case of disjunct distributions of closely related species in the poorwill radiation. In this case, none of the three species involved are found in Mesoamerica. *Antrostomus carolinensis* breeds in southeastern North America. It is also migratory and winters in Central America and the Caribbean. Its sister species is *A. cubanensis*, which breeds in the

Greater Antilles on Cuba and Hispaniola and they are sister to *A. rufus*, which has a large range extending from Panama through the lowlands of Colombia and Venezuela and most of tropical and subtropical Brazil (**Map 18**). The relationships among the three species are not completely resolved, however (**Figure 2**). *A. rufus* is predicted to have diverged from the other two 8.6 MYA with *A. carolinensis* and *A. cubanensis* separating 5.6 MYA (**Figure 4b**). The ancestral-area analysis cannot resolve the geographic origin of the ancestor of all three species (**Figure 6**) as the clade is embedded among mesoamerican taxa. It has been suggested that the avifauna of the Greater Antilles is closely related to the Central American avifauna (Vasquez-Miranda *et al.,* 2007), and the sister-group to this three-taxon clade is indeed of Central American origin with two species (*A. badius* and *A. salvini*) breeding in the Yucatan and Gulf of Mexico. Cuba and the Yucatan Peninsula are only separated by 125 miles, hence dispersal between the two areas is plausible for these birds. Likewise, Cuba and Florida are close to one another, and as the wintering sites of *A. carolinensis* overlap with the breeding range of *A. cubanensis* on both Cuba and Hispaniola, movements between the two areas is already present. *Antrostomus rufus* has succesfully colonized some of the Lesser Antilles, so a high propensity for dispersal across open water is present in all three species and may explain their disjunct distributions. Until the relationships of the three species are fully resolved, and the taxonomic status of the three subspecies of *A. cubanensis* fully understood (it has been suggested *A. cubanensis* represents at least two species – Cleere, 2010), the biogeographical history of this species-complex remains uncertain.

4.2.2.3. Biogeography of nighthawks in Central and North America.

Four nighthawk species breed in Central and North America, all members of the genus *Chordeiles*. Their presence there is considerably younger than the poorwill radiation and arose twice independently from an ancestral South American origin. (**Figure 8**). *Chordeiles minor* has the largest breeding range of any nightjar species in North America stretching from Panama in the south through the remainder of Central America, Mexico, the majority of the USA and southern half of Canada (**Map 19**). As there is little genetic structure throughout its range (this thesis), an expansion of its current breeding range throughout North America may have occured very rapidly during the Pleistocene, possibly after a previous reduction during glacial cycles as seen in many other avian taxa (ie. Zink, 1996; Avise & Walker, 1998; Milá *et al.,* 2000, 2007; Colbeck *et al.,* 2008). No population-level studies exist for the species, so the timing, origin and spatial patterns of this potential expansion into its current range are unknown.

Its sister-species, *Chordeiles gundlachii* breeds in the Caribbean on the Greater Antilles as well as the Bahamas and Turks & Caicos (**Map 19**). These two species split from one another around 4.2 MYA in the early Pliocene (**Figure 4a**). *Chordeiles minor* has a large wintering range in South and Central America as well as in the Caribbean. *C. gundlachii* is also migratory so the wintering grounds of the two species do not overlap in the Caribbean, although it is not known precisely where *C. gundlachii* winters (Holyoak, 2001). It is likely that the ancestral species of the two, had a large extensive range in North America with populations in the Caribbean diverging from the rest in the early Pliocene. The separation of the lineage leading to these two taxa from its sister-taxa dates back to 18 MYA (**Figure 4a**), but the exact timing of its dispersion out of South America into Central and North America later in the Miocene is unknown.

Chordeiles acutipennis and its sister-species *C. texensis* are found in Central America and Mexico, and the two species split from one another in the very late Pliocene or around 2.8 MYA (**Figure 4a**). The range boundaries of the two species are somewhat unclear, with *C. texensis* breeding in the arid regions of north and central Mexico, but two subspecies of *C. acutipennis, littoralis* and *micromeris,* have a joint distribution from central Mexico south to Panama. The ranges of *littoralis* and *acutipennis* are known to overlap (**Map 10**). The remaining *C. acutipennis* subspecies are found in South America. *C. a. littoralis* and *micromeris* form a distinct subclade within the species complex as presented in Chapter 2, and although the evidence is not strong enough to suggest that together they form a distinct species, they were treated as a separate taxon in the dating analysis and the results show it split from the nominate form in the mid-Pleistocene (1.4. MYA) (**Figure 4a**). Both the split between *C. acutipennis* and *C. texensis* and between *C. a. littoralis/micromeris* and the remaining *C. acutipennis* occured after the formation of the Isthmus of Panama around 3.5. MYA-4 MYA (Keigwin Jr, 1978; Coates & Obando, 1996; Kirby *et al*., 2008).

4.2.2.4. Recent trans-Panamian dispersion events

There are a number of trans-Panamian dispersion events within Caprimulgidae, particularly within the South American Clade. Within the genus *Nyctidromus* there are two independent dispersion events from South America to Central America (**Map 14**). First, the divergence of *N. merrilli* from *N. albicollis* and *N. derbyanus,* may have happened as a result of dispersion and vicariance across the still-forming Isthmus of Panama, around 4.5 MYA (**Figure 4c**). *N. merrilli* is strictly found in Mexico and Central America but the current range of *N. albicollis* extends from northern South America into

Central America as far as Honduras while *N. derbyanus* is distributed more distantly south of the Amazon (**Map 14**). The presence of *N. albicollis* in Central America might represent a recent dispersion, but is not known with certainty where *N. albicollis* and *N. merrilli* meet and whether possible hybridization may be occurring.

Another more recent example of a trans-Panamian dispersion event occurred in the species *Lurocalis semitorquatus*, but two of its subspecies *L. s. stonei* and *L. s. noctivagus* breed in Guatemala/Honduras and Panama respectively whereas the other three subspecies are found in the Amazon Basin, Guianas and across Brazil to the Atlantic Forest. There is some genetic structure within the species (this thesis), with *L. s. stonei* diverging from the nominate *semitorquatus*, which is distributed north of the Amazon in the Guianas and in coastal areas of Colombia and Venezuela, very recently (between 1-1.5 MYA) (**Figure 4c**), but better sampling of the different subspecies is needed to fully understand if and how dispersion into Central America may have induced divergence between populations, or if vicariant sea-level changes in northwestern South America may have played a part (Nores, 2004).

4.3 ECOLOGICAL TRAIT EVOLUTION IN THE NEW WORLD CAPRIMULGIDAE

4.3.1 PATTERNS OF HABITAT CHOICE DIVERSIFICATION

Habitat choice diversity differs considerably among the three New World nightjar radiations (**Figures 9-13**). Despite having the largest overall range of the three radiations (**Map 3**), habitat diversity is the lowest among the nighthawks as they are strictly found in open or semi-open habitats and mainly in lowlands (**Figures 9** and **11**). This

preference for open habitats can be explained by their feeding ecology but unlike the majority of nightjar species, all nighthawks feed only by "hawking", catching prey items in continuous flight, often quite high above the ground in a similar manner to swifts (Apodidae). This foraging behavior relies on adequate room to maneuver and is therefore more suitable to open areas. It also relies on light which is why nighthawks are generally less nocturnal than other nightjars. In contrast, most forest-dwelling nightjar species forage by "sallying", or flying upwards from the ground or a perch to catch a single prey item (Cleere & Nurney, 1999; Holyoak, 2001).

The poorwills, on the other hand, are predominantly found in forests, and the ancestral trait reconstruction analysis suggests this habitat preference is primitive in the group (**Figure 9**). Only one species, *Phalaenoptilus nuttalli,* prefers open habitats, in this case arid scrubland and prairies, whereas the other five poorwill species are generalists, preferring semi-open forests and forest edges but are sometimes also found in grassland habitats (i.e., *Antrostomus rufus*) or dense forest (i.e., *A. ridgwayi*). Poorwills do inhabit a wide variety of forest types at different altitudes, humid and dry, deciduous and evergreen. Most of the species prefer a single type of forest, which may explain why their distributions are limited to small areas such as the pine-oak woodlands in the highlands of Western Mexico (*Nyctiphrynus mcleodii*), the thorny brushland in the coastal area of the Gulf of Mexico (*Antrostomus salvini*), and the cloud forests of the Talamancan Cordillera in Costa Rica (*Antrostomus saturatus*).

Diversity of habitat choice is highest within the South American radiation (**Figures 10** and **12**), with forest and open habitat specialists equally represented, and 10 species inhabit intermediate or both kinds of habitats. The majority of the species are

found in lowlands, and except for *Lurocalis rufiventris*, all highland species are in the genus *Hydropsalis*. The ancestral habitat reconstruction in **Figure 13** provides a better picture of the evolution of habitat choice within the South American radiation than the simpler analyses depicted in **Figures 10** and **12**. Lowland tropical forests were most important in the early history of the whole radiation as well as within the genera *Lurocalis, Nyctiprogne* and *Nyctidromus*. Montane forests are much more common in *Hydropsali*s, with six species inhabiting the Andes or the Tepuis; montane forests are the ancestral habitat type for the genus.

Habitat shifts from forests to open habitats occurred repeatedly within the South American radiation, including six times within *Hydropsalis* and three times in *Nyctidromus*. There are four independent shifts into dry forest or scrubland habitats. All four lineages lead to a single species (*Hydropsalis decussatus, Nyctidromus anthonyi, N. hirundinaceus, Nyctiprogne vielliardi*). With the exception of *N. vielliardi*, these habitat shift events occurred early in the history of the group, dating back to the early-mid Miocene (15-18 MYA). Habitat shifts into more widespread grassland and savannah habitats occurred at least six times (**Figure 14**), including five times in *Hydropsalis*.

The majority of the shifts into grasslands took place in the latter half of the Miocene (10-12 MYA), when increased aridification and cooling led to significant expansion of open grasslands and dry semi-open woodlands (Pascual & Jaureguizar, 1990; Flower & Kennett, 1994; MacFadden *et al.,* 1996; Latorre *et al.,* 1997; Pagani *et al.,* 1999; Ortiz-Jaureguizar & Cladera, 2006; Barreda & Palazzesi, 2007). The appearance of open grassland and savannah habitats that gradually expanded over a large area apparently enabled many of species to extend their ranges and achieve a wide

distribution, in particular those that are able to live in various types of open and semi-open habitats (grassland, savannah, farmlands, forest edges etc.). Not all grassland species are widespread and generalists, and at least two species, *H. anomalus* and *H. candicans*, are highly specialized to a particular type of grassland (Chaco swamps and dry open Cerrado grasslands respectively), and hence have small ranges.

The differences in habitat choice among the three radiations, whose histories are largely temporally congruent in the New World, raise questions about how habitat diversity and its evolution impacts spatial distribution in related groups. It is difficult to compare the poorwill and South American radiation as they are almost completely spatially separated but the nighthawks, on the other hand, overlap the distributions of the two other radiations. Perhaps due to restrictions related to their foraging style, ecological diversification in the nighthawk radiation has been limited and they inhabit broadly similar open habitats in both North and South America. Nevertheless, as a group they have successfully extended their distributions extensively on both continents, in some cases relatively rapidly. In South America, other habitat types such as forests and montane habitats are inhabited by members of the South American radiation (and four poorwill species), but numerous shifts from forests into various open habitats have occurred in the history of the South American radiation whereas the poorwills have been much less successful in shifting into available open habitats in Central and North America. The generally small and ecologically specific ranges of the poorwills in Central America may be a result from this historical inability to take advantage of increasing availability of open habitats with *Phalaenoptilus nuttalli* being the only real exception.

Habitat choice conservatism seems to be prevalent in both the nighthawk and poorwill radiations, much more so than in the larger South American radiation. This may be explained by the slightly younger age of these radiations (**Figure 3b**) or to differences in total diversity, but the spatial diversification histories of the two radiations are very different despite the presence of several migratory species suggesting high dispersal propensity in both groups. How the strong differences in habitat choice between the two radiations impacted their diversification and distribution is difficult to test.

4.3.2 EVOLUTION OF MIGRATORY BEHAVIOR

The relevance of the evolution of migratory behavior within the three New World nightjar radiations to the biogeographic history of individual taxa has been discussed in previous sections. Unsurprisingly, the majority of the long-distance migratory species are members of the two radiations that are present in North America, namely the nighthawks and the poorwills. The only long-distance migrant in the South American radiation is also the only true austral migrant (**Figure 14**). The presence of partial migratory behavior, such as nomadic movements (seasonal or not) within the breeding range and altitudinal movements, is evenly distributed throughout the phylogeny, which indicates that migratory behavior has evolved independently numerous times within the family. This is congruent with patterns seen in other groups of birds in which phylogenetic signal for migratory behavior tends to be weak and the trait thus highly labile (Joseph *et al.*, 1999; Outlaw *et al*., 2003; Outlaw & Voelker, 2006; Winker & Pruett, 2006; Kondo & Omland, 2007). The effect of the presence of migratory behavior on distributions and how they may change through time is difficult to evaluate. Information about wintering habits of nightjars and breeding site fidelity are scarce. It is

suspected in other species, that some individuals of migratory species at their wintering sites may become sedentary and even diverge from their ancestral species (Kondo *et al*., 2008), but whether that is a common phenomenon is not well understood. Seasonal migration increases movements of individuals and populations and thus may increase the chances of long-distance dispersal, as well as greatly increasing the distrubutional range of a species. In groups with a high occurrence of migration such as the poorwills, it is possible that thie behavior may have played an important part in creating some of the disjunct distributions of sister-species seen today, as well as have allowed for the colonization of isolated areas such as islands in the Caribbean.

5. CONCLUSIONS

The history of nightjar diversification in the New World should be viewed as three independent stories, as the biogeography and ecological diversification of the three New World radiations are highly different. The onset of diversification in the three groups is not temporally congruent, with the nighthawk radiation being 10 million years younger than the South American radiation, whereas the poorwill radiation is intermediate in age. Nevertheless, the bulk of extant lineage generation in all three radiations occurred in the last 20 million years.

The pathways of spatial distribution differ greatly among the three. The South American radiation is almost strictly limited to South America, where it radiated into multiple different areas across the continent. The diversity is evenly distributed with areas renowned for avian species richness, such as the Amazon Basin and the Andes, not being exceptionally diverse. The most important area for diversification was the Central-South American Corridor, a composite area of dry forests and open habitats, which is inhabited by numerous widespread species as well as endemics. The core area of poorwill diversity is Mesoamerica, but high dispersal propensity of taxa within the clade has allowed for numerous independent colonizations of distant areas in North America, on the Caribbean Islands and in South America. The nighthawk radiation is the least diverse, but has the largest distribution, covering both continents, and most species are widespread.

Ecological diversification is also highly different among the three groups with regard to habitat choice and migratory behavior, the two ecological traits investigated in

this study. The nighthawks are open-habitat specialists and are restricted to lowland areas. The majority of poorwill species live in forest but inhabit a variety of both lowland and highland forest habitats. The diversity of habitat choice is the highest in the South American radiation, and despite a strong phylogenetic signal for ancestral distributions being tropical forests (both lowland and montane), numerous independent habitat shifts into drier, more open habitats have occurred within the radiation, a likely response to the increased availability of those habitats in the Miocene and Pliocene. Migratory behavior has evolved in all three radiations, but is most prominent in the poorwill and nighthawk radiations.

Distributions of extant avian taxa are the result of a complex interplay of events such as allopatric speciation, dispersion between adjacent areas and long-distance dispersal, and are directly shaped by the availability of areas, creation and disappearance of geographic barriers, as well as the evolution of ecological traits that may either induce or decrease movements between areas. All these processes and their impact can change at various rates over time and affect taxa differently. The New World nightjars are no different as is evident by the diverse diversification histories described in this study.

The distinct patterns and differences in spatial distribution and ecological specialization of these three, temporally concurrent radiations raises questions about the generality of the processes shaping large-scale continental diversification of radiations that share similarities in their morphology, lifestyle or ecology, and that are broadly distributed in the same or adjacent areas. Is the degree of spatial separation and/or habitat choice differentiation seen among the three New World nightjar radiations observed among sub-groups in other diverse avian radiations?

Even without knowledge about intrinsic causal processes, investigating whether similar patterns of such spatial (i.e., allopatry, frequent dispersal events, range size diversity, range overlap) and ecological differentiation (i.e., niche conservatism, niche shifts) on a continental scale are seen in other New World avian groups is an important next step. Groups that are somewhat constrained morphologically because of a particular lifestyle but are both diverse and widespread (such as hummingbirds, swifts or owls) are potentially good candidates for comparison with the nightjars. Complete species phylogenies, distributional data, and ecological information are required for such comparisons. How levels of diversity, phylogenetic distance or spatial distance affect the presence of unique patterns also need evaluation.

Investigating biogeography and diversification in groups that are distributed across whole continents is extremely complex as it involves a larger number and variety of areas, habitats, ecological conditions, and time periods than more local studies. But as this study on the New World nightjars shows, spatial diversification patterns can be inferred from well-sampled calibrated phylogenies, and information about broadly defined ecological traits can cast light on general trends in niche evolution within groups on a large, continental scale.

6. FIGURES AND MAPS

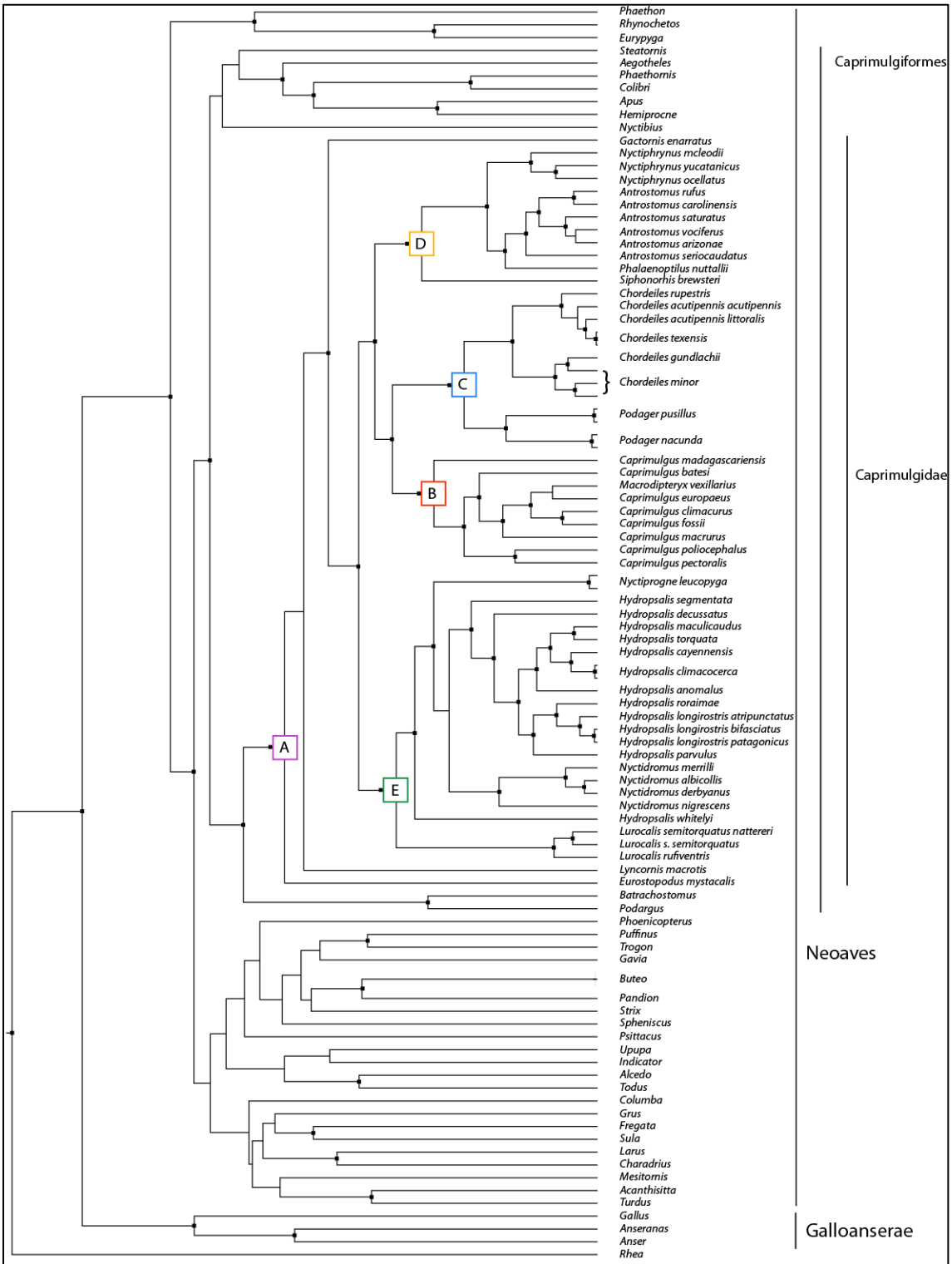


FIGURE 1: A phylogeny of modern birds with emphasis on the caprimulgiform taxa in particular the caprimulgids based on a Bayesian analysis in Beast v1.6.2 of a *RAG-1* dataset (2,877bp). Nodes with posterior probability values higher than 0.95 are marked by a black square. The clades indicated by letters arethe following:
A - All nightjars (Caprimulgidae)
B - Crown Old World radiation.
C - Nighthawk clade
D - Poorwill clade
E - South American radiation.

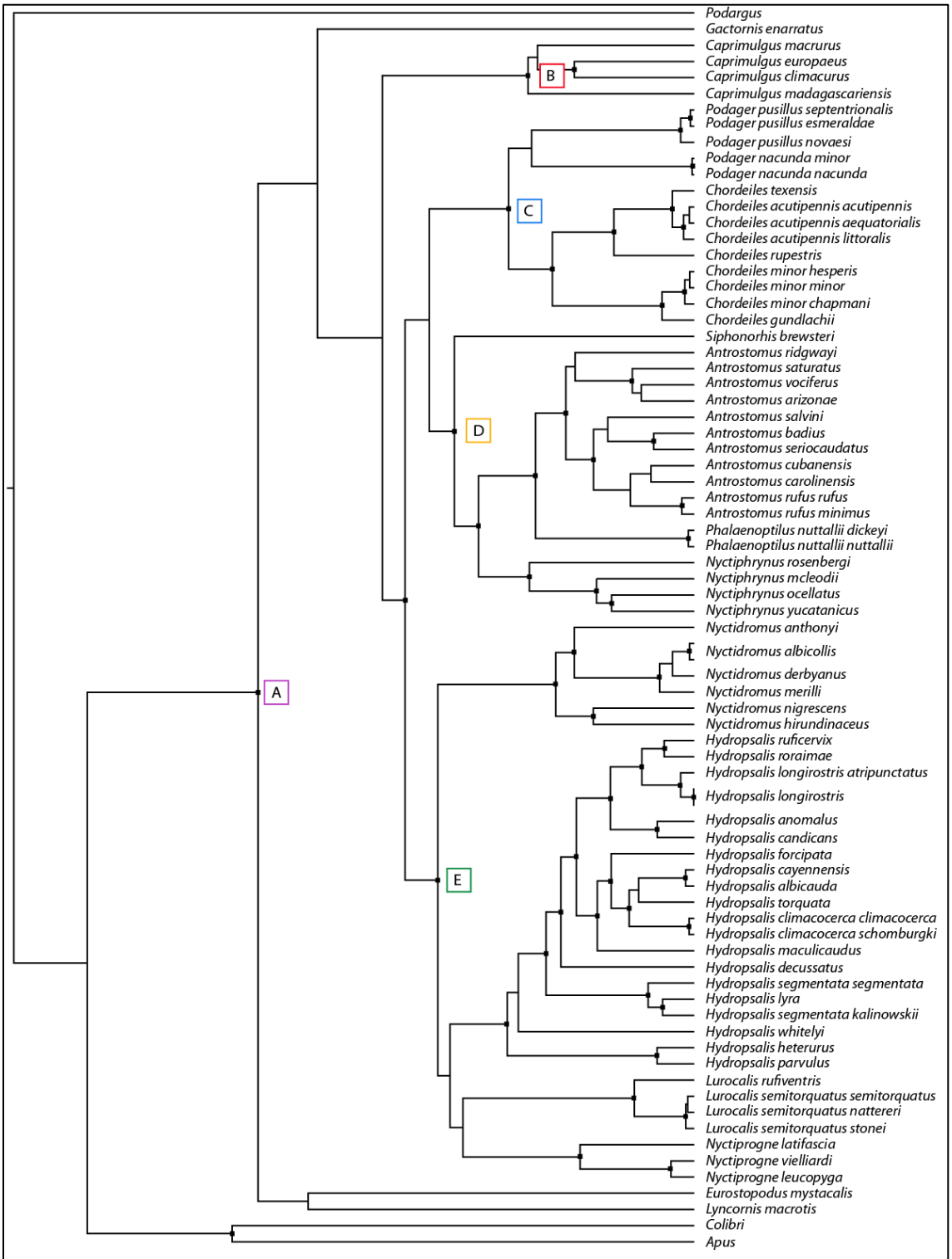


FIGURE 2: A phylogeny of the Caprimulgidae and three outgroup taxa based on a Bayesian analysis in Beast v1.6.2 of a *mtDNA* dataset (2,185bp). Nodes with posterior probability values higher than 0.95 and bootstrap values higher than 70 (from a ML analysis of the same data) are marked by a black square. The clades indicated by letters are the following:
A - All nightjars (Caprimulgidae)
B - Crown Old World radiation.
C - Nighthawk clade
D - Poorwill clade
E - South American radiation.

