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Molecular systematics of the genus *Chaetura* (Aves: Apodidae)

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Introduction

Swifts are among the most aerial of birds. Various morphological features, many related to the shape of their wings, are likely adaptations to a lifestyle that regularly involves prolonged flight (Chantler 1999, Lentink et al. 2007). Swift morphology is notoriously conservative and *Chaetura* is one of the most monomorphic genera of swifts; species in this genus are difficult to identify both in the field and in the specimen drawer.

Until 1970, *Chaetura* contained all species that constitute the present tribe Chaeturini and included numerous Old World species, but the genus is currently considered to consist of nine species endemic to the New World (Brooke 1970, Chantler 1999). Marín (1997, 2000) used morphological characteristics to divide *Chaetura* into two groups, the brown-rumped and the gray-rumped swifts, and to further divide the gray-rumped group into gray-rumped and pale-rumped species (Table 1). Not suprisingly, given the lack of morphological variation, some species limits with *Chaetura* are controversial.

In this project we used molecular data to:

- determine whether *Chaetura* is a monophyletic (natural evolutionary) group
- establish whether the brown- and gray-rumped groups, and pale- and gray-rumped subgroups, are monophyletic
- assess the monophyly of each species of *Chaetura*
- evaluate the genetic status of putative species *richmondi*, *viridipennis*, *fumosa*, and *egregia* relative to their proposed conspecifics *vauxi*, *chapmani*, *spinicauda*, and *cinereiventris*/*spinicauda*, respectively

Species	Phenotype	Range	No. Subspp./ No. Sampled	Total Samples
C. pelagica	Brown-rumped	breeds e. North America; winters w. South America	monotypic	2
C. vauxi	Brown-rumped	breeds w. N. A.; winters s. N. A. and Central America	6/2	4
C. chapmani	Brown-rumped	n. South America	2/2	4
C. brachyura	Brown-rumped	n. South America	4/2	3
C. andrei	Brown-rumped	n. and c. South America	2/1	3
C. cinereiventris	Gray-rumped (Gray)	s. Caribbean and C. and S. America	7/2	4
C. spinicauda	Gray-rumped (Pale)	s. C. A. and n. S. A.	5/4	7
C. martinica	Gray-rumped (Pale)	Lesser Antilles	monotypic	0
C. egregia	Gray-rumped (Pale)	c.-w. South America	monotypic	2

Table 1. Selected characteristics of species of *Chaetura* (Chantler 1999; Marín 2000).

Materials and Methods

- Tissue samples were obtained for 32 individuals representing eight of the nine *Chaetura* species and three outgroups (Table 1). Two outgroup species were representatives of other genera within the Chaeturini (*Neafrapus* and *Hirundapus*) and the third outgroup species (*Apus apus*) was a representative of the broader Apodidae.
- DNA was extracted using Qiagen extraction kits, and the mitochondrial gene NADH dehydrogenase 2 (ND2) and intron 5 of the nuclear gene muscle specific receptor tyrosine kinase (MUSK) were amplified using standard PCR protocols.
- Sequences were obtained using an ABI PRISM 3130 automated sequencer, edited using Sequencher 4.9, and analyzed using maximum likelihood (ML) and maximum parsimony (MP) as implemented in RAxML (Stamatakis et al. 2008) and PAUP* 4.0 (Swofford 2003).

