

INDEPENDENT EVOLUTION OF TWO DARWINIAN MARSH-DWELLING OVENBIRDS (FURNARIIDAE: *LIMNORNIS*, *LIMNOCTITES*)

Storrs L. Olson¹, Martin Irestedt^{2, 3}, Per G. P. Ericson², & Jon Fjeldså⁴

¹Division of Birds, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, DC 20013-7012, U.S.A. *E-mail*: olsons@si.edu

²Department of Vertebrate Zoology and Molecular Systematics Laboratory, Swedish Museum of Natural History, P.O. Box 50007, SE-104 05 Stockholm, Sweden.

E-mail: martin.irestedt@nrm.se & per.ericson@nrm.se

³Department of Zoology, University of Stockholm, SE-106 91 Stockholm, Sweden.

⁴Vertebrate Department, Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark. *E-mail*: jfjeldsaa@zmuc.ku.dk

Resumen. – Evolución independiente de dos horneros de pantano (Furnariidae: *Limnornis*, *Limnocitites*). – La Pajonalera Pico Curvo (*Limnornis curvirostris*) y la Pajonalera Pico Recto (*Limnocitites rectirostris*) son dos especies de hornero de pantano colectados por primera vez por Charles Darwin en Uruguay. Ambas tienen una distribución limitada a Uruguay, el sur de Brasil y el norte de Argentina, área en la cual ocupan hábitat muy diferentes. Descritas originalmente como congéneres debido a sus similitudes en plumaje, las dos especies han sido consideradas parientes cercanas a pesar de diferencias estructurales obvias entre ambas. Analizamos secuencias de ADN de tres genes de estas dos especies y las comparamos con una amplia variedad de otras especies de Furnariidae y varios grupos externos. *Limnocitites rectirostris* pertenece al grupo de especies tradicionalmente agrupadas en *Cranioleuca*, estando más cercanamente relacionada al Curutié Ocráceo (*C. sulphurifera*) entre las especies muestreadas. Estos resultados están respaldados por vocalizaciones y nidificación. *Limnornis curvirostris* forma un clado con el Junquero (*Phleocryptes melanops*); este clado tiene al Macuquiño (*Lochmias nematura*) como grupo hermano. Una relación cercana entre *Limnornis* y *Phleocryptes* es respaldada por el color azul de los huevos y la arquitectura del nido, la cual es aparentemente única en estos dos géneros.

Abstract. – The Curve-billed Reedhaunter (*Limnornis curvirostris*) and the Straight-billed Reedhaunter (*Limnocitites rectirostris*) are marsh-dwelling ovenbirds that were first collected by Charles Darwin in Uruguay. Each has a limited distribution in southernmost Brazil, Uruguay, and northern Argentina, within which the birds occupy very distinct habitats. Originally described as congeners because of overall similarity of plumage, the two species have been treated as close relatives through most of their history despite obvious structural differences. We analyzed DNA sequences from three different genes of these species, comparing them with a wide variety of other species of Furnariidae and several outgroup taxa. *Limnocitites rectirostris* belongs among the species traditionally placed in *Cranioleuca*, being most closely related to the marsh-dwelling Sulphur-throated Spinetail (*C. sulphurifera*) among the species we sampled. This is supported by vocalizations and nidification. *Limnornis curvirostris* forms a clade with the Wren-like Rushbird (*Phleocryptes melanops*), with the Sharp-tailed Streamcreeper (*Lochmias nematura*) as a rather distant sister-taxon. A close relationship between *Limnornis* and *Phleocryptes* is supported by the apparently unique nest architecture and blue-green egg color. *Accepted 5 April 2005.*

Key words: Furnariidae, *Limnocitites*, *Limnornis*, molecular systematics, nidification, ovenbirds.

INTRODUCTION

Charles Darwin was the first naturalist to collect two paludicolous species of ovenbirds that are now known to be of very limited distribution in southeastern South America. These were obtained in June 1833 (Steinhilber 2004; not 1832 as per Vaurie 1980: 211) in what is now the province of Maldonado in the Republica Oriental del Uruguay. When John Gould (1839: 80–81, pl. 25–26) identified and described the birds from the voyage of H. M. S. *Beagle*, he created a new genus, *Limnornis*, for these two species, calling the first *L. rectirostris*, for its very straight, pointed bill, and the second *L. curvirostris*, for its bill with a more typically curved tip. In English these species are now called the Straight-billed and the Curve-billed reedhaunters, respectively.