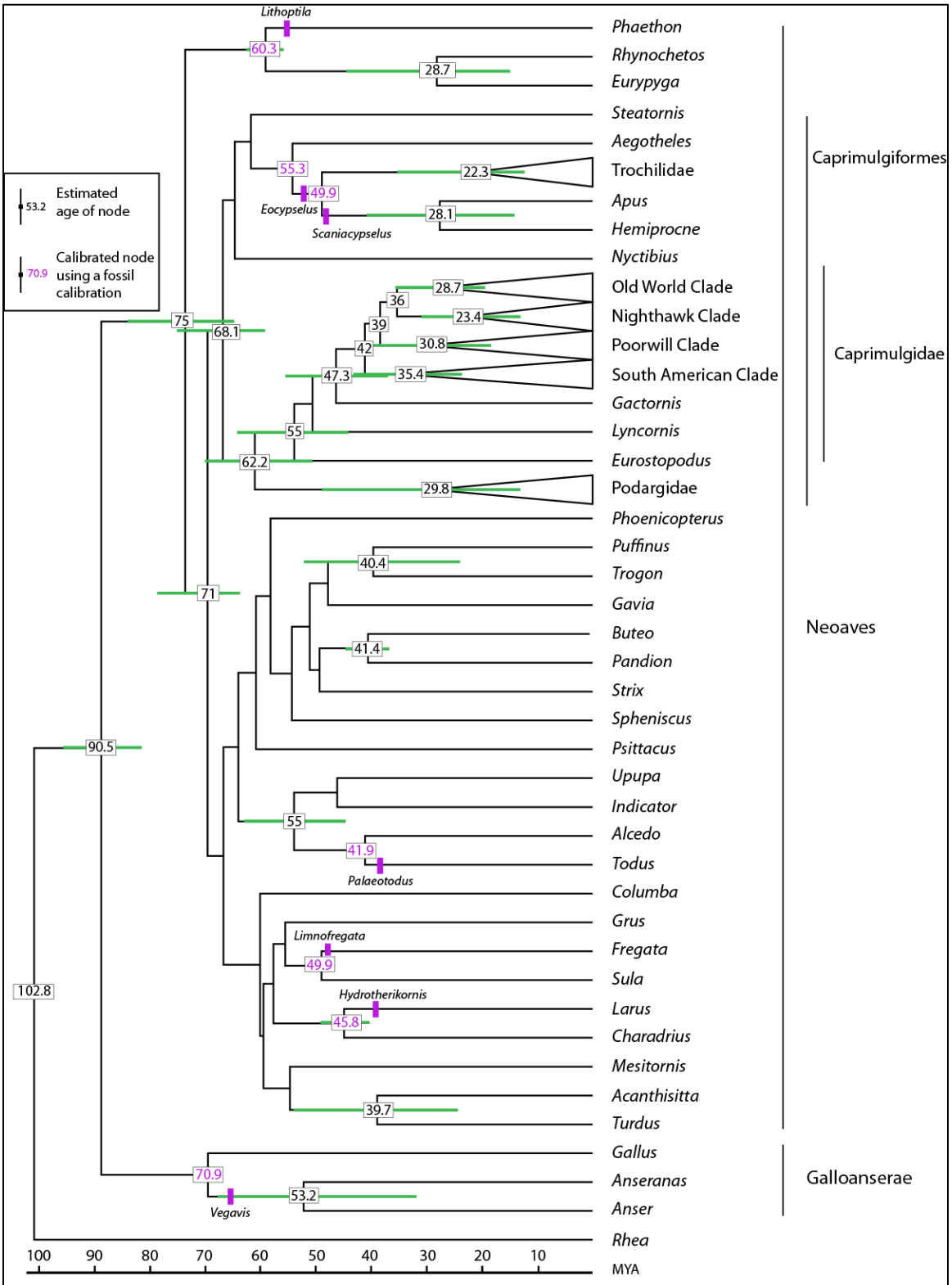
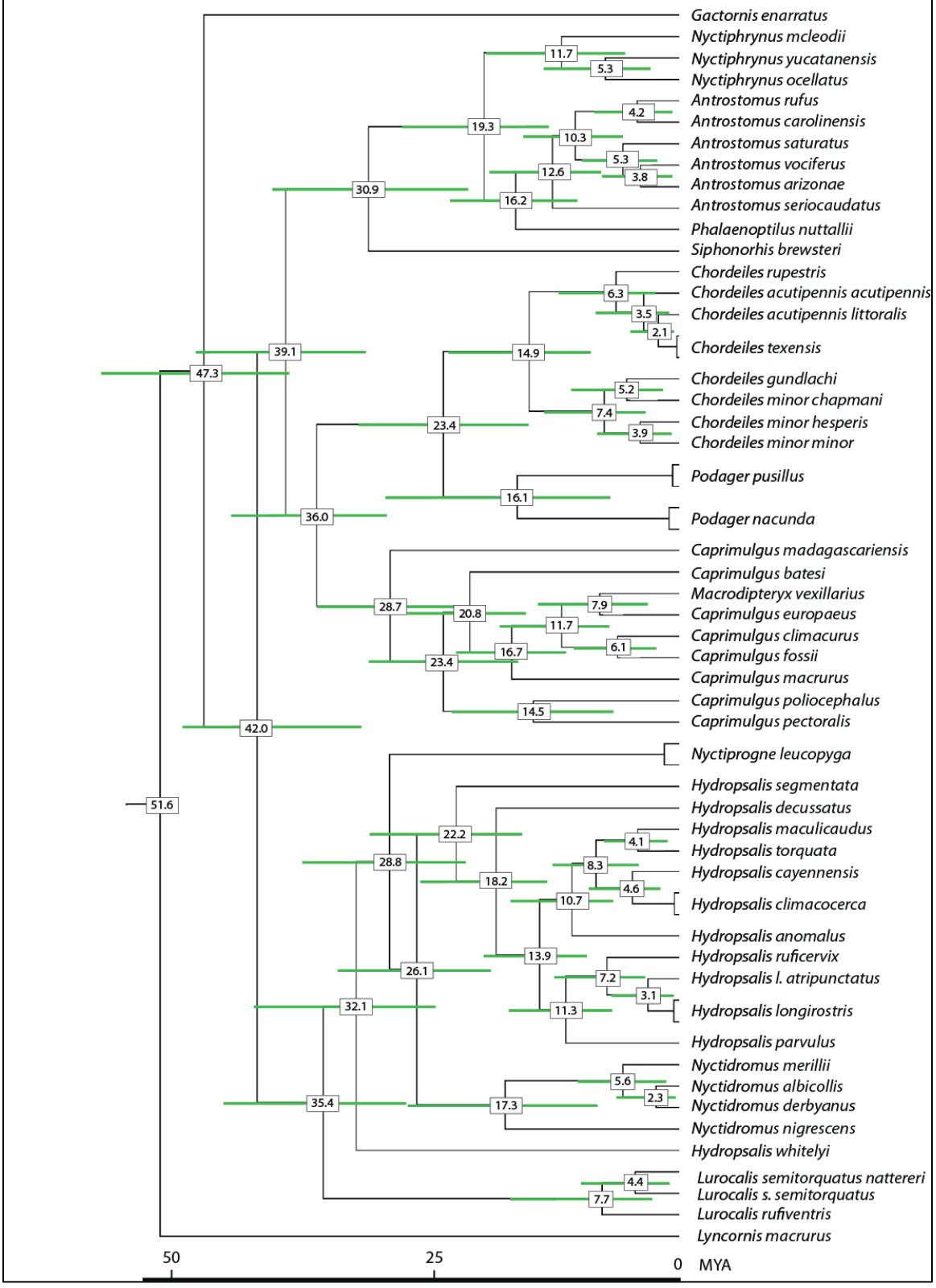


FIGURE 3a: A chronogram of modern birds with emphasis on the caprimulgiform taxa based on a relaxed molecular clock dating analysis in Beast v1.6.2 of a *RAG-1* dataset (2,877bp). Dates of divergence are depicted on nodes with dates and fossils used for calibration are placed on the stem lineages.
95% confidence limits are also displayed as green lines.

FIGURE 3b: A chronogram of the caprimulgids (except *Eurostopodus*) based on the results of a relaxed molecular clock analysis of a *RAG-1* dataset (2,877bp) in Beast v1.6.2. 95% confidence limits placed on the dates.



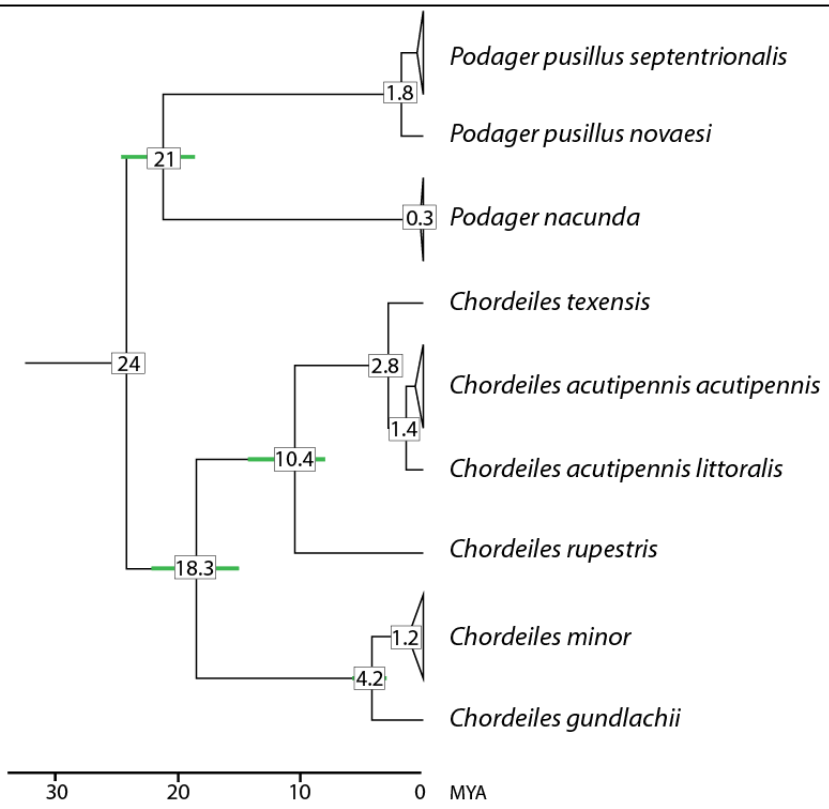


FIGURE 4a: A chronogram of the Nighthawk clade from the results of a relaxed molecular clock analysis of a mitochondrial dataset (2,185bp) in Beast v1.6.2. Dates of divergence are depicted on the nodes. A normal distributed calibration was placed on the root based on its estimated age from the analysis of a RAG-1 dataset. 95% confidence limits are displayed as green lines.

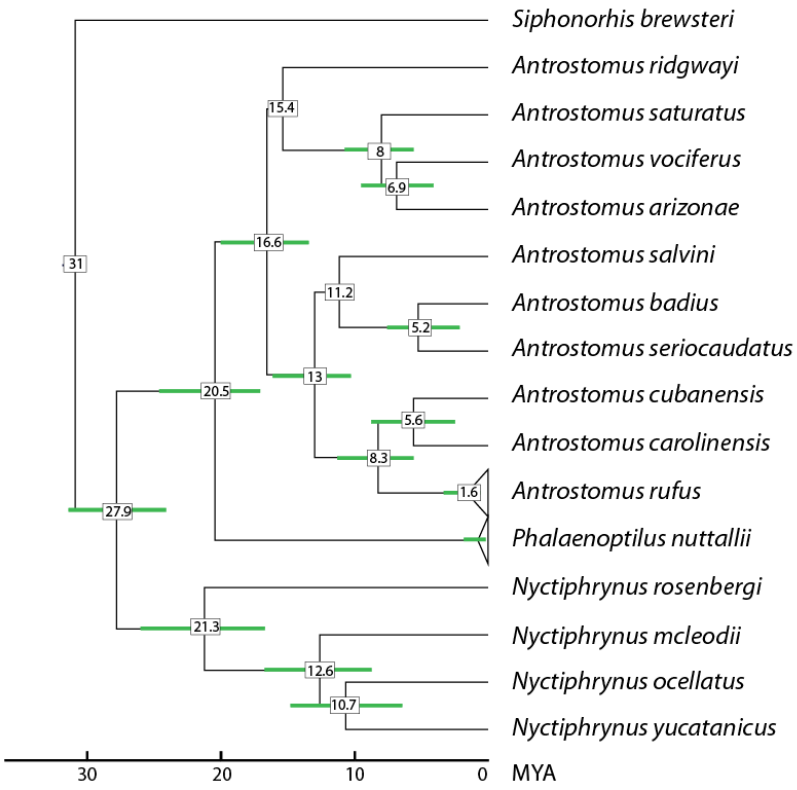


FIGURE 4b: A chronogram of the Poorwill clade based on the results of a relaxed molecular clock analysis of a mitochondrial dataset (2,185bp) in Beast v1.6.2. Dates of divergence are depicted on the nodes. A normal distributed calibration was placed on the root based on its estimated age from the analysis of a RAG-1 dataset. 95% confidence limits are displayed as green lines.

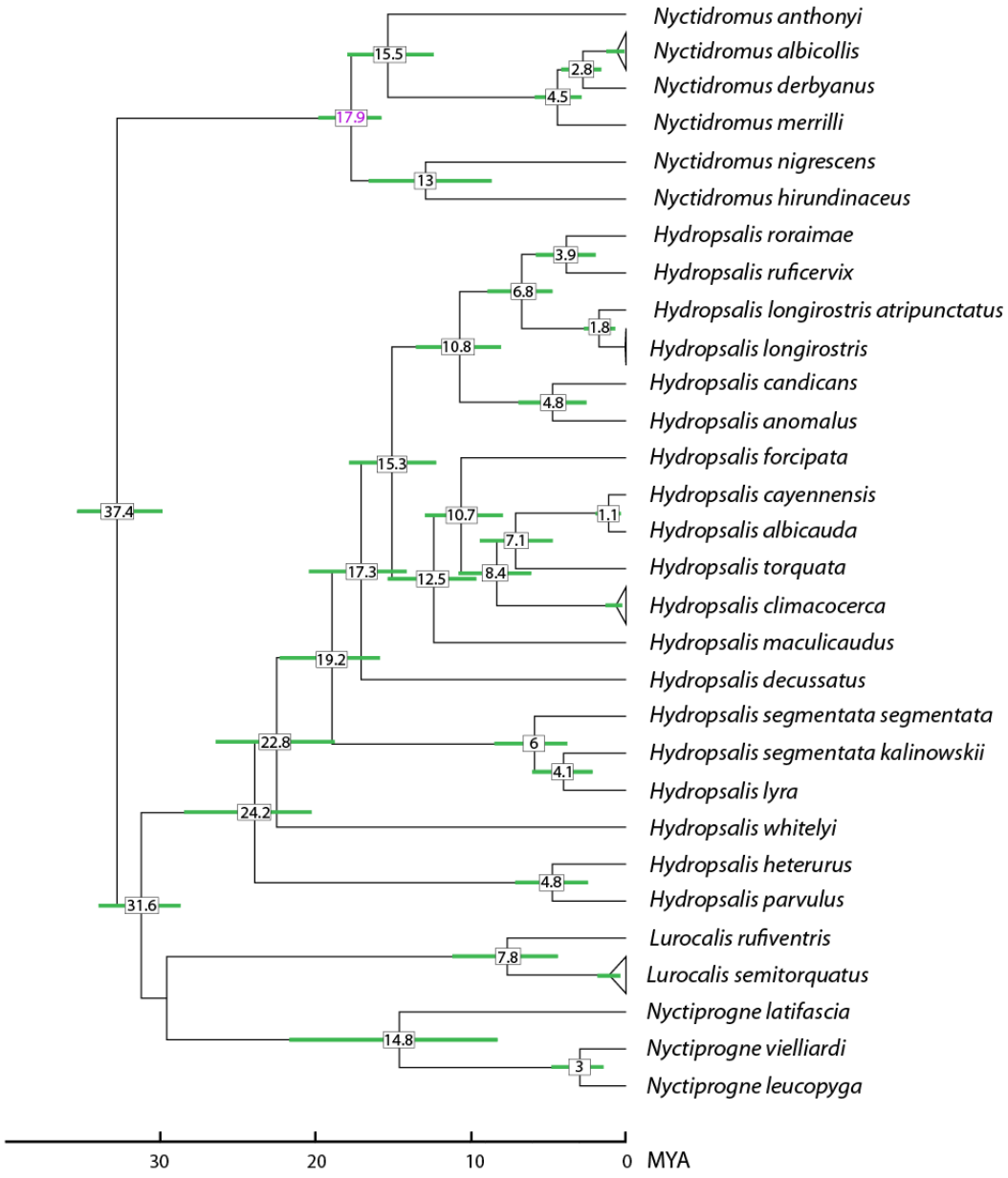
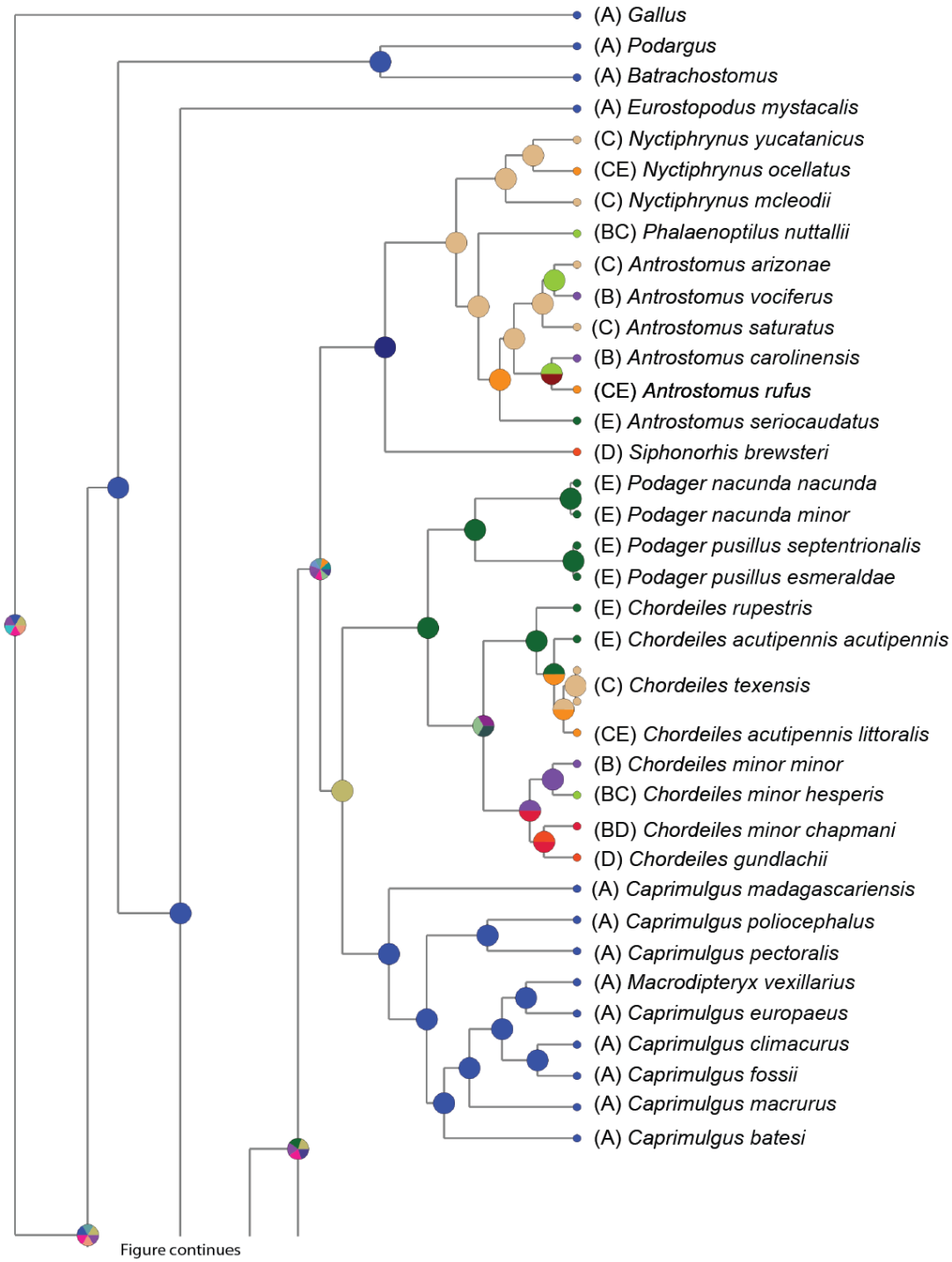


FIGURE 4c: A chronogram of the South American clade based on the results of a relaxed molecular clock analysis of a mitochondrial dataset (2,185bp) in Beast v1.6.2. Dates of divergence are depicted on the nodes. A normal distributed calibration was placed on the root based on its estimated age from the analysis of a RAG-1 dataset. 95% confidence limits are displayed as green lines.

FIGURE 5: An ancient area reconstruction plot for the Caprimulgidae and other caprimulgiform taxa from a BBM analysis in RASP using a *RAG-1* phylogeny. Distributions of extant taxa are shown next to their names. Pie charts on nodes show the inferred reconstructed ancestral areas for the clades in question. Each color represents either a single area or combinations of areas as explained in the legend.