Photo Credit: Peter LaTourrette

Results

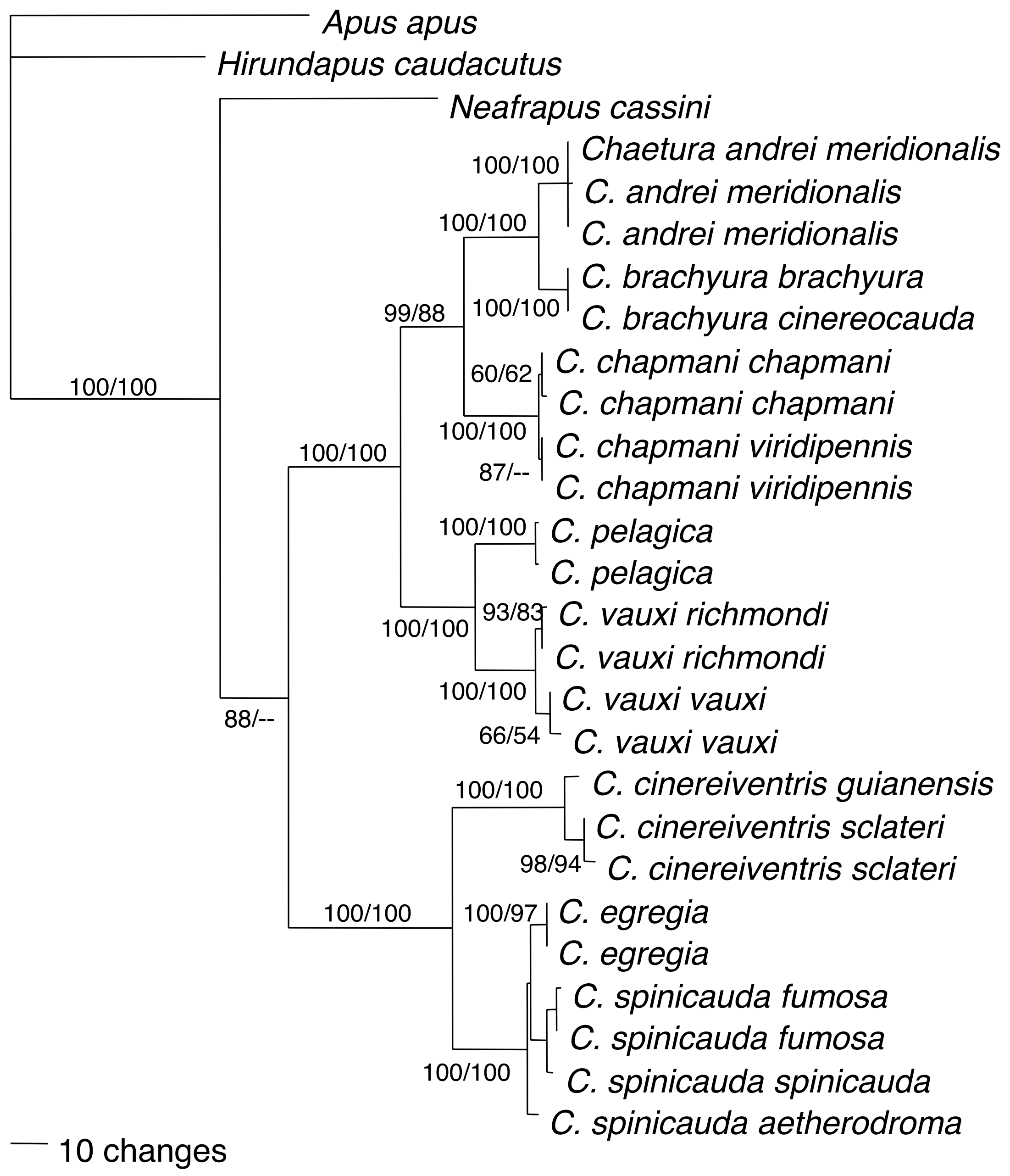

Figure 1. Most likely phylogenetic tree, obtained through analysis of the combined mitochondrial and nuclear data (figures on the tree are ML/MP bootstrap support values).

- Complete mitochondrial sequence (1041 bp) was obtained for 27 individuals and complete nuclear sequence (612 aligned bp) for 22 individuals.
- Most trees (all ML trees and the nuclear MP tree; Fig.1) indicated that the genus *Chaetura* was monophyletic. The brown- and gray-rumped groups and the pale- and gray-rumped subgroups were monophyletic in all trees.
- Individual species were monophyletic with the exception of *C. spinicauda*, which in most trees was paraphyletic with respect to *C. egregia*. Mean mitochondrial divergence between sister species ranged from 1.5% (between *andrei* and *brachyura*) and 5.5% (between *cinereiventris* and *spinicauda*/*egregia*).
- Putative conspecifics *vauxi vauxi* and *v. richmondi* were sister taxa in all trees; mean mitochondrial divergence was 0.5%. Nominate *chapmani* and *c. viridipennis* formed a clade and were sister taxa in some trees; mean sequence divergence between these taxa was only 0.1%. Nominate *spinicauda* and *s. fumosa* formed part of a clade that also included the other representative of *spinicauda* (*aetherodroma*) and *C. egregia*. Mean mitochondrial divergence was 0.5% between *s. spinicauda* and *s. fumosa* and 1.0% between *C. spinicauda* and *C. egregia*. *Chaetura egregia* was not sister to or nested within *C. cinereiventris* and differed from it by 5.5% mean sequence divergence.

Discussion

- Our results indicate that the genus *Chaetura* is likely monophyletic, consistent with the restricted definition of the genus (Brooke 1970). However, *Neafrapus* is closely related and some analyses (mitochondrial MP) place it within *Chaetura*.
- The basic structure of our phylogenetic tree is consistent with previous views based on morphological variation in *Chaetura*. Marín's division of the genus into brown- and gray-rumped groups and pale- and gray-rumped subgroups is supported by all of our trees. Our results also support a close relationship between *egregia* and *spinicauda* (cf. Marín 2000), in contrast to previous views suggesting that *egregia* is conspecific with *cinereiventris*. *Chaetura egregia* is nested within *C. spinicauda* in most trees.
- Morphology and vocalizations are frequently used to distinguish avian species. However, such characters are of limited utility in swifts, and views on species status in the group have often been based on one or a few characters subject to varying interpretations. Under the biological species concept, genetic data on allopatric taxa are insufficient to determine species limits; however, they can provide additional perspective in cases of equivocal morphological and behavioral data. We found low levels of genetic divergence separating *richmondi*, *viridipennis*, and *fumosa* from their conspecifics, relative to levels of divergence between sister species in *Chaetura*. These findings are more consistent with treatment of these taxa as conspecifics than as different species.

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