Both species were said by Darwin (*in* Gould 1839:80–81) to live in the same habitat “amongst the reeds on the borders of lakes” and that he was “unable to point out any differences” in the habits of the two. This mistaken impression probably colored much of the subsequent thinking about these birds. Apart from the supposedly shared habitat, the main similarity between the two reedhaunters is in general coloration and plumage pattern. This is doubtless what lead Gould (1839) to his original decision to place them both in the same genus and also why Vaurie (1980) rather vigorously defended this course. On the other hand, there are manifest differences between the two, so that they have most often been placed in separate monotypic genera (*Limnornis* and *Limnoctites*). Regardless, the two reedhaunters first collected by Darwin have long been regarded as each other’s closest relative. This also appeared to receive support from a phylogenetic analysis of nest structure (Zyskowski & Prum 1999) in which *Limnornis* and *Limnoctites* were said to form a group with the Wren-like Rushbird (*Phleocryptes melanops*).

We decided to test this hypothesis by reviewing the information on morphology, ecology, and nidification, and by comparing this with new molecular evidence.

SYNOPSIS OF MORPHOLOGY AND NOMENCLATURAL HISTORY

Both reedhaunters are plain brownish or dull rufous above, with rufous tails, dull whitish undersides, and no adornment apart from a whitish superciliary stripe. *Limnornis curvirostris* is a reasonably robust bird (26.7–33.3 g, mean 29.0 g, n = 10, according to USNM specimen data; mean of 21 eggs 24.6 x 17.9 mm, according to Narosky *et al.* 1983) with a longish, rounded tail and a stout, curved bill. It has very much the appearance of a drab version of one of the smaller species of *Furnarius*. *Limnoctites rectirostris* is a much slighter bird (15.6–24.5 g, mean 19.2 g, n = 5, according to USNM specimen data [the heaviest was a very fat laying female]; mean of 3 eggs 20.3 X 15.3 mm, according to Ricci & Ricci 1984) with an extremely long, straight, slender bill, and a shorter, graduated tail with very pointed, usually worn, rectrices. The nomenclatural history of the two species has revolved around whether to emphasize their similarities or their differences.

Gould (1839) did not designate a type species for *Limnornis* and Gray (1840) subsequently selected *L. curvirostris* as the genotype. Sclater (1889) overlooked Gray’s action and applied a new name, *Limnophyes*, to *L. curvirostris*, reserving the name *Limnornis* for *L. rectirostris*. But *Limnophyes* was preoccupied by a genus of Diptera, so Oberholser (1899) proposed *Thryolegus* as a replacement. Hellmayr (1925) pointed out Gray’s (1840) type designation, returned *curvirostris* to *Limnornis*, and proposed the new generic name *Limnoctites* for *L. rectirostris*. Since then, most authors have maintained the two species in monotypic genera, usually placing them next to one

another.

The first exception appears to be Esteban (1949), who advocated removing *Limnortites rectirostris* to the subfamily Synallaxinae near *Certhiopsis*, presumably leaving *Limnortis curvirostris* in the Philydorinae, where both were placed by Sclater (1890). Peters (1951) also dissociated the two, placing *Limnortis* immediately after *Furnarius*, with 12 genera between it and *Limnortites*, which was placed between *Certhiopsis* and *Poecilurus/Craniolenca*. Although Meyer de Schauensee (1966) followed Peters' sequence almost exactly, one of his few departures was to place *Limnortites* immediately after *Limnortis*. Vaurie (1971, 1980) and Sibley & Monroe (1990) returned to the original Gouldian nomenclature and combined both species in *Limnortis*. Other authors (e.g., Ridgely & Tudor 1994) have preferred to emphasize differences by recognizing two genera for the reed-haunters, although still maintaining their close association. Remsen (2003) maintained them as adjacent in his linear sequence but noted that differences in tail structure, nesting materials, and egg color called into question their proposed sister relationship.