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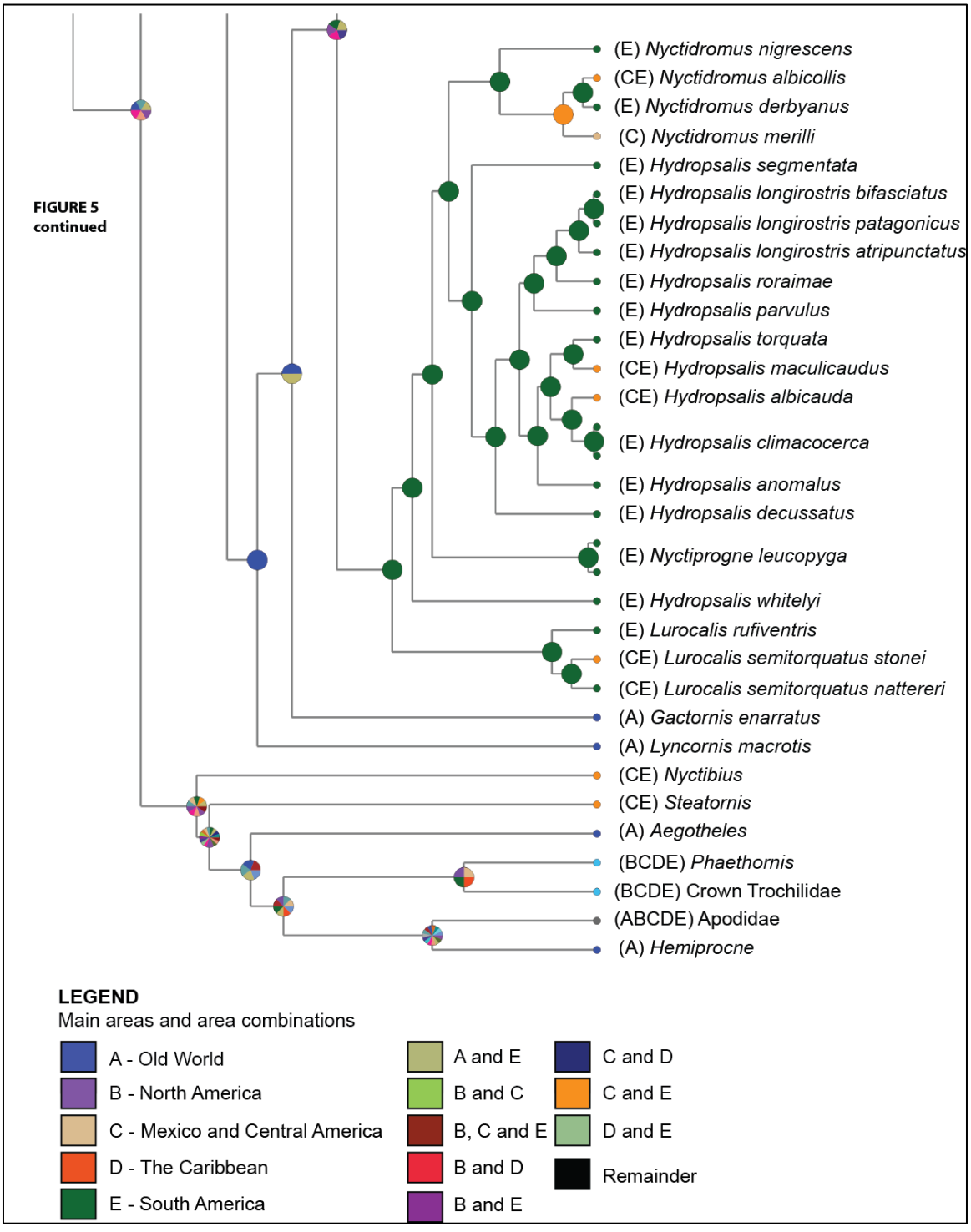


FIGURE 5
continued

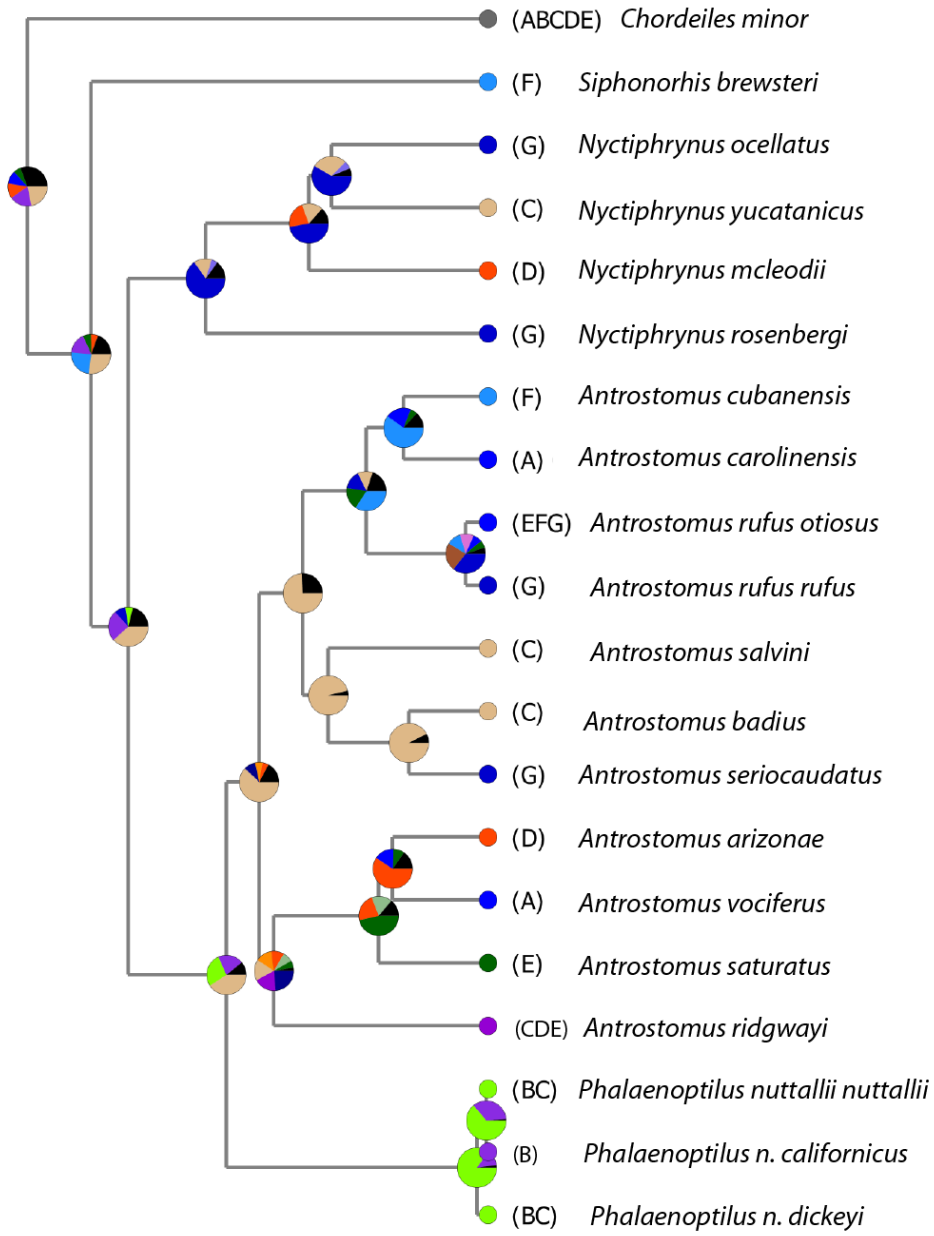
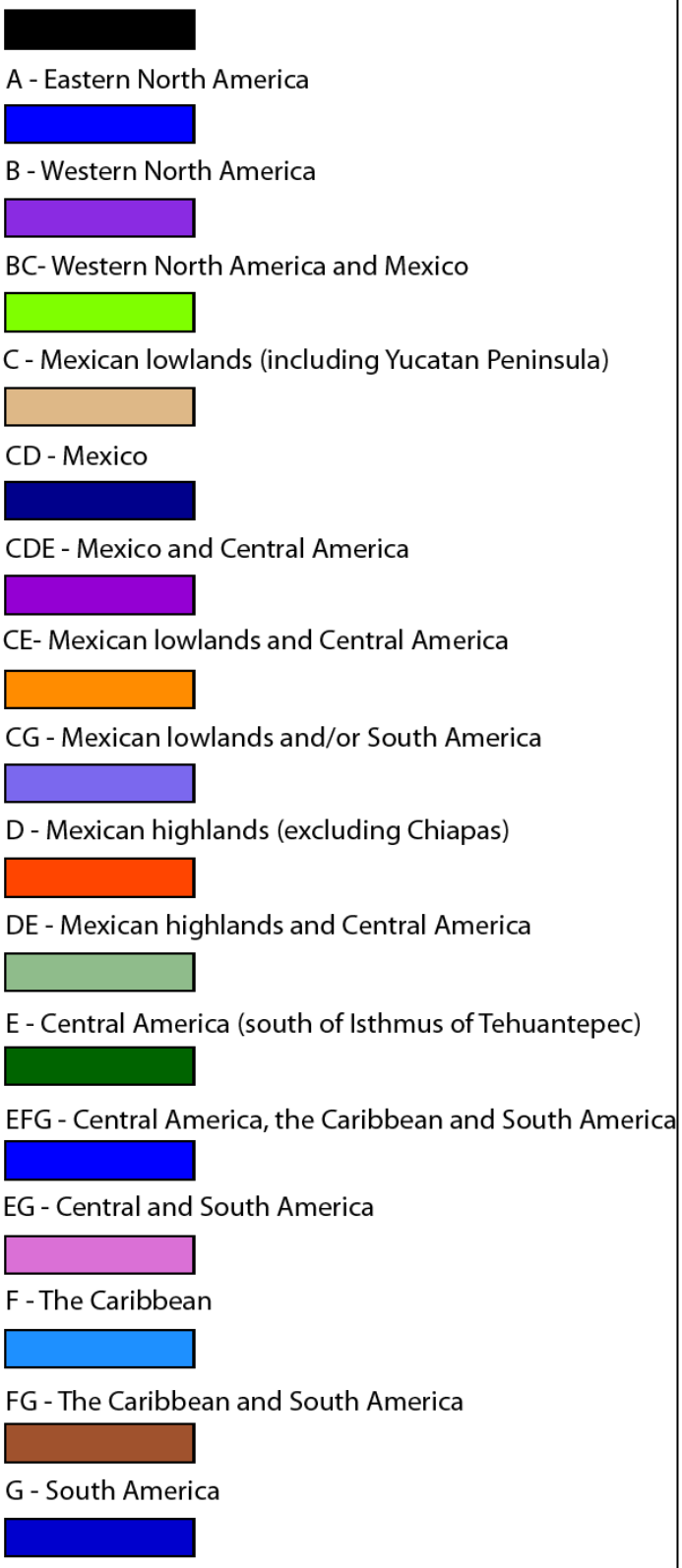


FIGURE 6a: An ancient area reconstruction plot for the Poorwill clade from a BBM analysis in RASP using a mitochondrial phylogeny. Distributions of extant taxa are shown next to their names. Pie charts on nodes show the inferred reconstructed ancestral areas for the clades in question. Each color represents either a single area or combinations of areas as explained in the legend (**Figure 6b**).

Figure 6b - Legend for Figure 6a



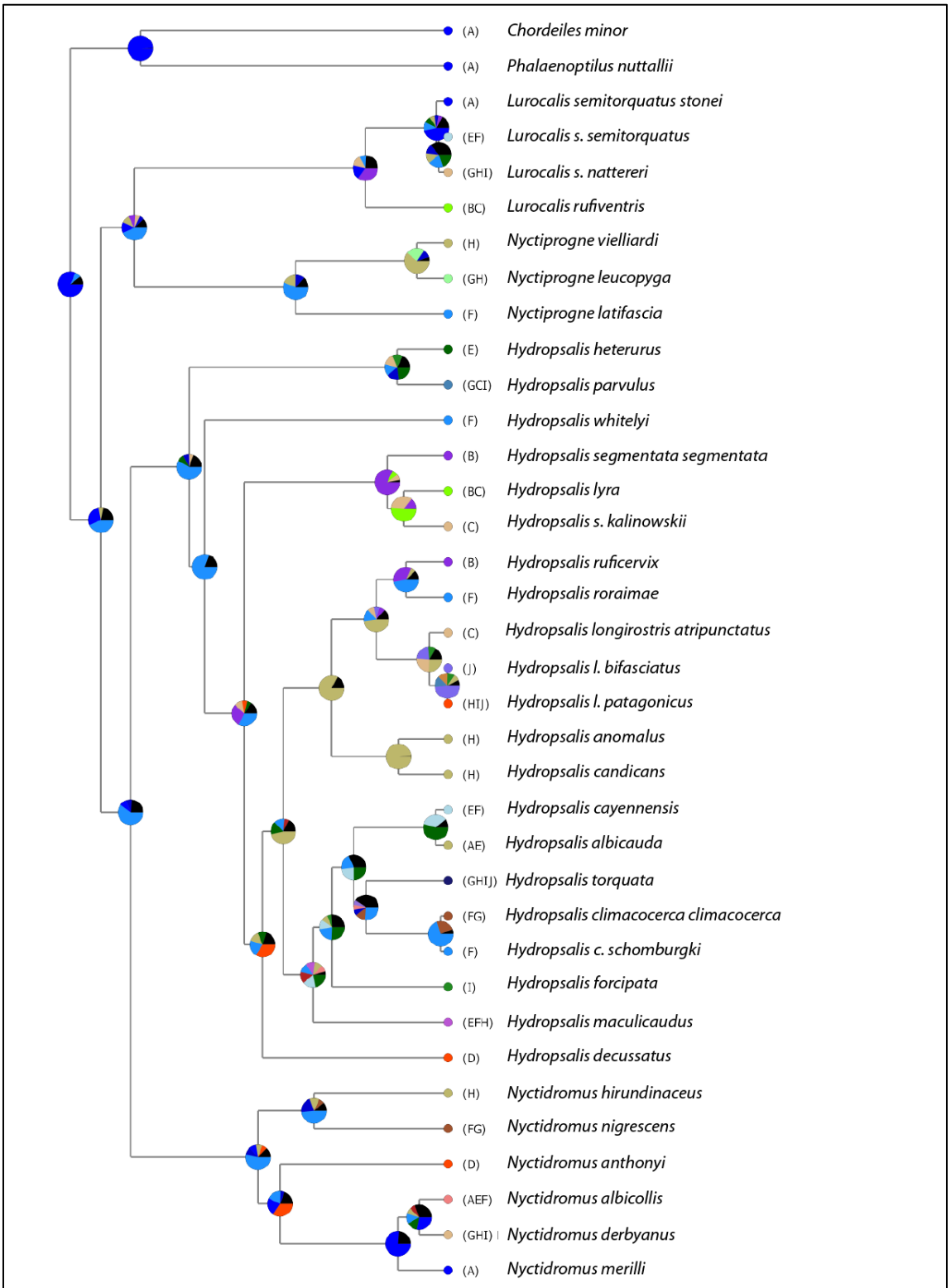
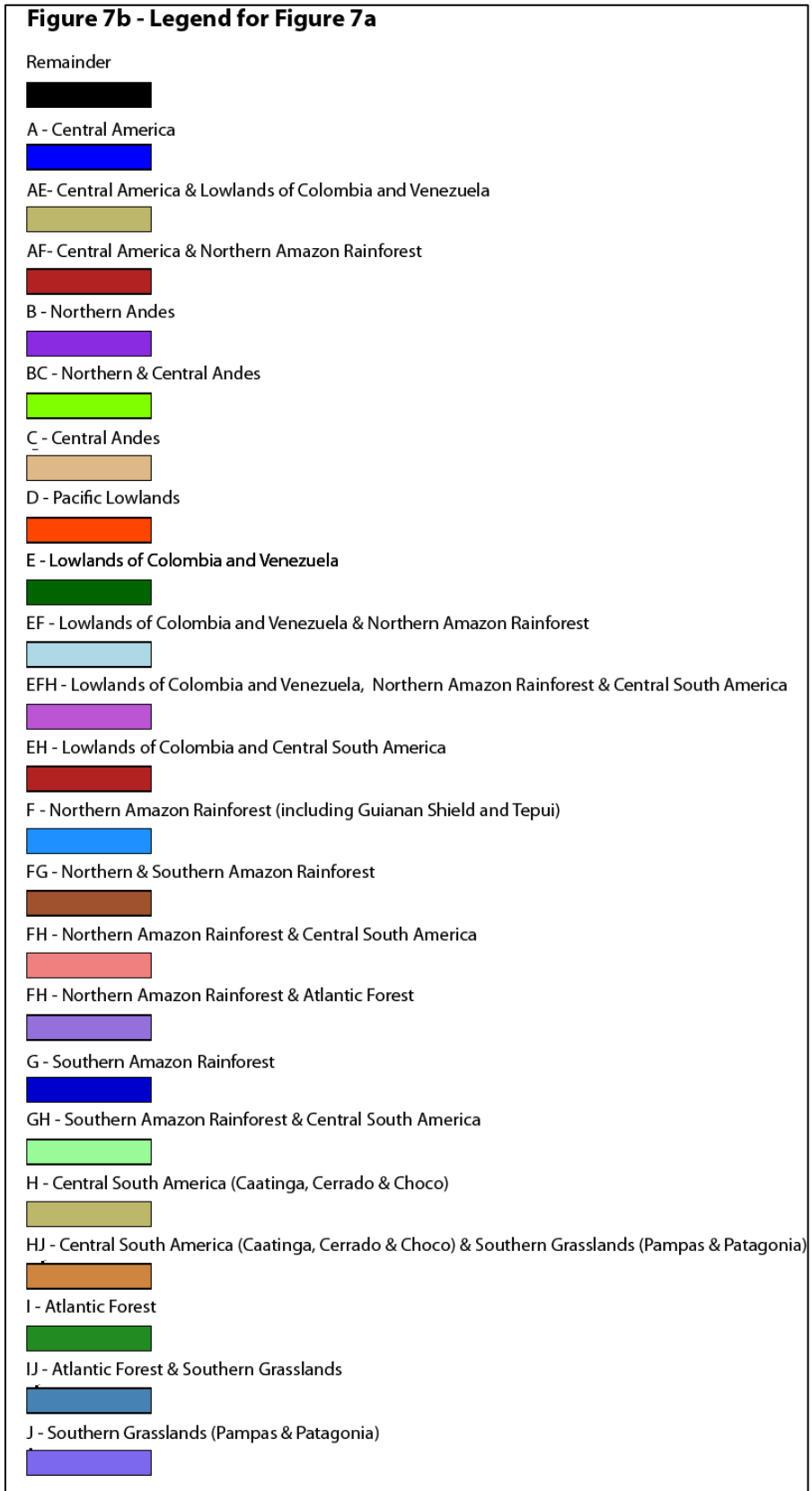


FIGURE 7a: An ancient area reconstruction plot for the South American clade from a BBM analysis in RASP using a mitochondrial phylogeny. Distributions of extant taxa are shown next to their names. Pie charts on nodes show the inferred reconstructed ancestral areas for the clades in question. Each color represents either a single area or combinations of areas as explained in the legend (**Figure 7b**).

Figure 7b - Legend for Figure 7a



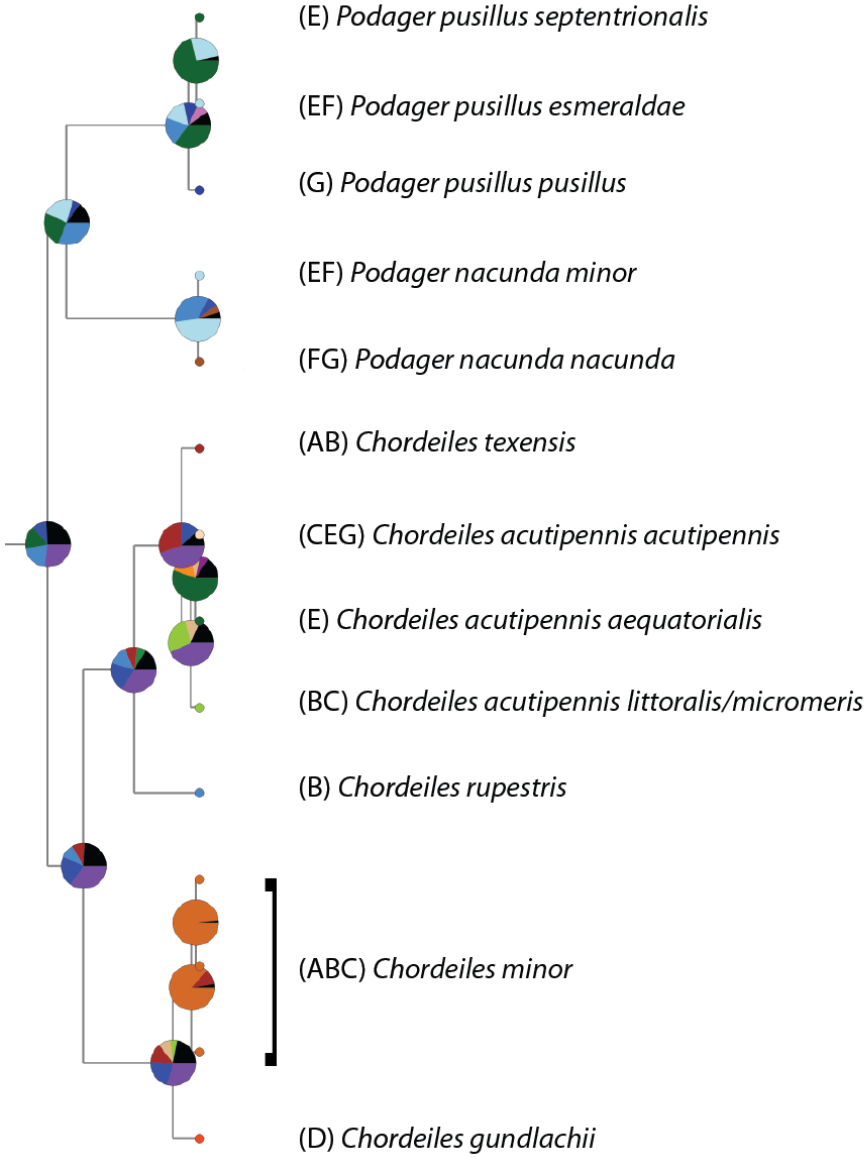
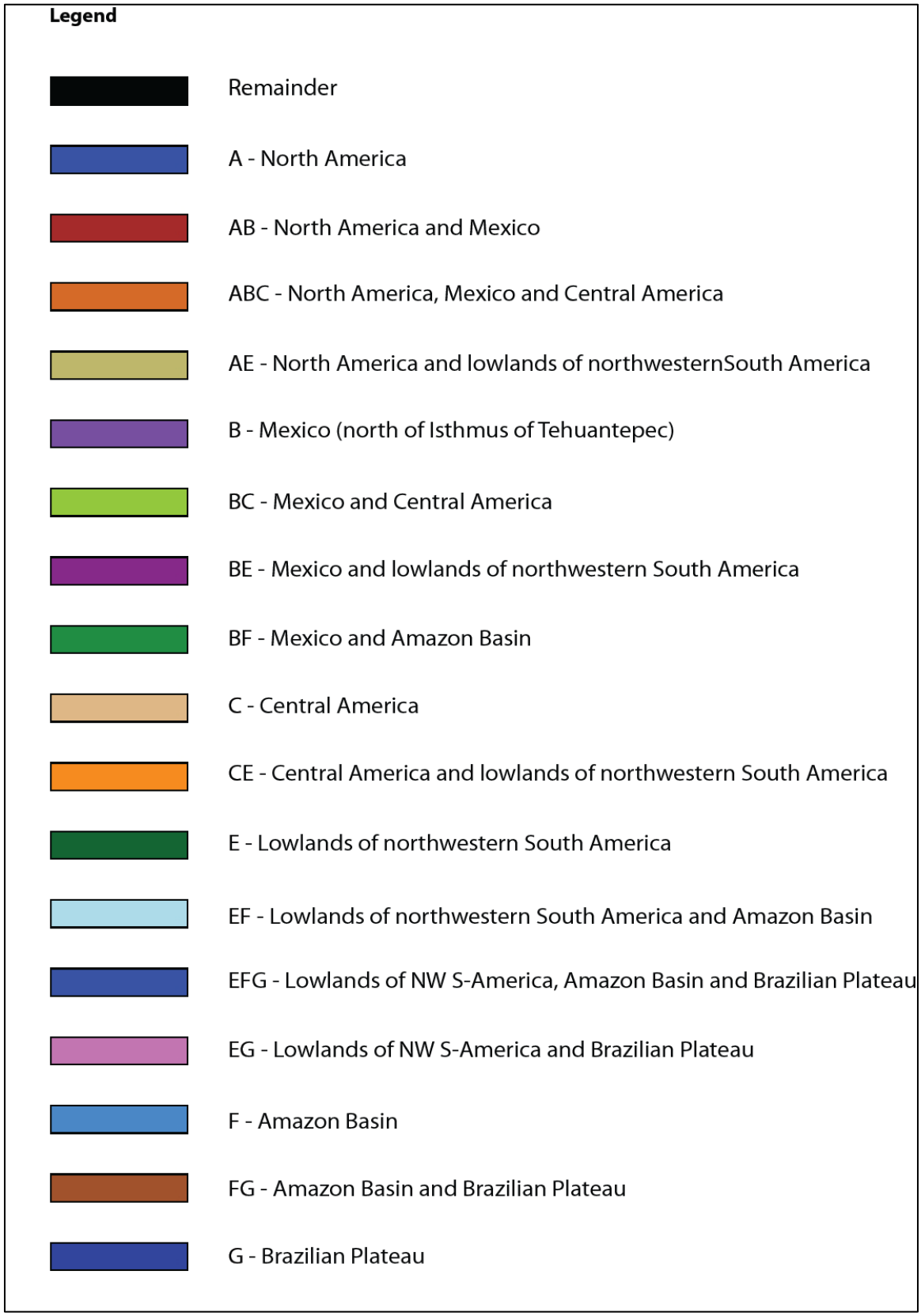


FIGURE 8a: An ancient area reconstruction plot for the nighthawk clade from an BBM analysis in RASP using a mitochondrial phylogeny. Distributions of extant taxa are shown next to their names. Pie charts on nodes show the inferred reconstructed ancestral areas for the clades in question. Each color represents either a single area or combinations of areas as explained in the legend (**Figure 8b**).


Legend
Remainder
A - North America
AB - North America and Mexico
ABC - North America, Mexico and Central America
AE - North America and lowlands of northwesternSouth America
B - Mexico (north of Isthmus of Tehuantepec)
BC - Mexico and Central America
BE - Mexico and lowlands of northwestern South America
BF - Mexico and Amazon Basin
C - Central America
CE - Central America and lowlands of northwestern South America
E - Lowlands of northwestern South America
EF - Lowlands of northwestern South America and Amazon Basin
EFG - Lowlands of NW S-America, Amazon Basin and Brazilian Plateau
EG - Lowlands of NW S-America and Brazilian Plateau
F - Amazon Basin
FG - Amazon Basin and Brazilian Plateau
G - Brazilian Plateau

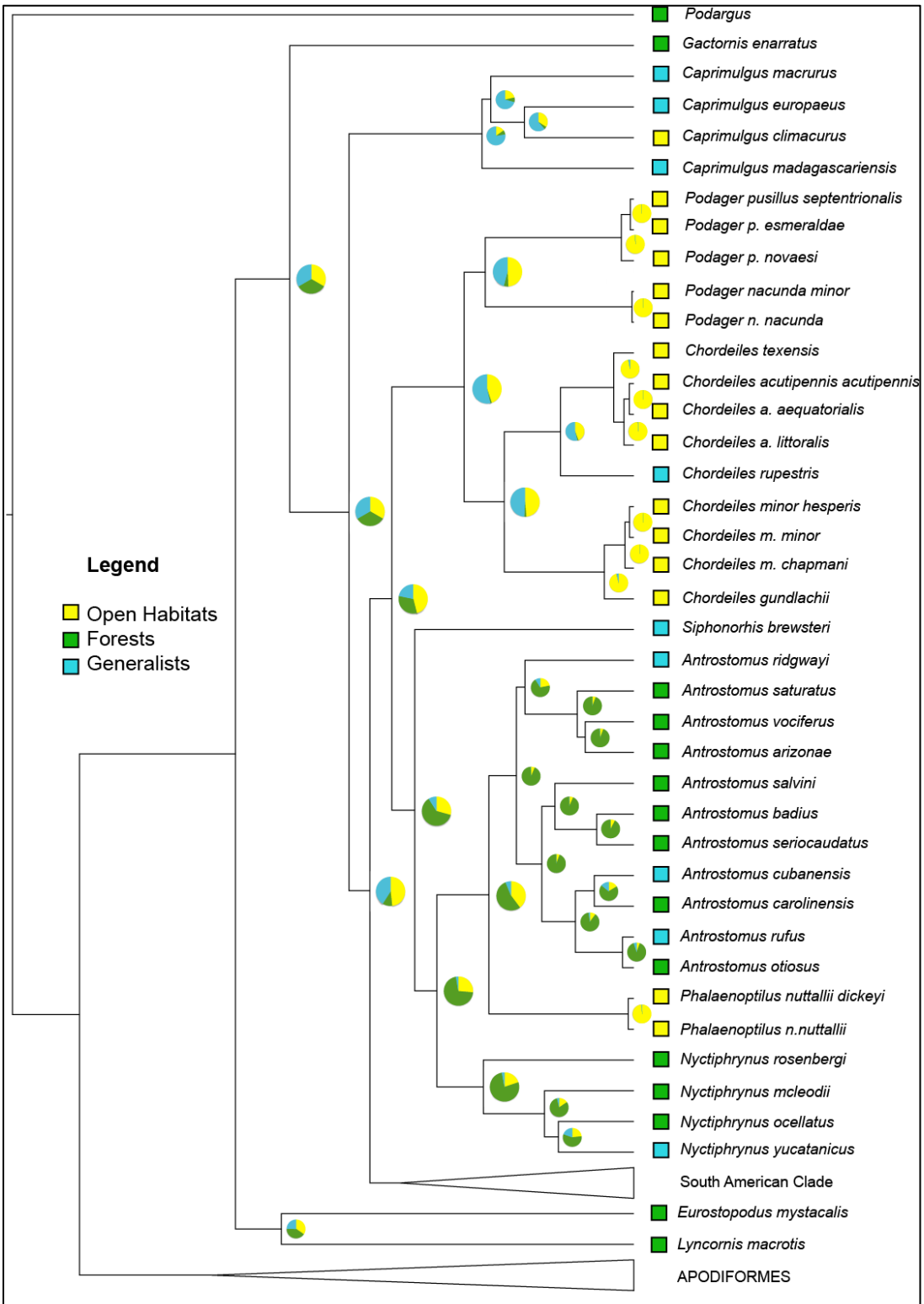


FIGURE 9: An ancestral trait reconstruction plot showing habitat type (forests vs open habitats) for the Nighthawk and Poorwill clades based on results from a BayesTraits analysis using a mitochondrial phylogeny. Habitat types of extant taxa are displayed next to their names. Pie charts on nodes represent the inferred reconstructed ancestral states for the clades in question.

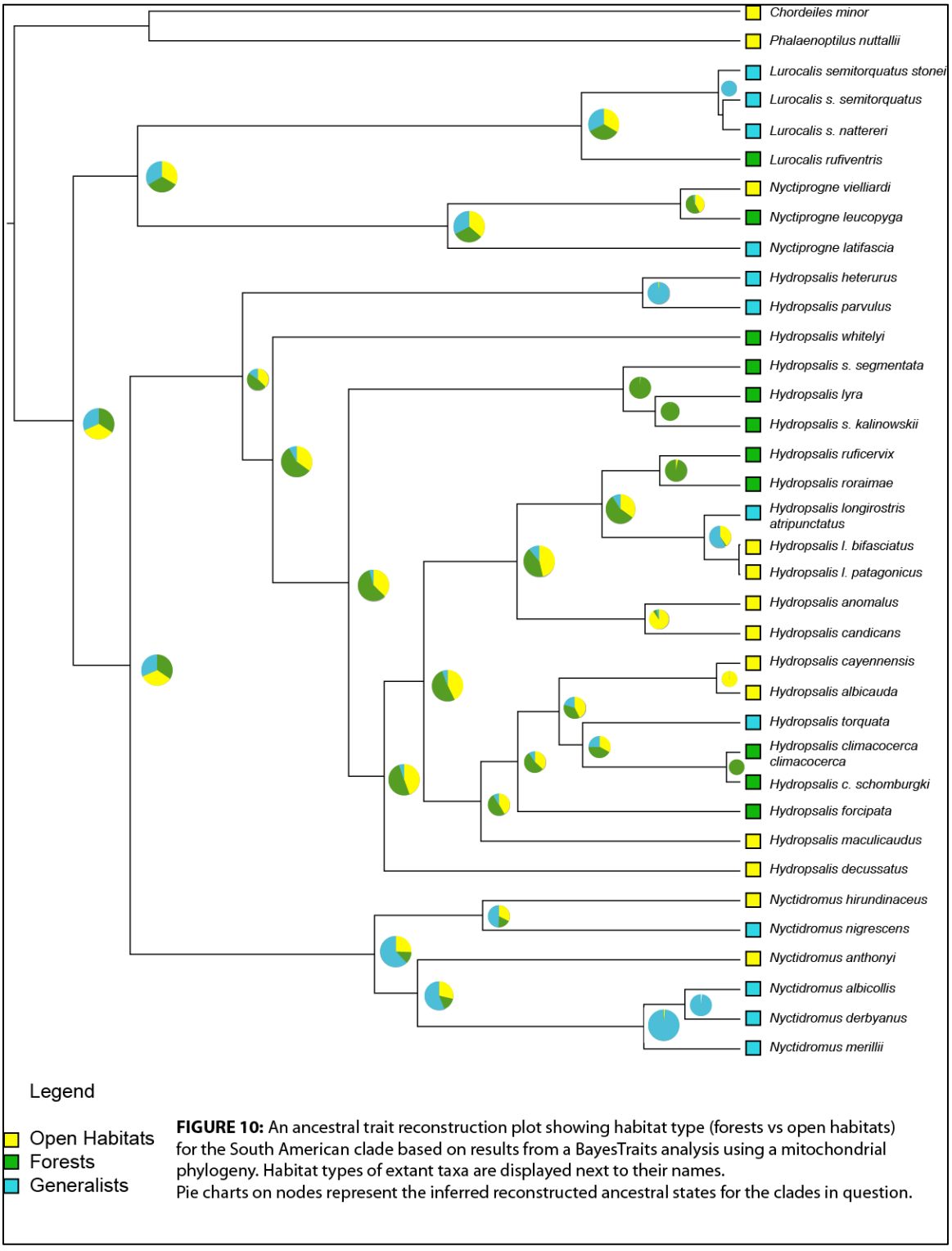


FIGURE 10: An ancestral trait reconstruction plot showing habitat type (forests vs open habitats) for the South American clade based on results from a BayesTraits analysis using a mitochondrial phylogeny. Habitat types of extant taxa are displayed next to their names.
Pie charts on nodes represent the inferred reconstructed ancestral states for the clades in question.

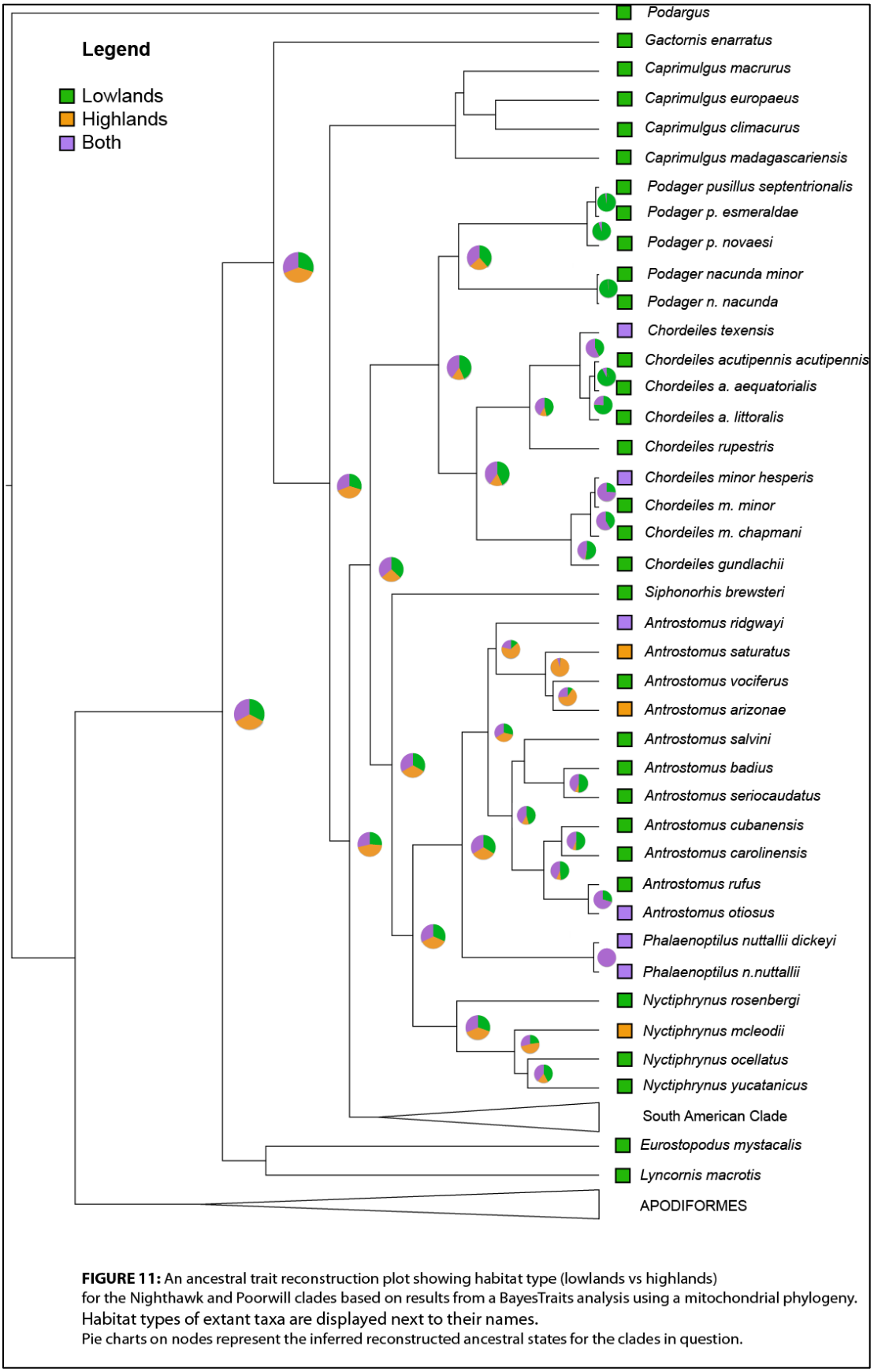


FIGURE 11: An ancestral trait reconstruction plot showing habitat type (lowlands vs highlands) for the Nighthawk and Poorwill clades based on results from a BayesTraits analysis using a mitochondrial phylogeny. Habitat types of extant taxa are displayed next to their names. Pie charts on nodes represent the inferred reconstructed ancestral states for the clades in question.

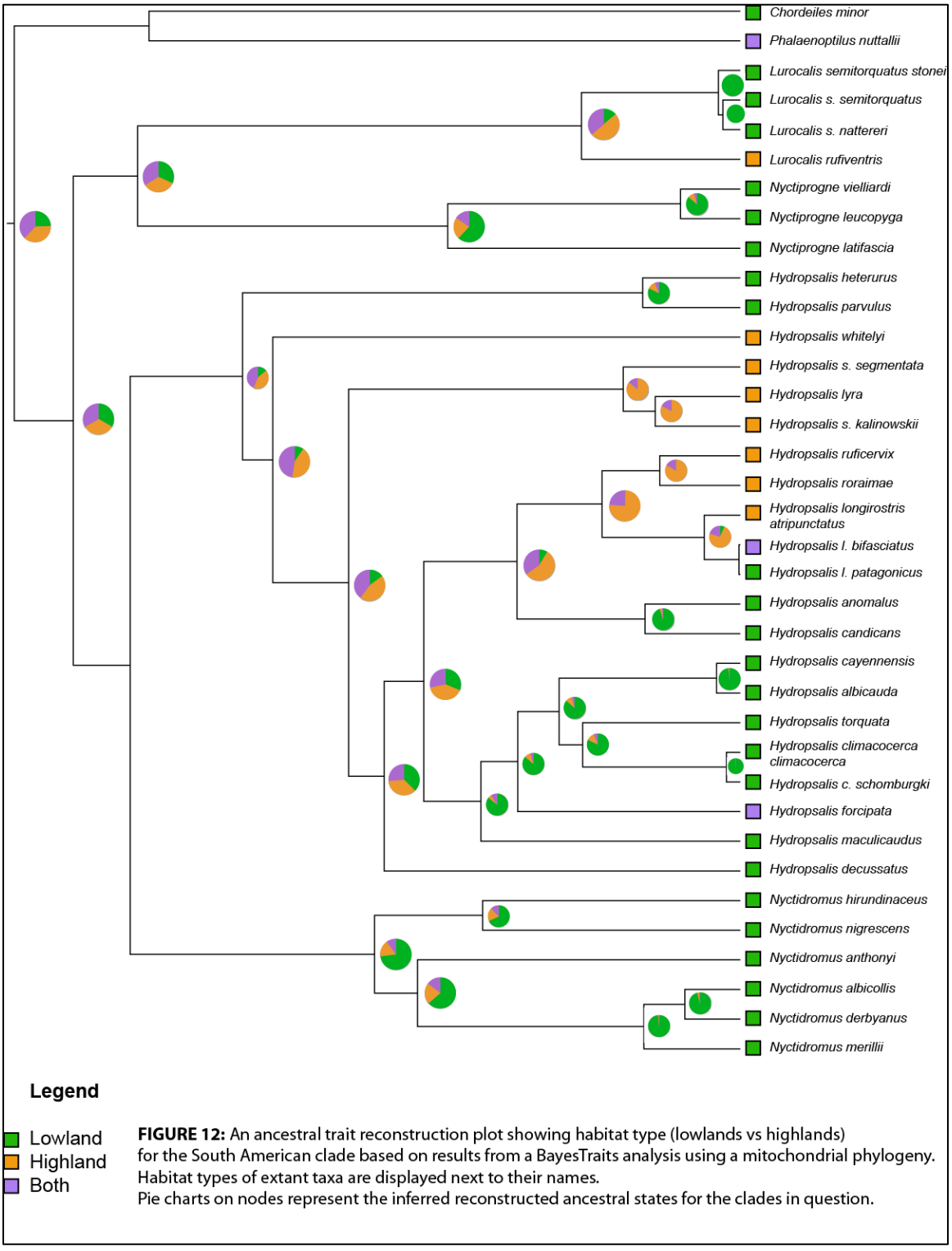


FIGURE 12: An ancestral trait reconstruction plot showing habitat type (lowlands vs highlands) for the South American clade based on results from a BayesTraits analysis using a mitochondrial phylogeny. Habitat types of extant taxa are displayed next to their names. Pie charts on nodes represent the inferred reconstructed ancestral states for the clades in question.

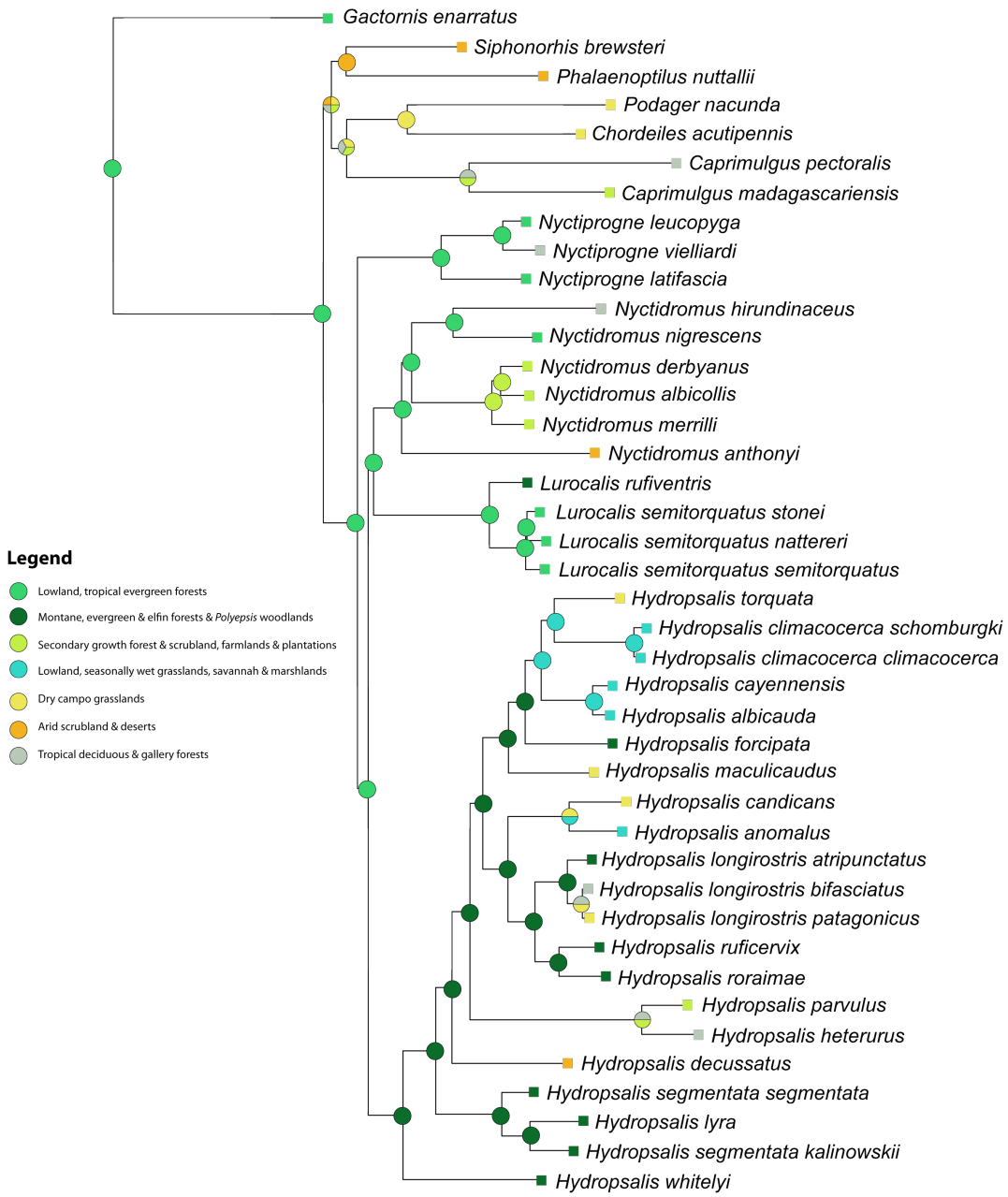


FIGURE 13: An ancestral trait reconstruction plot showing habitat type (with seven habitat categories) for the South American clade based on results from a parsimony analysis in R, using a mitochondrial phylogeny. Pie charts on nodes represent the inferred reconstructed ancestral states for the clades in question.

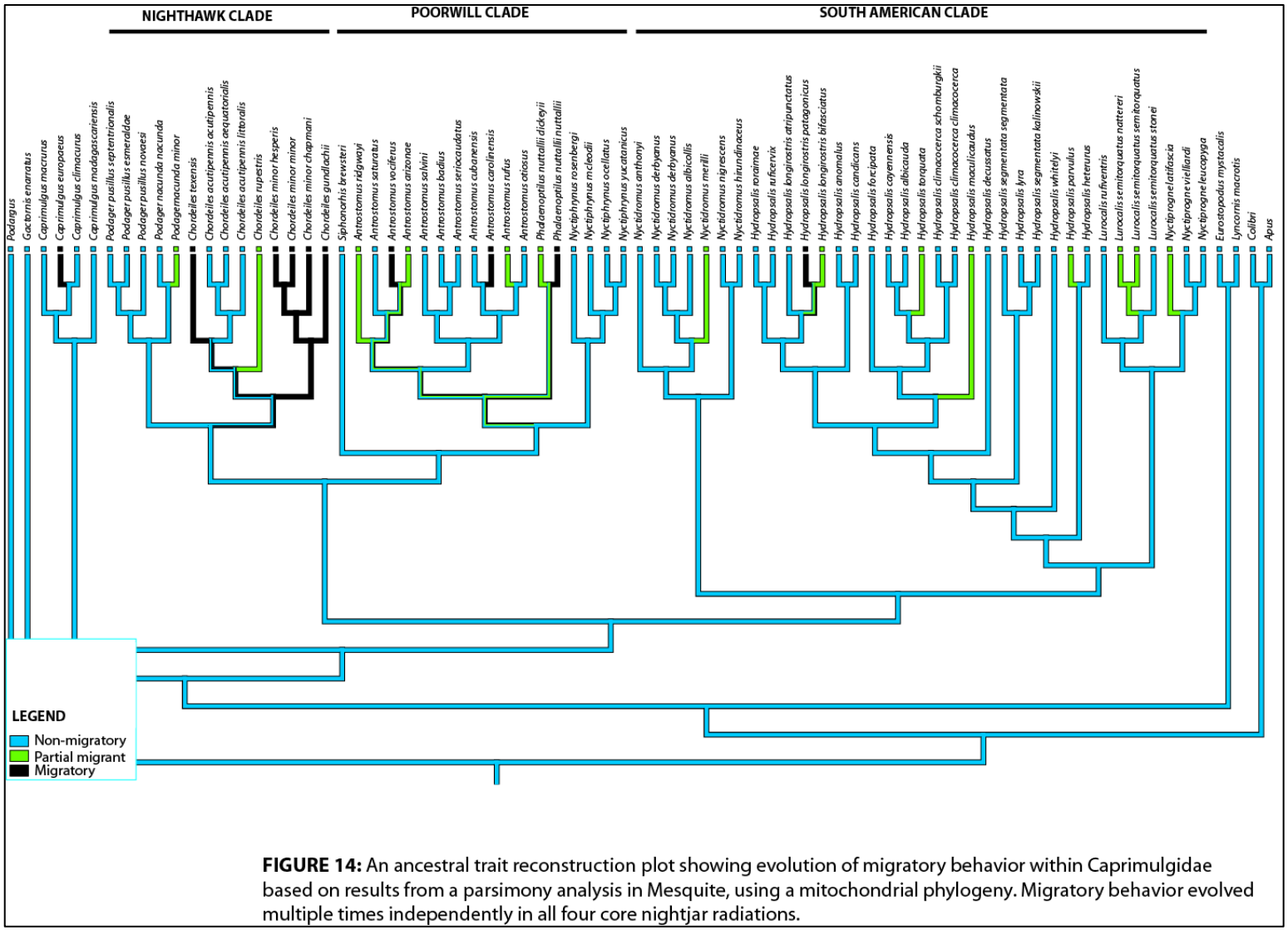
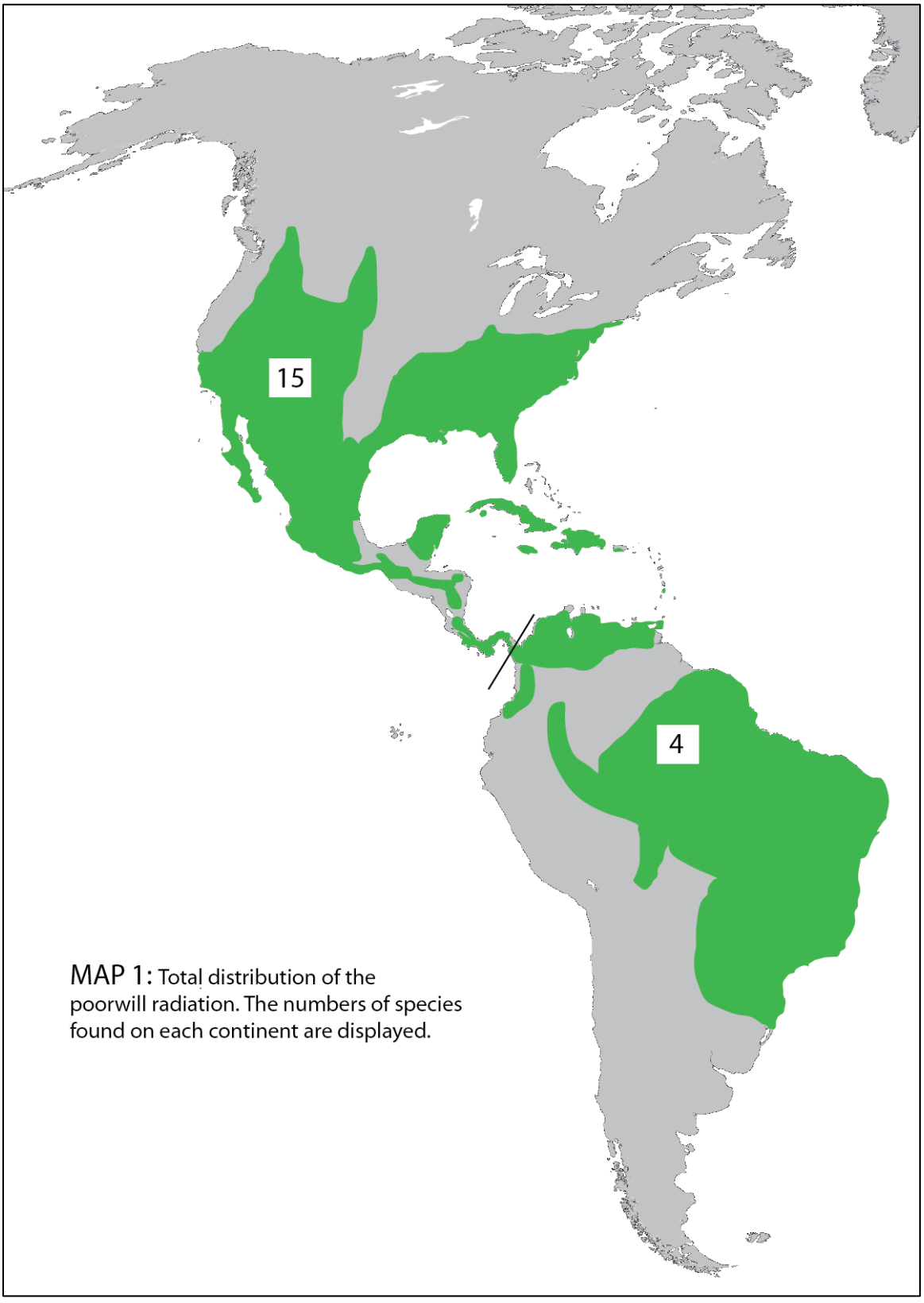
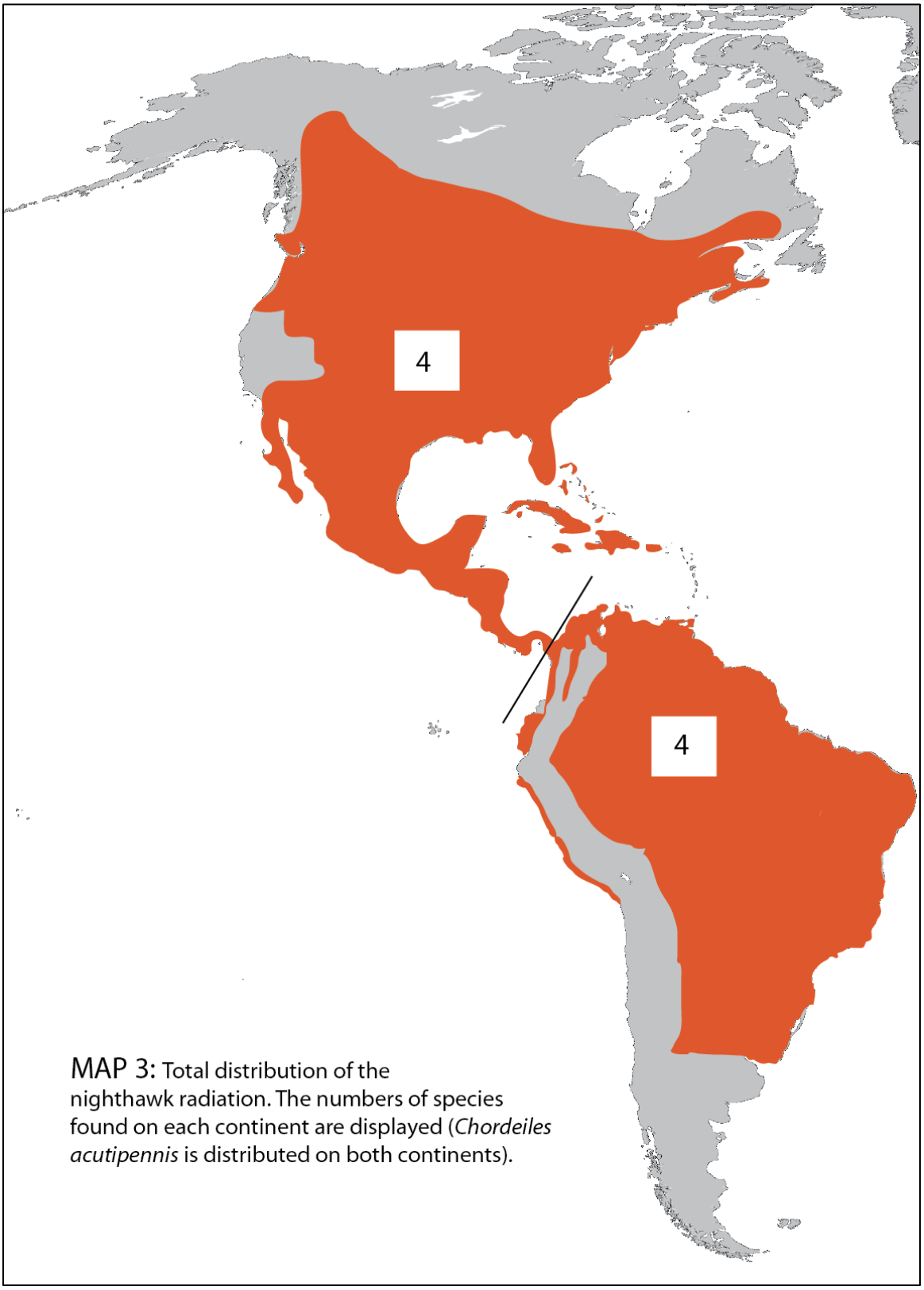


FIGURE 14: An ancestral trait reconstruction plot showing evolution of migratory behavior within Caprimulgidae based on results from a parsimony analysis in Mesquite, using a mitochondrial phylogeny. Migratory behavior evolved multiple times independently in all four core nightjar radiations.



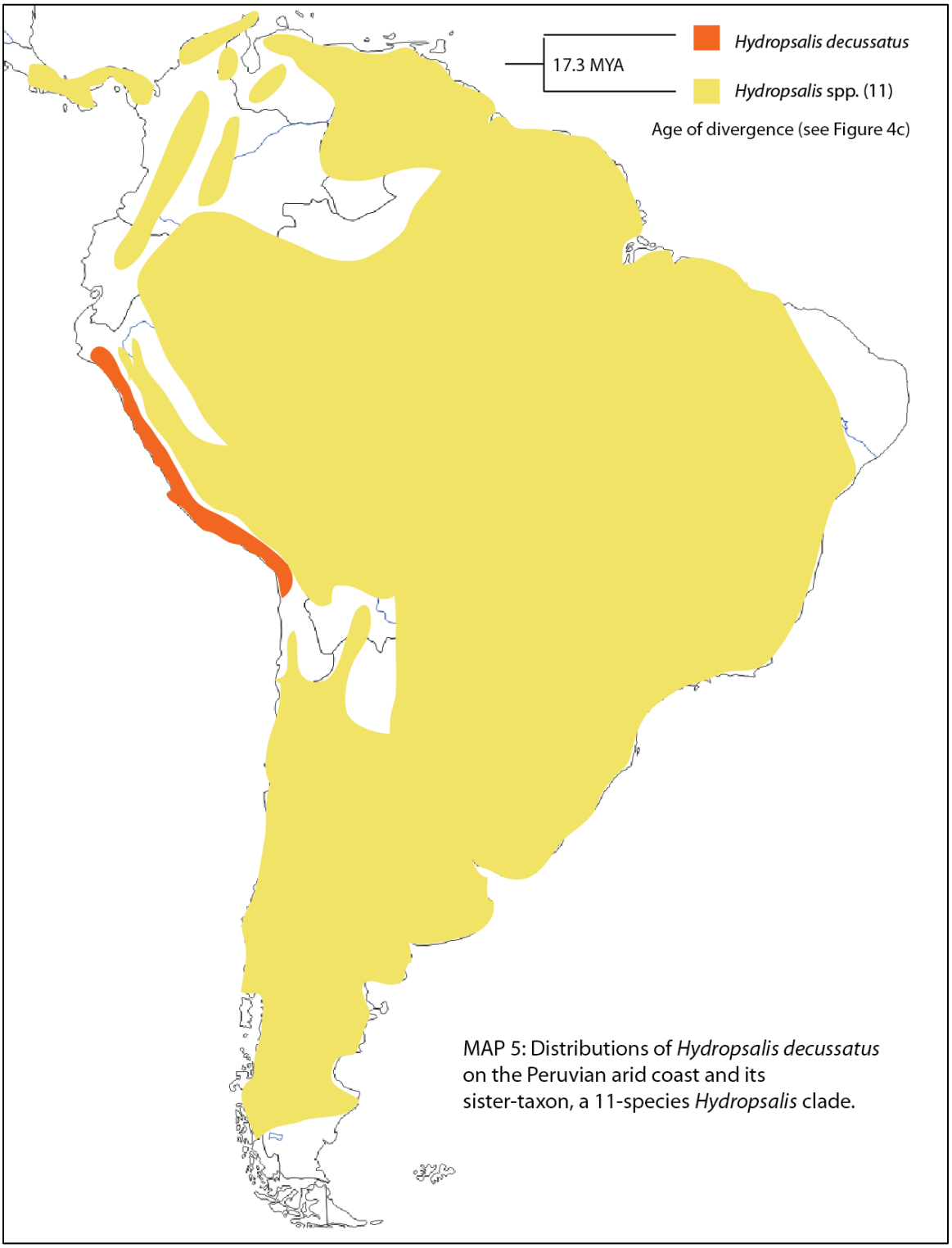
MAP 1: Total distribution of the poorwill radiation. The numbers of species found on each continent are displayed.

MAP 2: Total distribution of the South American radiation. The numbers of species found on each continent are displayed (*Hydropsalis albicauda, Lurocalis semitorquatus* and *Nyctidromus albicollis* are distributed on both continents).

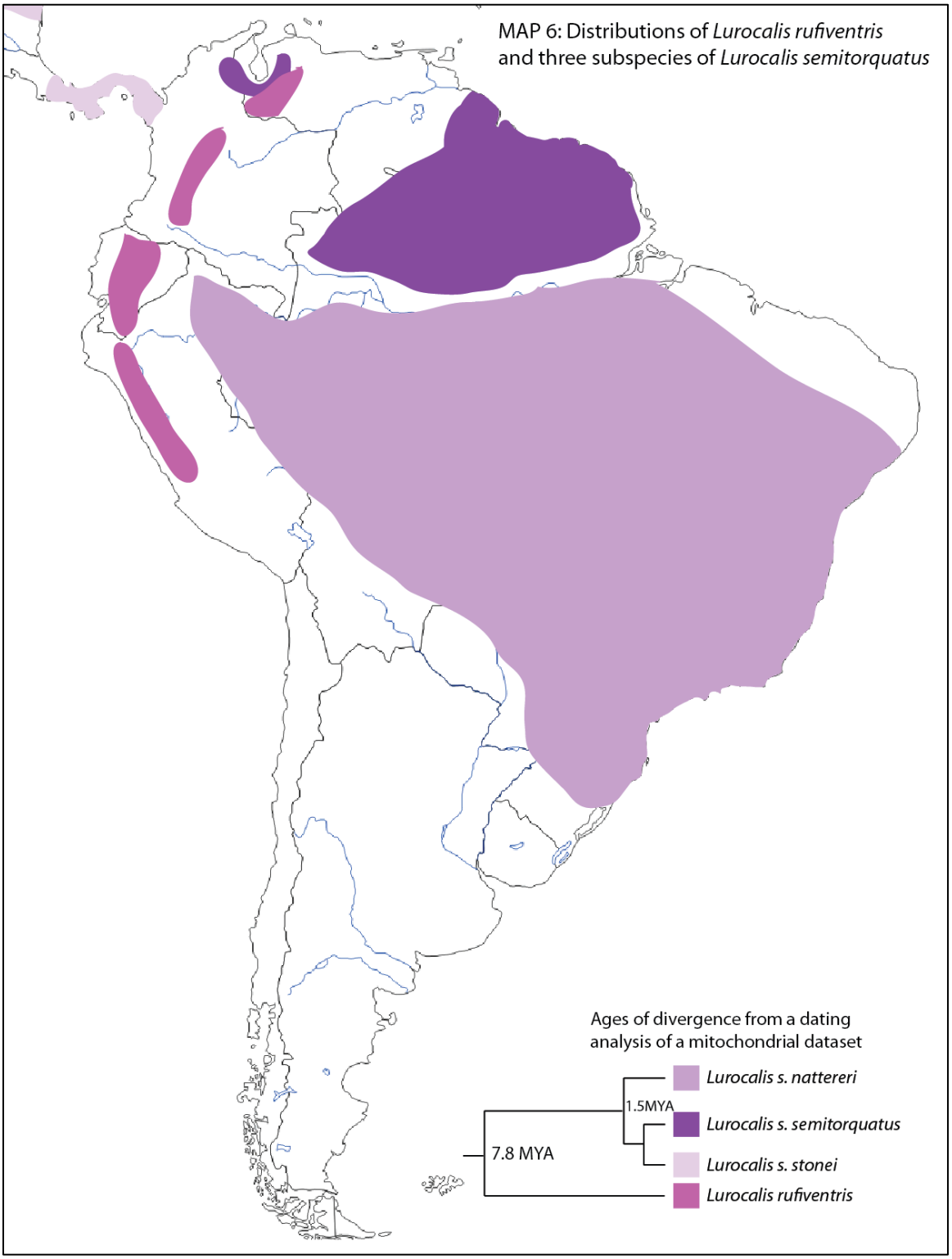


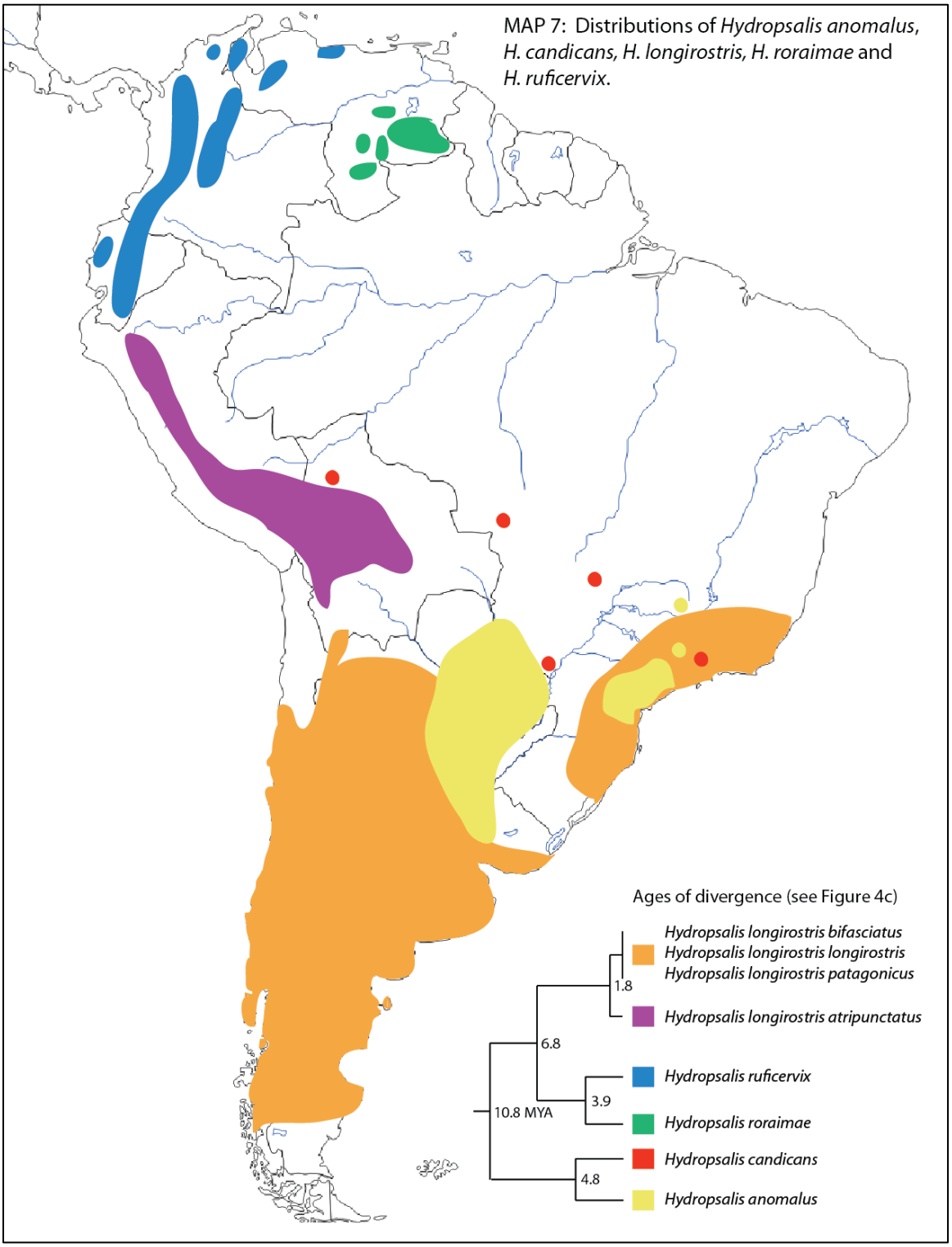
MAP 3: Total distribution of the nighthawk radiation. The numbers of species found on each continent are displayed (*Chordeiles acutipennis* is distributed on both continents).

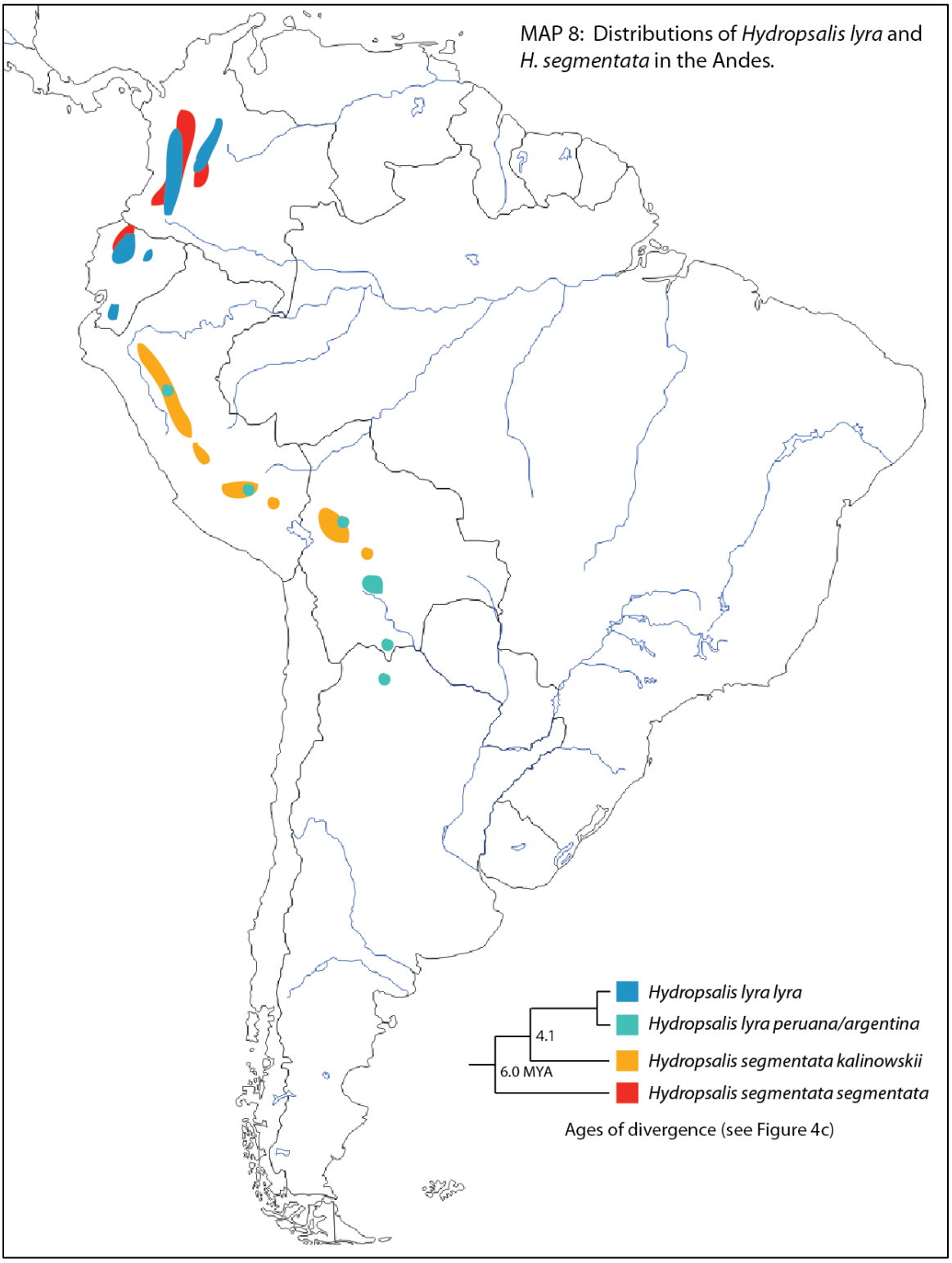

MAP 4: Distributions of *Nyctidromus anthonyi* in the Tumbesian area of endemism and its sister-taxon, the *N. albicollis* species-complex.
15.5 MYA
Nyctidromus anthonyi
Nyctidromus albicollis,
Nyctidromus derbyanus
Nyctidromus merrilli
Age of divergence (see Figure 4c)

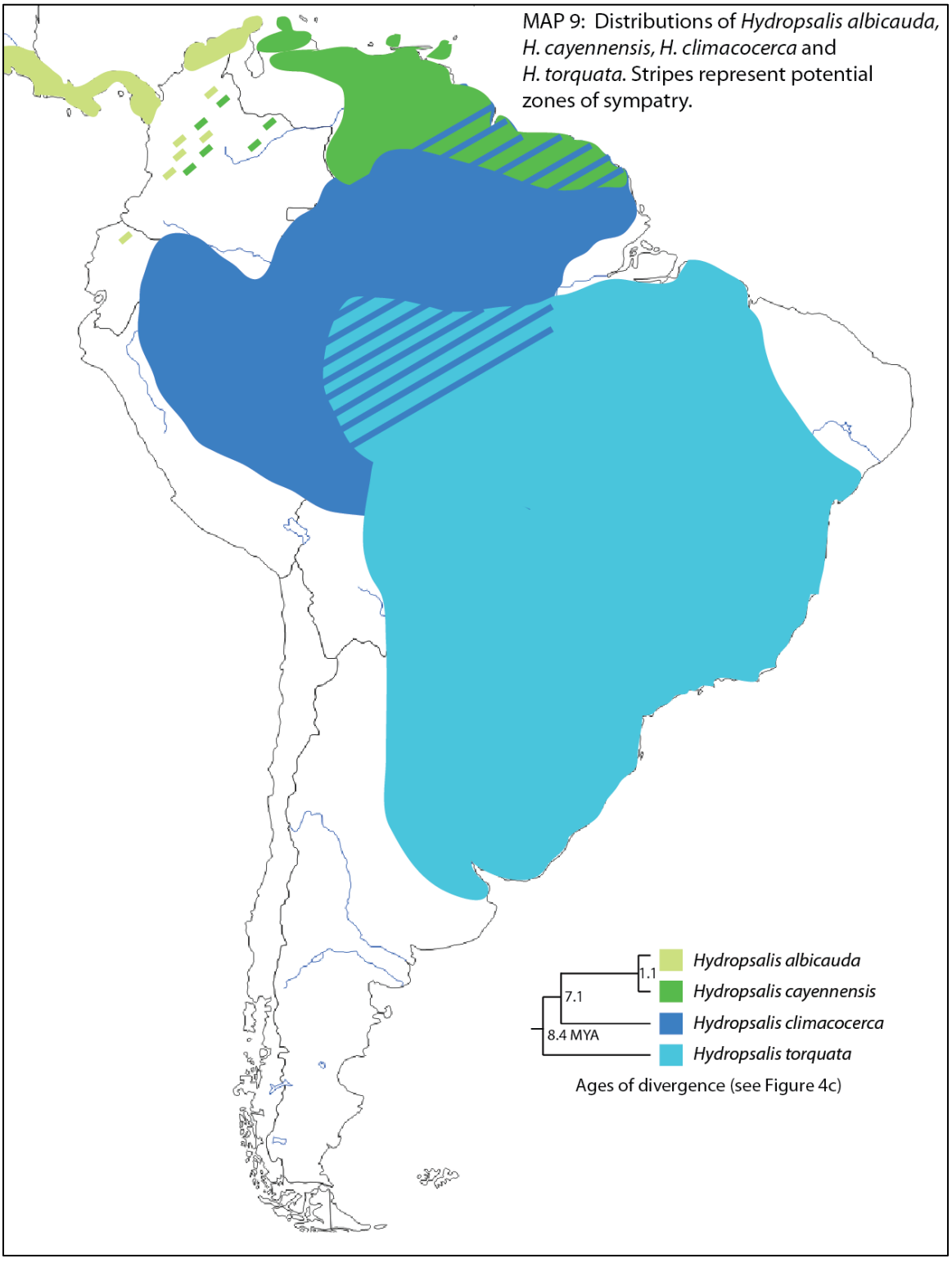


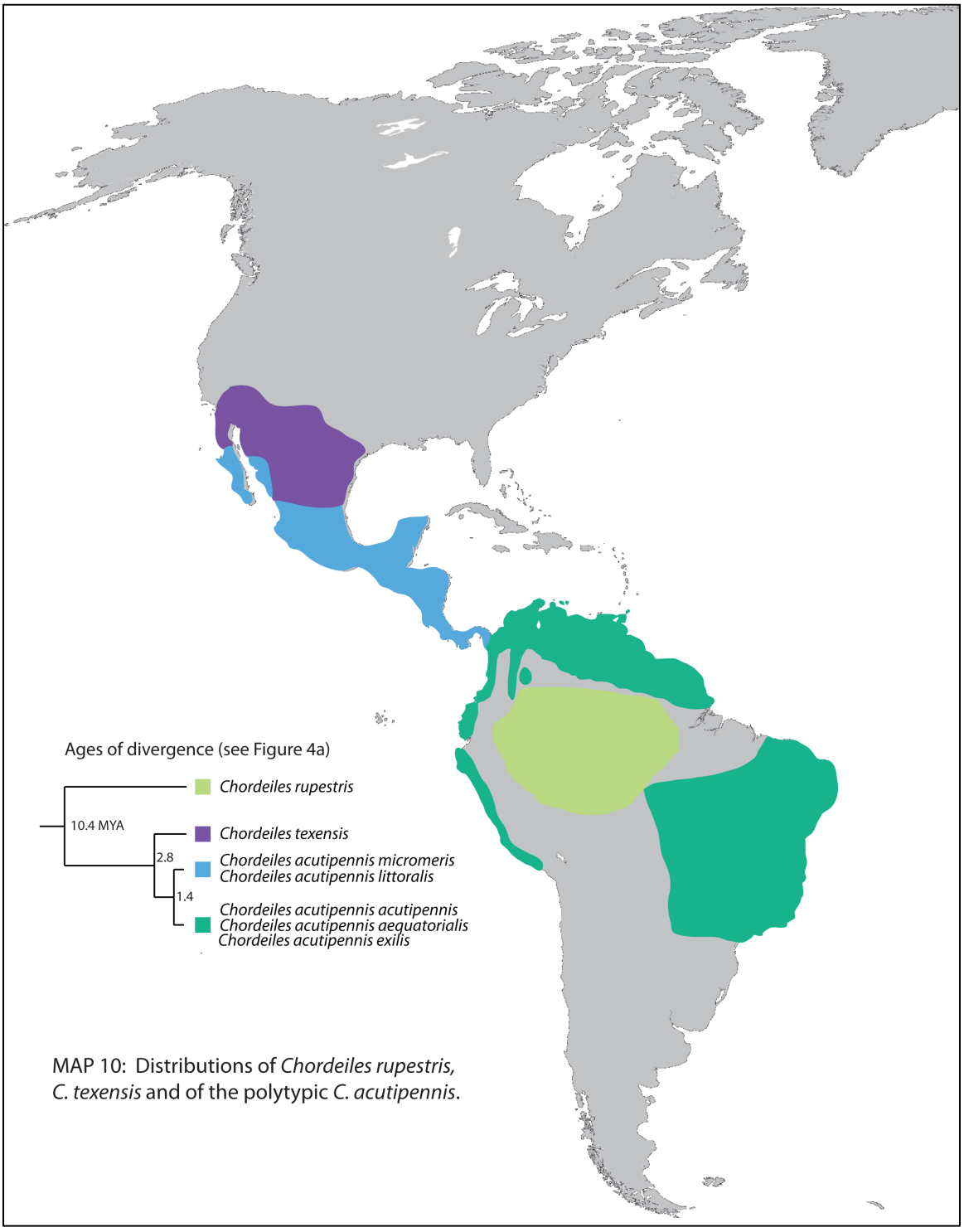
MAP 5: Distributions of *Hydropsalis decussatus* on the Peruvian arid coast and its sister-taxon, a 11-species *Hydropsalis* clade.


MAP 6: Distributions of *Lurocalis rufiventris* and three subspecies of *Lurocalis semitorquatus*
Ages of divergence from a dating analysis of a mitochondrial dataset
Lurocalis s. nattereri
1.5MYA
Lurocalis s. semitorquatus
7.8 MYA
Lurocalis s. stonei
Lurocalis rufiventris

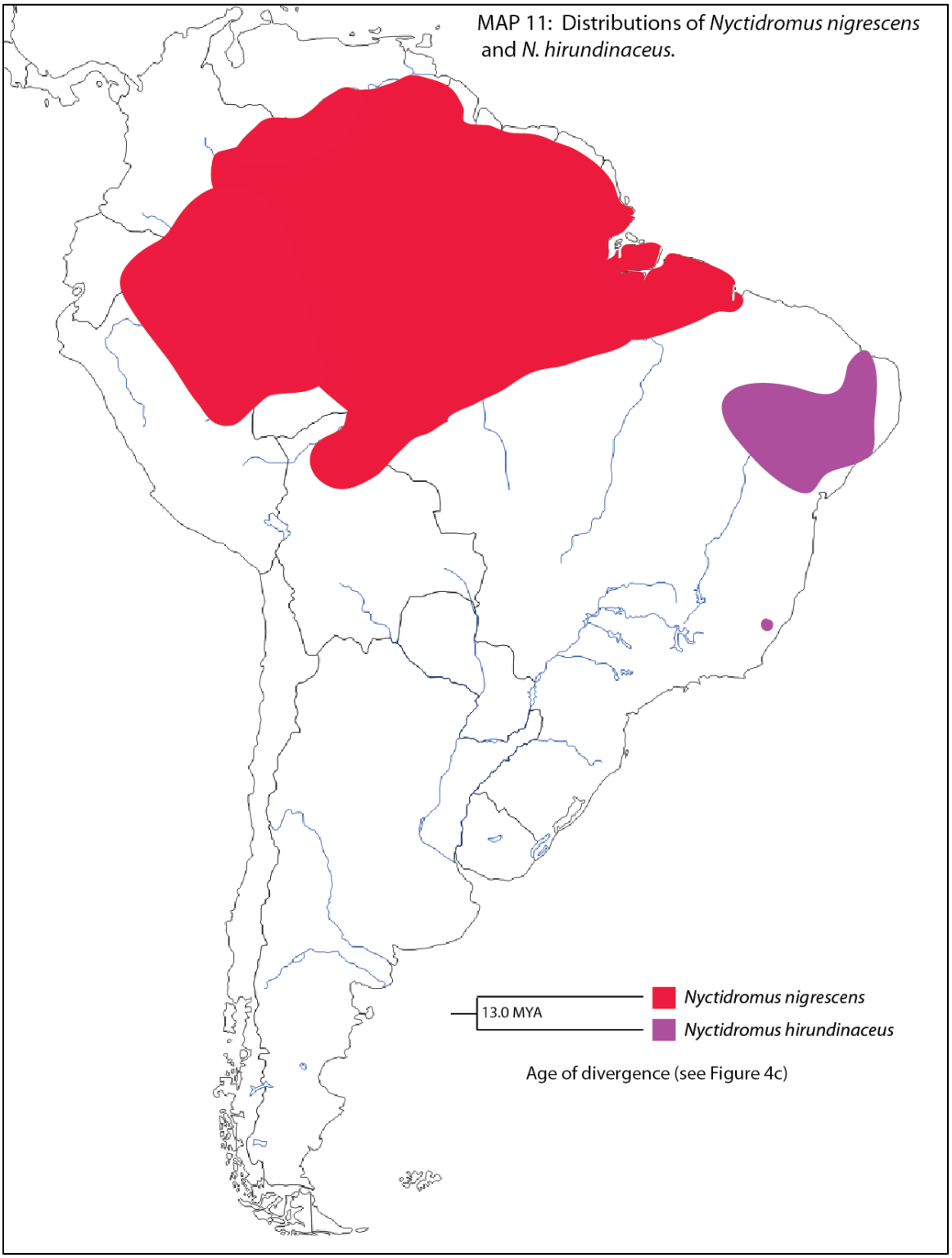

MAP 7: Distributions of *Hydropsalis anomalus*, *H. candicans*, *H. longirostris*, *H. roraimae* and *H. ruficervix*.
Ages of divergence (see Figure 4c)
Hydropsalis longirostris bifasciatus
Hydropsalis longirostris longirostris
Hydropsalis longirostris patagonicus
Hydropsalis longirostris atripunctatus
Hydropsalis ruficervix
Hydropsalis roraimae
Hydropsalis candicans
Hydropsalis anomalus
1.8
6.8
3.9
10.8 MYA
4.8

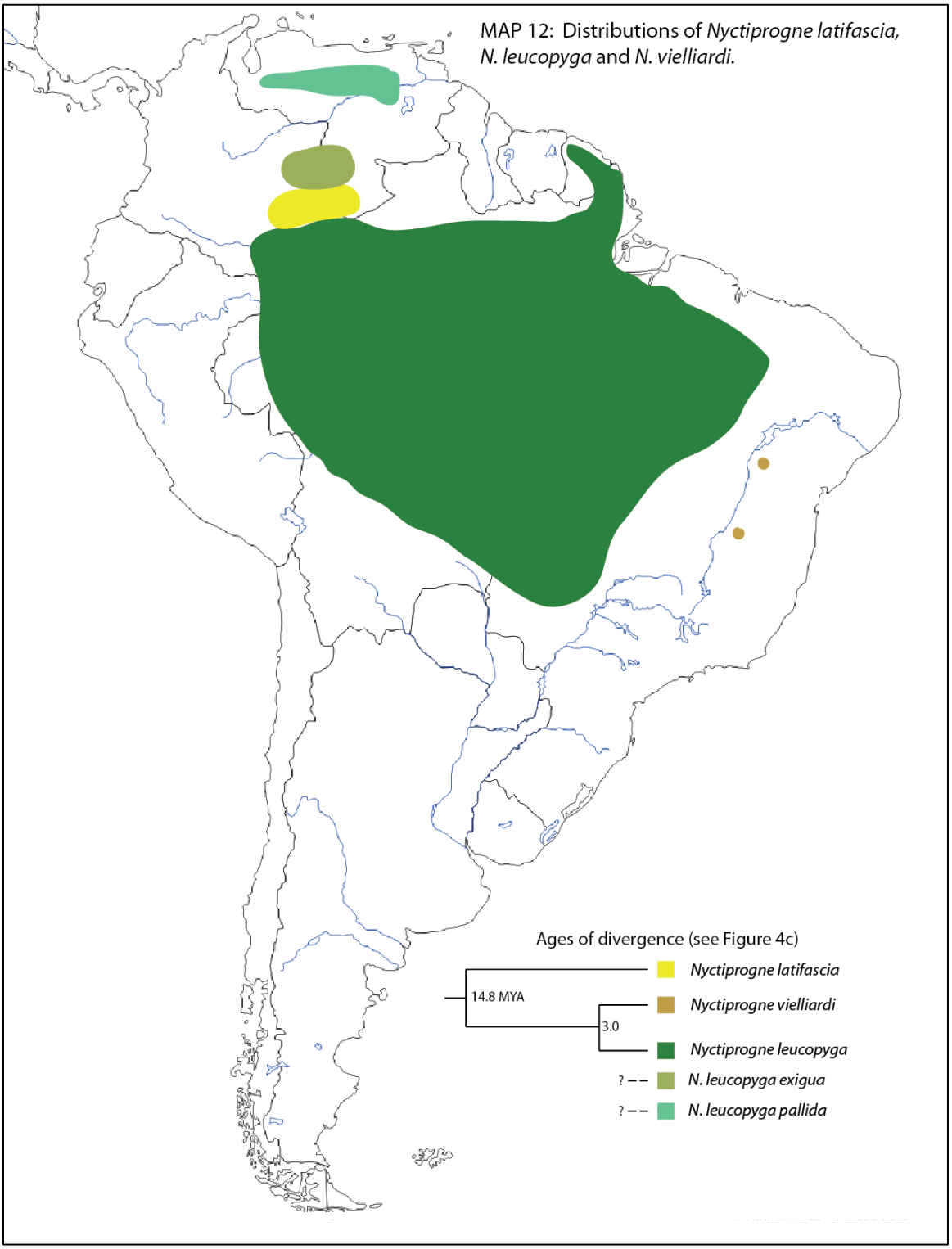

MAP 8: Distributions of *Hydropsalis lyra* and *H. segmentata* in the Andes.
Hydropsalis lyra lyra
Hydropsalis lyra peruana/argentina
Hydropsalis segmentata kalinowskii
Hydropsalis segmentata segmentata
4.1
6.0 MYA
Ages of divergence (see Figure 4c)


MAP 9: Distributions of *Hydropsalis albicauda, H. cayennensis, H. climacocerca* and *H. torquata*. Stripes represent potential zones of sympatry.
1.1
7.1
8.4 MYA
Hydropsalis albicauda
Hydropsalis cayennensis
Hydropsalis climacocerca
Hydropsalis torquata
Ages of divergence (see Figure 4c)

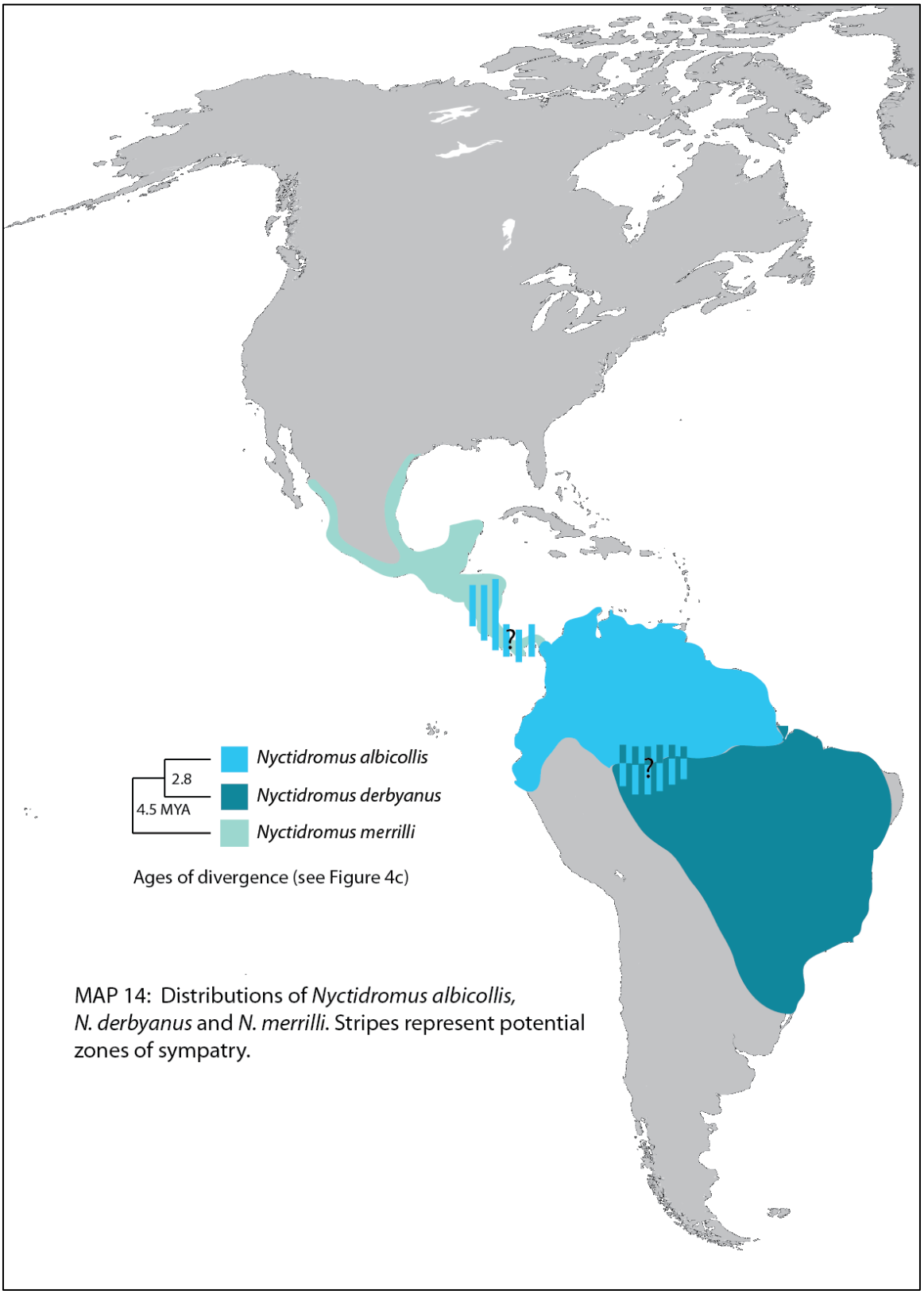


MAP 10: Distributions of *Chordeiles rupestris*, *C. texensis* and of the polytypic *C. acutipennis*.

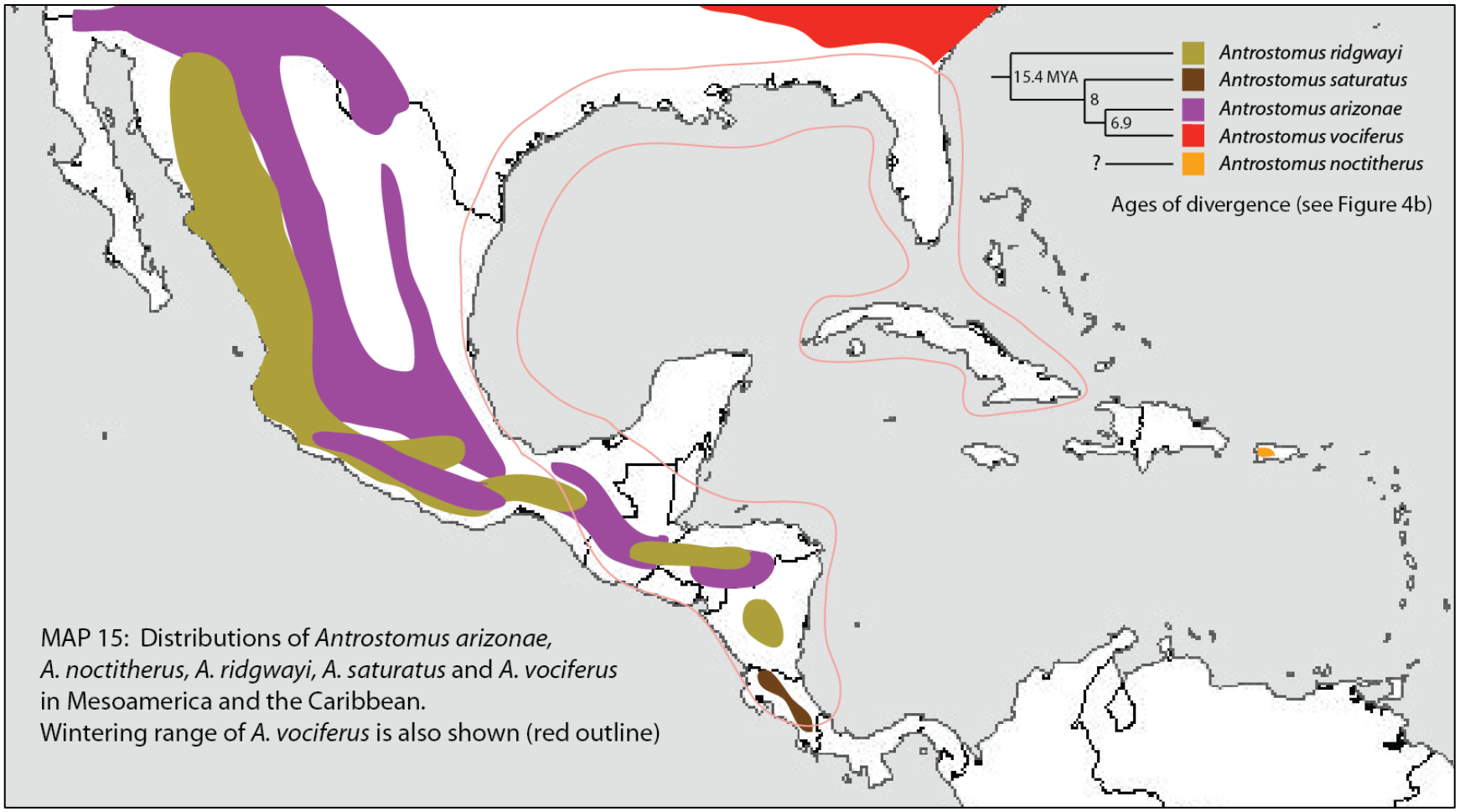

MAP 11: Distributions of Nyctidromus nigrescens and N. hirundinaceus.
13.0 MYA
Nyctidromus nigrescens
Nyctidromus hirundinaceus
Age of divergence (see Figure 4c)


MAP 12: Distributions of *Nyctiprogne latifascia, N. leucopyga* and *N. vielliardi*.
Ages of divergence (see Figure 4c)
14.8 MYA
3.0
Nyctiprogne latifascia
Nyctiprogne vielliardi
Nyctiprogne leucopyga
? – – *N. leucopyga exigua*
? – – *N. leucopyga pallida*

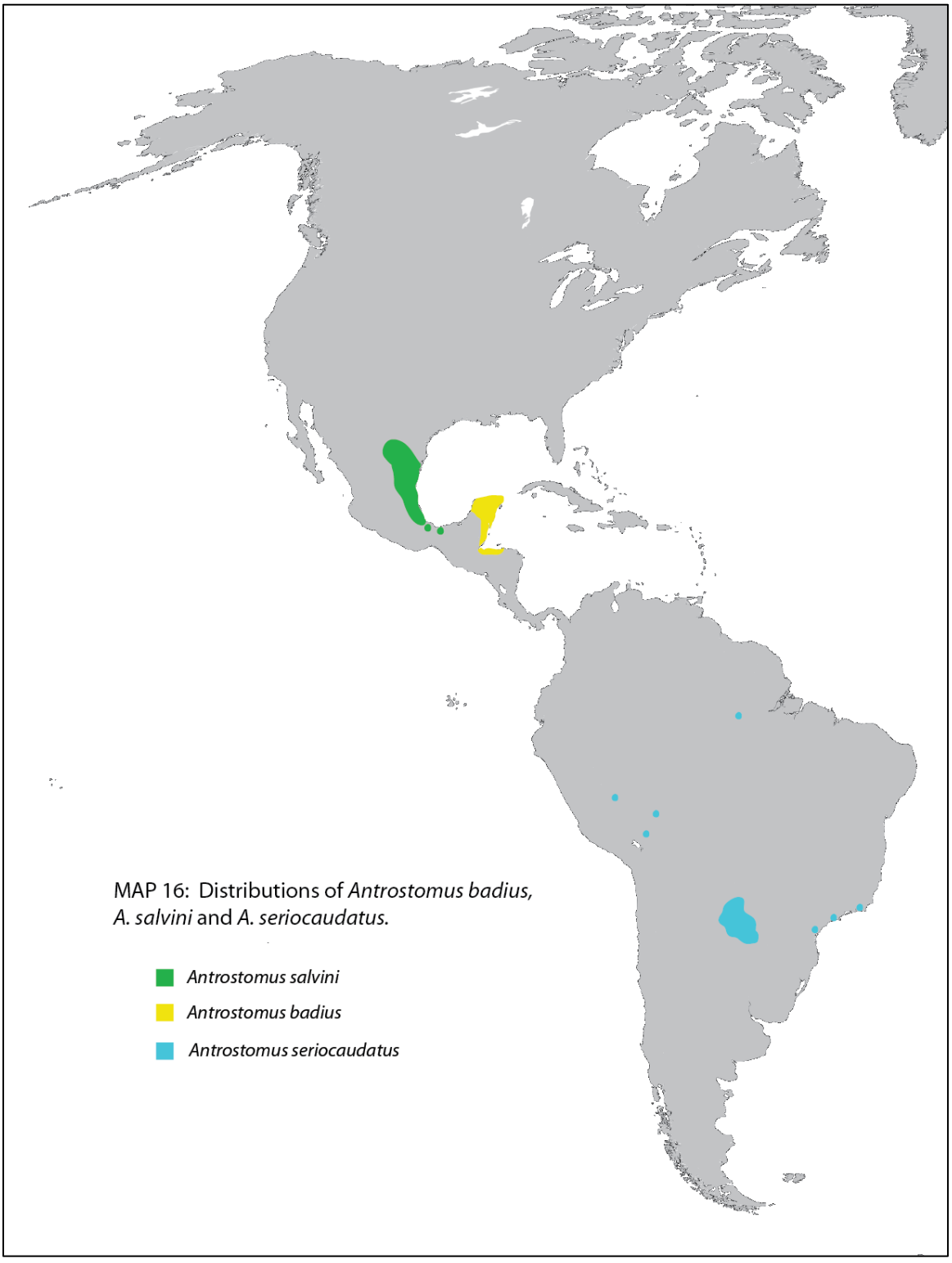
MAP 13: Distributions of *Hydropsalis heterurus*, and *H. parvulus*.

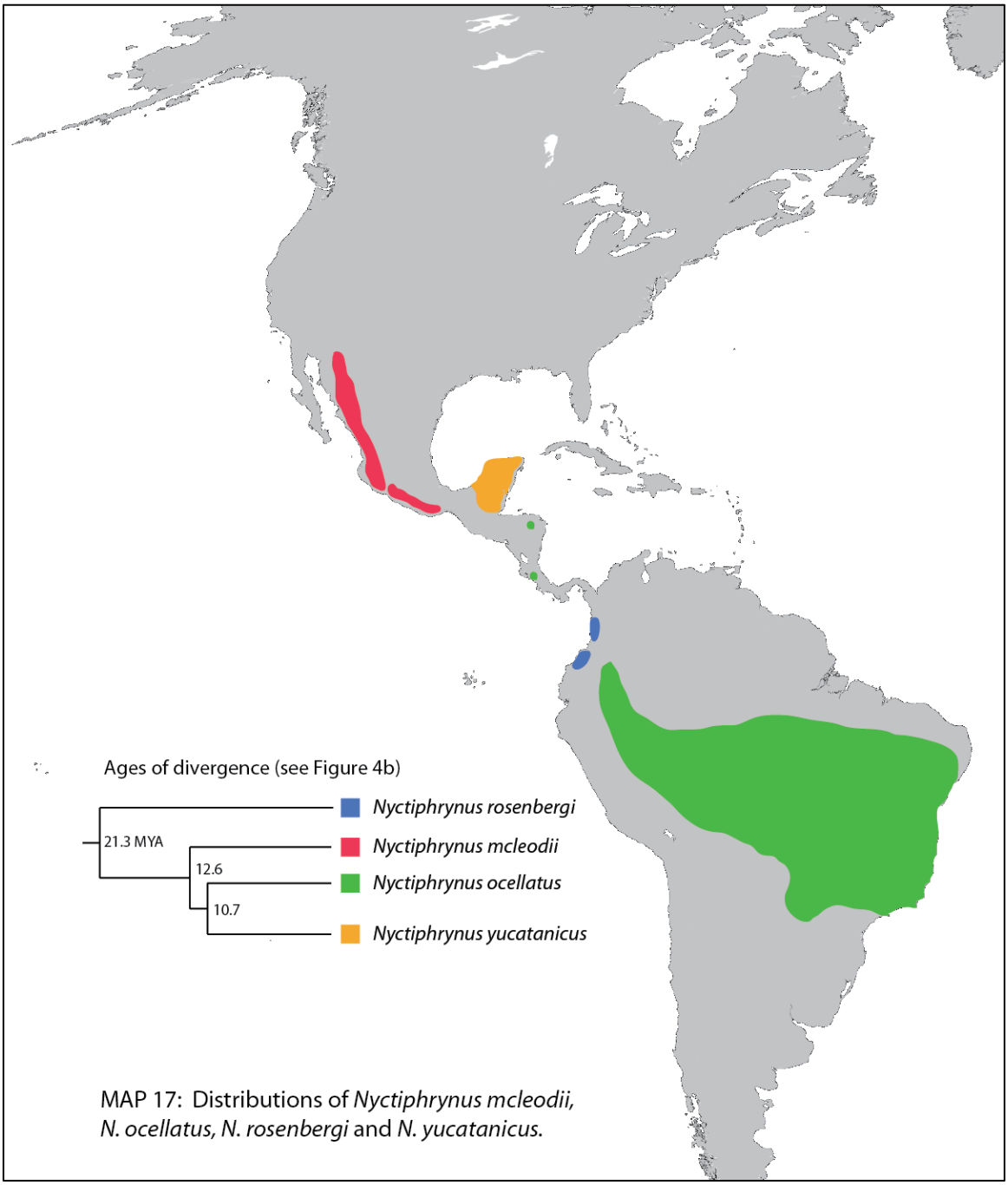


MAP 14: Distributions of *Nyctidromus albicollis, N. derbyanus* and *N. merrilli*. Stripes represent potential zones of sympatry.

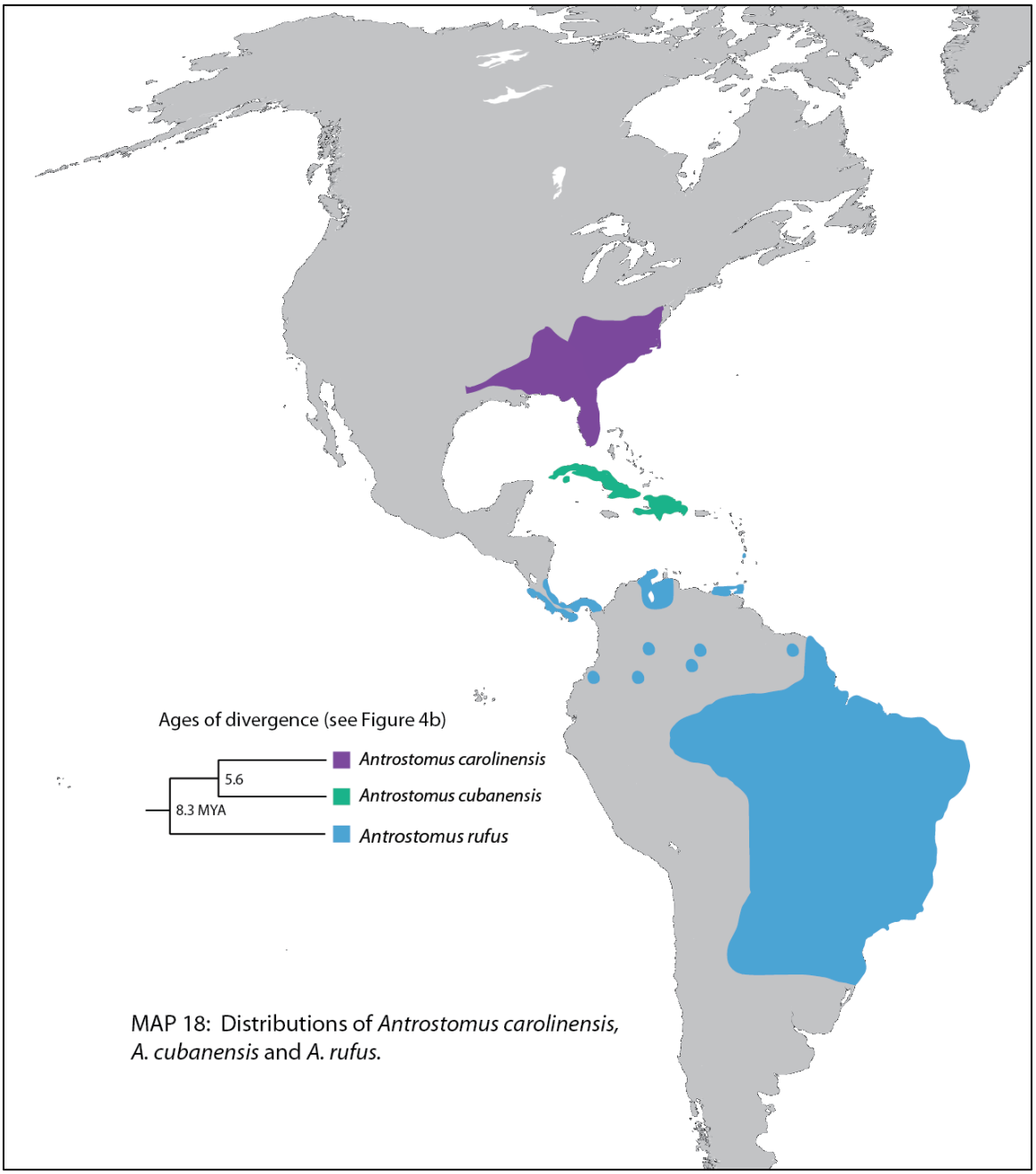


MAP 15: Distributions of *Antrostomus arizonae, A. noctitherus, A. ridgwayi, A. saturatus* and *A. vociferus* in Mesoamerica and the Caribbean.
Wintering range of *A. vociferus* is also shown (red outline)

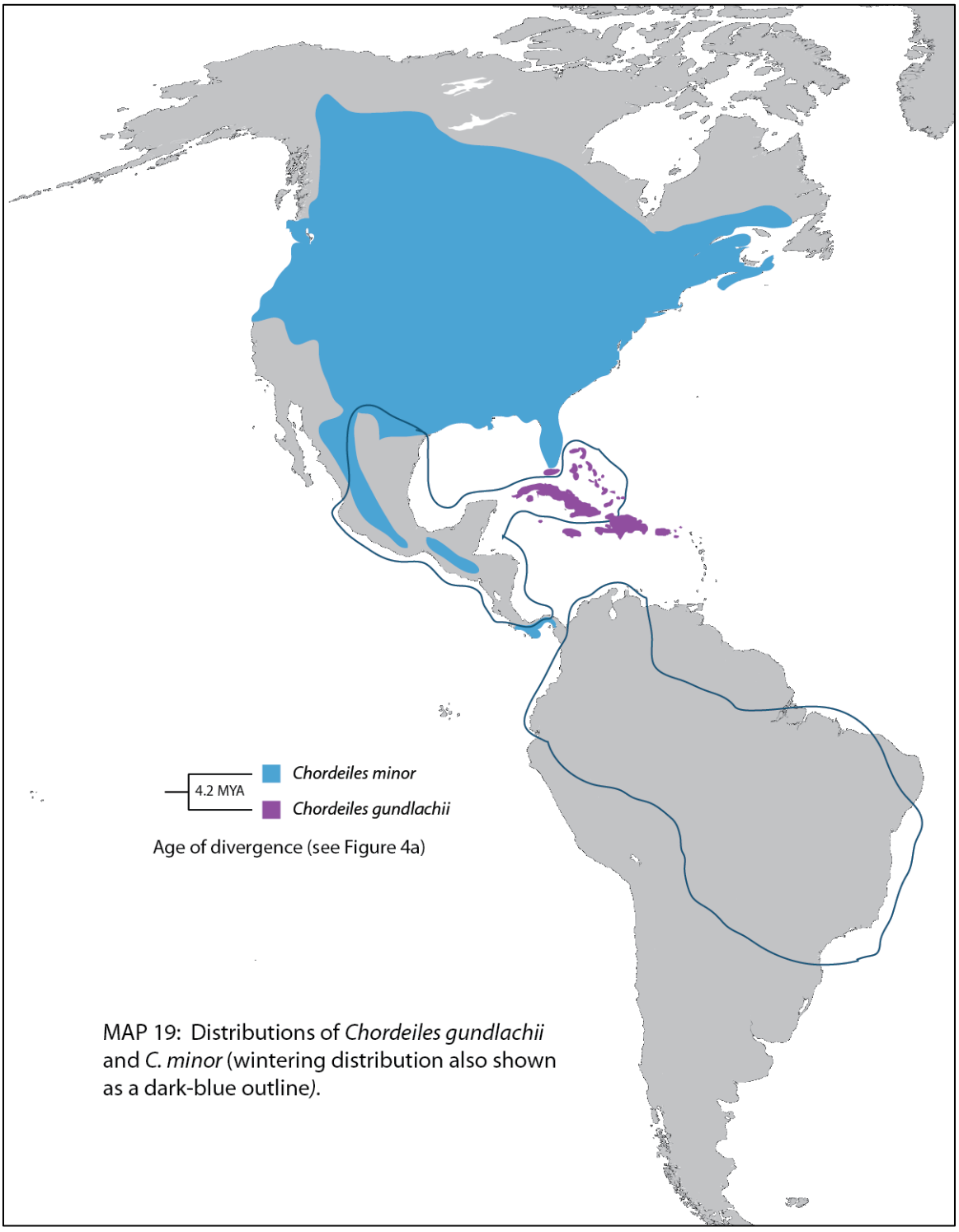

MAP 16: Distributions of *Antrostomus badius, A. salvini* and *A. seriocaudatus.*
Antrostomus salvini
Antrostomus badius
Antrostomus seriocaudatus



MAP 17: Distributions of *Nyctiphrynus mcleodii*, *N. ocellatus*, *N. rosenbergi* and *N. yucatanicus*.



MAP 18: Distributions of *Antrostomus carolinensis*, *A. cubanensis* and *A. rufus*.



MAP 19: Distributions of *Chordeiles gundlachii* and *C. minor* (wintering distribution also shown as a dark-blue outline).

7. TABLES

Table 1a. RAG-1 Phylogeny – Taxon list

Taxon name	Family	Source of RAG-1 sequence
Acanthisitta chloris	Acanthisittidae	Genbank – AY056975
Buteo jamaicensis	Accipitridae	Genbank – AY461394
Aegotheles insignis	Aegothelidae	Genbank – DQ482636
Alcedo leucogaster	Alcedinidae	Genbank – DQ111794
Anser albifrons	Anatidae	Genbank – DQ137227
Anseranas semipalmatus	Anseranatidae	Own sequence – Tissue # AMNH DOT 10264
Apus affinis	Apodidae	Genbank – AY056979
Antrostomus arizonae	Caprimulgidae	Own sequence – Tissue # FM 394005
Antrostomus carolinensis	Caprimulgidae	Own sequence – Tissue # AMNH DOT 13818
Antrostomus rufus	Caprimulgidae	Own sequence – Tissue # USNM B04420
Antrostomus saturatus	Caprimulgidae	Own sequence – Tissue # LSUMZ B-16198
Antrostomus seriocaudatus	Caprimulgidae	Own sequence – Tissue # LSUMZ B-28908
Antrostomus vociferus	Caprimulgidae	Own sequence – Tissue # AMNH DOT 7377
Caprimulgus batesi	Caprimulgidae	Own sequence – Tissue # USNM B09936
Caprimulgus climacurus	Caprimulgidae	Own sequence – Tissue # AMNH DOT 11123
Caprimulgus europaeus	Caprimulgidae	Own sequence – Tissue # AMNH DOT 10905
Caprimulgus fossii	Caprimulgidae	Own sequence – Tissue # AMNH DOT 2165
Caprimulgus macrurus	Caprimulgidae	Own sequence – Tissue # AMNH DOT 9565
Caprimulgus madagascariensis	Caprimulgidae	Own sequence – Tissue # FM 356643
Caprimulgus pectoralis	Caprimulgidae	Own sequence – Tissue # FM 444036
Caprimulgus poliocephalus	Caprimulgidae	Own sequence – Tissue # FM 357948
Chordeiles acutipennis acutipennis	Caprimulgidae	Own sequence – Tissue # FM 392639
Chordeiles acutipennis littoralis	Caprimulgidae	Own sequence – Tissue # KU 9367
Chordeiles gundlachii	Caprimulgidae	Own sequence – Tissue # LSUMZ B-48963
Chordeiles minor chapmani	Caprimulgidae	Own sequence – Tissue # FM 443599
Chordeiles minor minor	Caprimulgidae	Own sequence – Tissue # FM 428842

Taxon name	Family	Source of RAG-1 sequence
Chordeiles minor minor	Caprimulgidae	Own sequence – Tissue # FM 395875
Chordeiles rupestris	Caprimulgidae	Own sequence – Tissue # ANSP 17721
Chordeiles texensis	Caprimulgidae	Own sequence – Tissue # AMNH DOT 4164
Chordeiles texensis	Caprimulgidae	Own sequence – Tissue # LSUMZ B-18025
Eurostopodus mystacalis	Caprimulgidae	Own sequence – Tissue # AMNH DOT 2401
Gactornis enarratus	Caprimulgidae	Own sequence – Tissue # FM 352811
Hydropsalis anomalus	Caprimulgidae	Own sequence – Tissue # KU 3275
Hydropsalis cayennensis	Caprimulgidae	Own sequence – Tissue # ANSP 21440
Hydropsalis climacocerca schomburgki	Caprimulgidae	Own sequence – Tissue # ANSP 21533
Hydropsalis climacocerca climacocerca	Caprimulgidae	Own sequence – Tissue # USNM B06949
Hydropsalis decussatus	Caprimulgidae	Own sequence – Tissue # LSUMZ B-5262
Hydropsalis longirostris atripunctatus	Caprimulgidae	Own sequence – Tissue # FM 429897
Hydropsalis longirostris bifasciatus	Caprimulgidae	Own sequence – Tissue # AMNH DOT 13553
Hydropsalis longirostris patagonicus	Caprimulgidae	Own sequence – Tissue # USNM B14783
Hydropsalis maculicaudus	Caprimulgidae	Own sequence – Tissue # USNM B14678
Hydropsalis parvulus	Caprimulgidae	Own sequence – Tissue # AMNH DOT 2207
Hydropsalis roraimae	Caprimulgidae	Own sequence – Tissue # LSUMZ B-4783
Hydropsalis segmentata	Caprimulgidae	Own sequence – Tissue # DOT 2877
Hydropsalis torquata	Caprimulgidae	Own sequence – Tissue # ANSP 22420
Hydropsalis whitelyi	Caprimulgidae	Own sequence – Tissue # AMNH DOT 11875
Lurocalis rufiventris	Caprimulgidae	Own sequence – Tissue # LSUMZ B-32761
Lurocalis semitorquatus nattereri	Caprimulgidae	Own sequence – Tissue # KU 277
Lurocalis semitorquatus semitorquatus	Caprimulgidae	Own sequence – Tissue # USNM B11905
Lyncornis macrotis	Caprimulgidae	Genbank – DQ482615
Macrodipteryx vexillarius	Caprimulgidae	Own sequence – Tissue # AMNH DOT 10638
Nyctidromus albicollis	Caprimulgidae	Own sequence – Tissue # USNM B00440
Nyctidromus derbyanus	Caprimulgidae	Own sequence – Tissue # FM 399123
Nyctidromus merrilli	Caprimulgidae	Genbank – DQ482618

Taxon name	Family	Source of RAG-1 sequence
Nyctidromus nigrescens	Caprimulgidae	Own sequence – Tissue # AMNH DOT 12694
Nyctiphrynus mcleodii	Caprimulgidae	Own sequence – Tissue # FM 343199
Nyctiphrynus yucatanicus	Caprimulgidae	Own sequence – Tissue # KU 2110
Nyctiprogne leucopyga	Caprimulgidae	Own sequence – Tissue # USNM B19380
Nyctiprogne leucopyga	Caprimulgidae	Own sequence – Tissue # KU 3144
Phalaenoptilus nuttallii	Caprimulgidae	Own sequence – Tissue # LSUMZ B-40919
Podager nacunda	Caprimulgidae	Own sequence – Tissue # USNM B02768
Podager nacunda	Caprimulgidae	Genbank – DQ482630
Podager pusillus	Caprimulgidae	Own sequence – Tissue # ANSP 21634
Podager pusillus	Caprimulgidae	Own sequence – Tissue # FM 392642
Siphonorhis brewsteri	Caprimulgidae	Own sequence – Tissue # KU 8149
Charadrius vociferus	Charadriidae	Genbank – AF143736
Columba livia	Columbidae	Genbank – AY228768
Eurypyga helias	Eurypigidae	Own sequence – Tissue #AMNH DOT 2430
Fregata minor	Fregatidae	Own sequence – Tissue #AMNH DOT 10104
Gavia immer	Gaviidae	Genbank – AF143733
Grus canadensis	Gruidae	Genbank – AF143732
Hemiprocne mystacea	Hemiprocnidae	Genbank – DQ482637
Indicator variegatus	Indicatoridae	Own sequence – Tissue #AMNH DOT 14728
Larus marinus	Laridae	Genbank - AY228799
Mesitornis unicolor	Mesitornithidae	Own sequence (GFB)
Nyctibius grandis	Nyctibiidae	Genbank – DQ482612
Pandion haliaetus	Pandionidae	Genbank – EF078706
Phaethon lepturus	Phaethontidae	Own sequence – Tissue #AMNH DOT 7757
Gallus gallus	Phasianidae	Genbank - AF143730
Phoenicopterus ruber	Phoenicopteridae	Own sequence– Tissue #AMNH DOT 15589
Batrachostomus septimus	Podargidae	Genbank – DQ482613
Podargus strigoides	Podargidae	Genbank – DQ482614

Taxon name	Family	Source of RAG-1 sequence
Puffinus creatopus	Procellariidae	Own sequence – Tissue #AMNH DOT 10686
Psittacus erithacus	Psittacidae	Genbank – DQ482642
Rhea americana	Rheidae	Own sequence (GFB)
Rhynochetos jubatus	Rhynochetidae	Own sequence (GFB)
Spheniscus humboldti	Spheniscidae	Genbank – AF143734
Steatornis caripensis	Steatornithidae	Genbank – DQ482611
Strix occidentalis	Strigidae	Genbank – DQ482641
Sula sula	Sulidae	Own sequence – Tissue # AMNH 6553
Todus angustirostris	Todidae	Genbank – DQ111790
Colibri coruscans	Trochilidae	Genbank – DQ482639
Phaethornis griseogularis	Trochilidae	Own sequence – Tissue # AMNH DOT 8799
*Trogon person*atus	Trogonidae	Genbank – AY625227
Turdus falklandii	Turdidae	Genbank – AY057039
Upupa epops	Upupidae	Own sequence – Tissue # AMNH DOT 9335

Table 1b. Mitochondrial phylogeny – Taxon list

Taxon Name	Source	Specimen number	Specimen type
Antrostomus arizonae	FM	343200	Fresh Tissue
Antrostomus badius	AMNH	#824782	Skin
Antrostomus carolinensis	AMNH	DOT 13818	Fresh Tissue
Antrostomus cubanensis	AMNH	#477312	Skin
Antrostomus otiosus	AMNH	#389422	Skin
Antrostomus ridgwayi	AMNH	#817016	Skin
Antrostomus rufus	LSUMZ	B-44579	Fresh Tissue
Antrostomus salvini	Sequence from Genbank – as Caprimulgus salvini – GUS86656		
Antrostomus saturatus	LSUMZ	B-16198	Fresh Tissue
Antrostomus seriocaudatus	LSUMZ	B-28908	Fresh Tissue
Antrostomus vociferus	AMNH	DOT 7377	Fresh Tissue
Caprimulgus climacurus	AMNH	DOT 11123	Fresh Tissue
Caprimulgus europaeus	AMNH	DOT 10905	Fresh Tissue
Caprimulgus macrurus	USNM	B04000	Fresh Tissue
Caprimulgus madagascariensis	FM	356643	Fresh Tissue
Chordeiles acutipennis acutipennis	FM	392639	Fresh Tissue
Chordeiles acutipennis aequatorialis	ANSP	18986	Fresh Tissue
Chordeiles acutipennis littoralis	KU	9367	Fresh Tissue
Chordeiles gundlachii	LSUMZ	B-48963	Fresh Tissue
Chordeiles minor chapmani	FM	432665	Fresh Tissue
Chordeiles minor hesperis	AMNH	DOT 7786	Fresh Tissue
Chordeiles minor minor	AMNH	DOT 10080	Fresh Tissue
Chordeiles rupestris	LSUMZ	B-43037	Fresh Tissue
Chordeiles texensis	LSUMZ	B-18025	Fresh Tissue
Eurostopodus mystacalis	AMNH	DOT 2401	Fresh Tissue
Gactornis enarratus	FM	352811	Fresh Tissue
Hydropsalis albicauda	ANSP	19607	Fresh Tissue

Hydropsalis anomalus	KU	3275	Fresh Tissue
Hydropsalis candicans	Sequence from Genbank – as Caprimulgus candicans – DQ062140		
Hydropsalis cayennensis	USNM	B04364	Fresh Tissue
Hydropsalis climacocerca climacocerca	ANSP	19378	Fresh Tissue
Hydropsalis climacocerca schomburgki	ANSP	21533	Fresh Tissue
Hydropsalis decussatus	LSUMZ	B-5262	Fresh Tissue
Hydropsalis forcipata	AMNH	#317317	Skin
Hydropsalis heterurus	AMNH	#824104	Skin
Hydropsalis longirostris atripunctatus	LSUMZ	B-3571	Fresh Tissue
Hydropsalis longirostris bifasciatus	AMNH	DOT 13553	Fresh Tissue
Hydropsalis longirostris patagonicus	USNM	B14783	Fresh Tissue
Hydropsalis lyra	ANSP	19587	Fresh Tissue
Hydropsalis maculicaudus	USNM	B14678	Fresh Tissue
Hydropsalis parvulus	AMNH	DOT 2207	Fresh Tissue
Hydropsalis roraimae	LSUMZ	B-4783	Fresh Tissue
Hydropsalis ruficervix	ANSP	27189	Fresh Tissue
Hydropsalis segmentata kalinowskii	AMNH	DOT 2877	Fresh Tissue
Hydropsalis segmentata segmentata	ANSP	15766	Fresh Tissue
Hydropsalis torquata	USNM	B06315	Fresh Tissue
Hydropsalis whitelyi	AMNH	DOT 11875	Fresh Tissue
Lurocalis rufiventris	ANSP	19588	Fresh Tissue
Lurocalis semitorquatus nattereri	KU	277	Fresh Tissue
Lurocalis semitorquatus semitorquatus	USNM	B11905	Fresh Tissue
*Lurocalis semitorquatus stone*i	ANSP	18451	Fresh Tissue
Lyncornis macrotis	USNM	B03732	Fresh Tissue
Nyctidromus albicollis albicollis	LSUMZ	B-12198	Fresh Tissue
Nyctidromus albicollis yucatanensis	ANSP	27121	Fresh Tissue
Nyctidromus anthonyi	AMNH	DOT 16843	Fresh Tissue
Nyctidromus derbyanus	FM	399123	Fresh Tissue
Nyctidromus hirundinaceus	AMNH	#477244	Skin
Nyctidromus merrilli	LSUMZ	B-37032	Fresh Tissue

Nyctidromus nigrescens	LSUMZ	B-65861	Fresh Tissue
Nyctiphrynus mcleodii	AMNH	#702848	Skin
Nyctiphrynus ocellatus	USNM	B07024	Fresh Tissue
Nyctiphrynus rosenbergi	AMNH	#117635	Skin
Nyctiphrynus yucatanicus	KU	2110	Fresh Tissue
Nyctiprogne latifascia	AMNH	DOT 14305	Fresh Tissue
Nyctiprogne leucopyga	KU	3144	Fresh Tissue
Nyctiprogne vielliardi	AMNH	#291910	Skin
Phalaenoptilus nuttallii dickeyi	AMNH	#131568	Skin
Phalaenoptilus nuttallii nuttallii	LSUMZ	B-21804	Fresh Tissue
Podager nacunda minor	USNM	B12379	Fresh Tissue
Podager nacunda nacunda	USNM	B20909	Fresh Tissue
Podager pusillus esmeraldae	FM	392642	Fresh Tissue
Podager pusillus novaesi	AMNH	#241901	Skin
Podager pusillus septentrionalis	ANSP	21634	Fresh Tissue

TABLE 2 – ANCESTRAL AREA ANALYSES

ANALYSIS 1 – All taxa

Area definitions:

A – Old World (one or more of Africa, Asia, Australasia and Europe)
B – North America (Canada and United States)
C – Mexico and Central America (including Panama)
D – The Caribbean (Greater and Lesser Antilles but not Netherlands Antilles)
E – South America

Taxon distributions:

Antrostomus arizonae	C
Antrostomus carolinensis	B
Antrostomus rufus	CE
Antrostomus saturatus	C
Antrostomus seriocaudatus	E
Antrostomus vociferus	B
Caprimulgus batesi	A
Caprimulgus climacurus	A
Caprimulgus europaeus	A
Caprimulgus fossii	A
Caprimulgus macrurus	A
Caprimulgus madagascariensis	A
Caprimulgus pectoralis	A
Caprimulgus poliocephalus	A
Chordeiles acutipennis acutipennis	E
Chordeiles acutipennis littoralis	CE
Chordeiles gundlachii	D
Chordeiles minor chapmani	BD
Chordeiles minor hesperis	BC
Chordeiles minor minor	B
Chordeiles rupestris	E
Chordeiles texensis	C
Eurostopodus mystacalis	A
Gactornis enarratus	A
Hydropsalis albicauda	CE
Hydropsalis anomalus	E
Hydropsalis climacocerca climacocerca	E
Hydropsalis climacocerca schomburgki	E
Hydropsalis decussatus	E
Hydropsalis longirostris atripunctatus	E
Hydropsalis longirostris bifasciatus	E
Hydropsalis longirostris patagonicus	E

Hydropsalis maculicaudus	CE
Hydropsalis parvulus	E
Hydropsalis roraimae	E
Hydropsalis segmentata	E
Hydropsalis torquata	E
Hydropsalis whitelyi	E
Lurocalis rufiventris	E
Lurocalis semitorquatus nattereri	E
Lurocalis semitorquatus stonei	CE
Lyncornis macrotis	A
Macrodipteryx vexillarius	A
Nyctidromus albicollis	CE
Nyctidromus derbyanus	E
Nyctidromus merrilli	C
Nyctidromus nigrescens	E
Nyctiphrynus mcleodii	E
Nyctiphrynus ocellatus	CE
Nyctiphrynus yucatanicus	C
Nyctiprogne latifascia	E
Nyctiprogne leucopyga	E
Phalaenoptilus nuttallii	BC
Podager nacunda minor	E
Podager nacunda nacunda	E
Podager pusillus esmeraldae	E
Podager pusillus septentrionalis	E
Siphonorhis brewsteri	D

ANALYSIS 2 – Poorwill Clade

Area definitions:

A – Eastern North America (East of Mississippi)
B – Western North America (West of Mississippi)
C – Mexican lowlands (including Yucatan Peninsula)
D – Mexican highlands (excluding Chiapas)
E – Central America (south of Isthmus of Tehuantepec)
F – The Caribbean
G – South America

Taxon distributions:

Antrostomus arizonae	D
Antrostomus badius	C
Antrostomus carolinensis	A
Antrostomus cubanensis	F
Antrostomus ridgwayi	CDE
Antrostomus rufus otiosus	EFG
Antrostomus rufus rufus	G
Antrostomus salvini	C
Antrostomus saturatus	E
Antrostomus seriocaudatus	G
Antrostomus vociferus	A
Nyctiphrynus mcleodii	D
Nyctiphrynus ocellatus	G
Nyctiphrynus rosenbergi	G
Nyctiphrynus yucatanicus	C
Phalaenoptilus nuttallii californicus	B
Phalaenoptilus nuttallii dickeyi	BCD
Phalaenoptilus nuttallii nuttallii	BCD
Siphonorhis brewsteri	F

ANALYSIS 3 – South American Clade

Area definitions:

A – Central America
B – Northern Andes
C – Central Andes
D – Pacific Lowlands
E – Lowlands of Colombia and Venezuela
F – Northern Amazon Rainforest (including Guianan Shield and Tepuis)
G – Southern Amazon Rainforest
H – Central South America (Caatinga, Cerrado & Choco)
I – Atlantic Forest
J – Southern Grasslands (Pampas & Patagonia)

Taxon distributions:

Hydropsalis albicauda	AE
Hydropsalis anomalus	H
Hydropsalis candicans	H
Hydropsalis cayennensis	EF
Hydropsalis climacocerca climacocerca	FG
Hydropsalis climacocerca schomburgki	F
Hydropsalis decussatus	D
Hydropsalis forcipata	I
Hydropsalis heterurus	E
Hydropsalis longirostris atripunctatus	C
Hydropsalis longirostris bifasciatus	J
Hydropsalis longirostris patagonicus	HIJ
Hydropsalis lyra	BC
Hydropsalis maculicaudus	EFH
Hydropsalis parvulus	GCI
Hydropsalis roraimae	F
Hydropsalis ruficervix	B
Hydropsalis segmentata kalinowskii	C
Hydropsalis segmentata segmentata	B
Hydropsalis torquata	GHIJ
Hydropsalis whitelyi	F
Lurocalis semitorquatus nattereri	GHI
Lurocalis semitorquatus semitorquatus	EF
Lurocalis semitorquatus stonei	A
Nyctidromus albicollis	AEF
Nyctidromus anthonyi	D
Nyctidromus derbyanus	GHI
Nyctidromus hirundinaceus	H
Nyctidromus merrilli	A

Nyctidromus nigrescens	FG
Nyctiprogne latifascia	F
Nyctiprogne leucopyga	GH
Nyctiprogne vielliardi	H

ANALYSIS 4 – Nighthawk Clade

Area definitions:

A – North America
B – Mexico (north of the Isthmus of Tehuantepec)
C – Central America (between the Isthmus of Panama and the Isthmus of Tehuantepec)
D – The Caribbean Islands
E – Lowlands of Colombia, Venezuela, Ecuador and Peru (including Chocó, Guajira, Llanos and Tumbesian areas of endemism)
F – Amazon Basin
G – Central South America (Caatinga, Cerrado & Choco)

Taxon distributions:

Chordeiles acutipennis acutipennis	CEG
Chordeiles acutipennis aequatorialis	E
Chordeiles acutipennis littoralis/micromeris	C
Chordeiles gundlachii	D
Chordeiles minor	ABC
Chordeiles rupestris	F
Chordeiles texensis	BC
Podager nacunda minor	EF
Podager nacunda nacunda	FG
Podager pusillus esmeraldae	EF
Podager pusillus pusillus	G
Podager pusillus septentrionalis	E

TABLE 3 – Trait reconstruction for habitat types in the South American clade

Trait categories:

A – Lowland, tropical evergreen forests
B – Montane, evergreen & elfin forests & *Polyepsis* woodlands
C – Secondary growth forest & scrubland, farmlands & plantations
D – Lowland, seasonally wet grasslands, savannah & marshlands
E – Dry campo grasslands
F – Arid scrubland & deserts
G – Tropical deciduous & gallery forests

Hydropsalis albicauda	D
Hydropsalis anomalus	D
Hydropsalis candicans	E
Hydropsalis cayennensis	D
Hydropsalis climacocerca climacocerca	D
Hydropsalis climacocerca schomburgki	D
Hydropsalis decussatus	F
Hydropsalis forcipata	B
Hydropsalis heterurus	G
Hydropsalis longirostris atripunctatus	B
Hydropsalis longirostris bifasciatus	G
Hydropsalis longirostris patagonicus	E
Hydropsalis lyra	B
Hydropsalis maculicaudus	E
Hydropsalis parvulus	C
Hydropsalis roraimae	B
Hydropsalis ruficervix	B
Hydropsalis segmentata kalinowskii	B
Hydropsalis segmentata segmentata	B
Hydropsalis torquata	E
Hydropsalis whitelyi	B
Lurocalis rufiventris	B
Lurocalis semitorquatus nattereri	A
*Lurocalis semitorquatus semitor*quatus	A
Lurocalis semitorquatus stonei	A
Nyctidromus albicollis	C
Nyctidromus anthonyi	F
Nyctidromus derbyanus	C
Nyctidromus hirundinaceus	G
Nyctidromus merrilli	C
Nyctidromus nigrescens	A
Nyctiprogne latifascia	A
Nyctiprogne leucopyga	A
Nyctiprogne vielliardi	G

TABLE 4 – AGES OF DIVERGENCE DATES

A) Estimated ages of key nodes from a dating analysis in Beast v1.6.2 of a RAG-1 dataset of the caprimulgid, other caprimulgiform taxa and outgroups.

Node	**Mean**	**95 % confidence limits**
Root of phylogeny	110.6	85.4-151.2 MYA
Root of Neognathae	96.5	80.3-121.1 MYA
Root of Galloanserae	72.2	71.0-76.1 MYA
Root of Neoaves	76.5	66.5-89.5 MYA
Root of Caprimulgiformes	69.6	61.1-80.4 MYA
Root of Caprimulgidae (split between *Eurostopodus* and remainder)	56.1	46.1-67.0 MYA
Separation of *Lyncornis* and remaining nightjar taxa	52.6	42.3-63.2 MYA
Separation of *Gactornis* and the four core nightjar radiations	48.1	38.8-58.0 MYA
Separation of South American radiation from other three	42.6	33.9-51.8 MYA
Separation of Poorwill radiation from Nighthawk and Old World radiations	39.8	31.8-48.9 MYA
Separation between Nighthawk and Old World radiations	36.6	28.9-45.2 MYA

B) Estimated ages of key nodes within the New World nightjar radiations from a dating analysis in Beast v1.6.2 of a mitochondrial dataset of the Caprimulgidae

Node	**Mean**	**95 % confidence limits**
SOUTH AMERICAN RADIATION		
Root of the South American radiation	33.2	31.0-35.4 MYA
Root of *Nyctidromus*	17.9	16.2-19.8 MYA
Split between *N. nigrescens* and *N. hirundinaceus*	13.1	8.7-16.6 MYA
Split between *N. anthonyi* and *N. albicollis/N. derbyanus/N. merrilli*	15.5	12.5-18.1 MYA
Split between *N. merrilli* and *N. albicollis/N. derbyanus*	4.5	2.8-6.3 MYA
Root of *Nyctiprogne*	14.8	8.9-21.8 MYA
Split between *N. leucopyga* and *N. vielliardi*	3.0	1.3-5.2 MYA
Root of *Lurocalis*	7.7	4.7-12.0 MYA
Root of *Hydropsalis*	24.2	20.3-28.2 MYA
Split between *H. heterurus* and *H. parvulus*	4.8	2.6-7.9 MYA
Root of *H. lyra/ H. segmentata* – group	6.0	3.8-8.6 MYA
Split between *H. decussatus* and sister-group	17.3	14.4-20.5 MYA
Split between *H. longirostris*- group and *H. cayennensis*-group	15.3	12.6-18.2 MYA
Split between *H. anomalus/H. candicans* and sister-group	10.8	2.5-7.3 MYA
Split between H. *longirostris* and *H. roraimae/H. ruficervix*	6.8	4.6-9.2 MYA
Split between *H. roraimae* and *H. ruficervix*	3.9	2.1-6.0 MYA
Split between *H. maculicaudus* and sister-group	12.5	9.8-15.5 MYA
Split between *H. forcipata* and sister-group	10.8	8.2-13.7
Root of *H. albicauda/H. cayennensis/H. climacocerca/ H. torquata* – group	8.4	6.2-11.0 MYA

Node	Mean	95 % confidence limits
POORWILL RADIATION		
Root of the Poorwill radiation	31.0	28.9-33.2 MYA
Split between *Nyctiphrynus* and *Antrostomus/Phalaenoptilus*	27.9	24.7-31.0 MYA
Split between *Antrostomus* and *Phalaenoptilus*	20.5	16.8-24.2 MYA
Split between *A. vociferus*-group and *A. carolinensis*-group	16.6	13.6-19.9 MYA
Split between *A. saturatus* and *A. arizonae/ A. vociferus*	8.0	5.5-10.9 MYA
Split between *A. arizonae* and *A. vociferus*	6.9	4.5-9.7 MYA
Root of *A. carolinensis/A. cubanensis/A. rufus*	8.3	5.6-11.3 MYA
Split between *Nyctiphrynus rosenbergi* and sister-group	21.3	16.7-25.7 MYA
Split between *N. mcleodii* and *N. ocellatus/N. yucatanensis*	12.6	8.9-16.8 MYA
Split between *N. ocellatus* and *N. yucatanensis*	10.7	6.9-15.0 MYA
NIGHTHAWK RADIATION		
Root of the Nighthawk radiation (split between *Chordeiles* and *Podager*)	24.0	21.7-26.2 MYA
Split between *Chordeiles acutipennis*-group and *C. minor*-group	18.3	14.6-21.7 MYA
Split between *C. rupestris* and *C. acutipennis/C. texensis*	10.4	7.1-13.9 MYA
Split between *C. acutipennis* and *C. texensis*	2.9	1.8-4.2 MYA
Split between *C. gundlachii* and *C. minor*	4.2	2.6-6.2 MYA
Slit between *Podager nacunda* and *P. pusillus*	21.0	16.9-24.6 MYA

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