DISTRIBUTION AND HABITAT

For nearly a century, Darwin's original two specimens of *L. rectirostris* were the only ones known. Sanborn (1929) next obtained the species at another locality in Uruguay in 1926. Gradually, its range was extended from the provinces of Entre Rios and Buenos Aires, Argentina, to Rio Grande do Sul and Santa Catarina, in southernmost Brazil, and the species was also found more extensively in Uruguay (Daguerre 1933, Pereyra 1938, Esteban 1949, Escalante 1956, Gerzenstein & Achaval 1967, Zorilla de San Martín 1963, Alda do Rosário 1996, Babarskas & Fraga 1998).

After Darwin's original collection, *Limnortis curvirostris* was next collected from 1866 to 1868 at Conchitas, Buenos Aires Province,

Argentina, by W. H. Hudson (Sclater & Salvin 1868). Durnford (1877: 182) found the species common in the same province and was "at a loss to understand how this bird could have escaped the observation of naturalists till Mr. Darwin's visit to South America." Additional specimens were obtained in Uruguay (Sclater & Hudson 1888, Sclater 1890, Hellmayr 1925), Sanborn's (1929) assertion that his 1926 specimens from Uruguay were the first since Darwin being erroneous. By 1899, the range of the species was extended to Rio Grande do Sul, Brazil (Ihering 1899).

Although Darwin stated (*in* Gould 1839) that the two reedhaunters occurred together and Vaurie (1980: 212) asserted that "*L. rectirostris* shares the same habitat [as *L. curvirostris*], but its requirements are less rigid," this is not, in fact, the case. Ridgely & Tudor (1994: 61) note that the two species "appear never to occur together in the same marsh." Belton (1984: 622) shows no overlap in range between the species in Rio Grande do Sul, Brazil. Olson has experience with *L. curvirostris* in Argentina, and with both species through much of Uruguay, and has not yet visited a site where both species might be expected to occur in proximity.

Limnortites rectirostris typically occurs in marshes. Although a variety of plants may occur in such sites, particularly at the edges, the bird is found only where the spiny *caraguatá*, *Eryngium* spp., dominates. In the ornithological literature this plant has erroneously been referred to as a sedge (e.g., Ridgely & Tudor 1994, Remsen 2003: 226, but correctly as an "apiaceous herb" on 261) or a grass (Gerzenstein & Achaval 1967, Vaurie 1980, Babarskas & Fraga 1998). It is actually a dicot that belongs in the carrot family (Apiaceae or Umbelliferae). Ricci & Ricci (1984: 205) correctly describe the plants as growing in "bromeliad-like rosettes," the leaves of which are beset with sharp spines that make the pursuit of birds in this habitat a decided challenge to

the ornithologist's flesh and clothing. The species that have been mentioned in connection with *Limnortites* are *Eryngium borridum* (Belton 1984, Remsen 2003), *E. pandanifolium* (Gerzenstein & Achaval 1967, Babarskas & Fraga 1998, Remsen 2003), and *E. eburneum* (Ricci & Ricci 1984). The ranges of these plants are given as southern Brazil to NE Argentina, with the last two extending to Paraguay (Cabrera 1965).

That the birds are tied to the plant and not necessarily to marshy environments is shown by their occurrence at 200 to 250 m in rocky scrub forest where *Eryngium pandanifolium* occurs in 5 to 20 m wide patches along streams (Gerzenstein & Achaval 1967). That *L. rectirostris* occurs as high as 1100 m (Ridgely & Tudor 1994, BirdLife International 2000, Remsen 2003) is presumably based on the populations in Aparados da Serra National Park mentioned by Belton (1984: 621), though no substantive documentation of their occurring so high appears to exist.

Although also a marsh bird, *L. curvirostris* is found in extensive reedbeds, especially of the giant sedge or pajonal (*Scirpus giganteus*), the grass known as *espadaña* (*Zizaniopsis bonariensis*), and also cattails (*Typha*). Although its briefly stated range from Rio Grande do Sul to Buenos Aires is the same as that of *L. rectirostris*, within that area it is much the more abundant and widespread of the two species because of the greater extent of its habitat.

In summary, although the distributions of the two reedhaunters are superficially similar, they are adapted to distinct habitats and are probably never syntopic.

NIDIFICATION

Nest structure in the Furnariidae is extremely diverse and has been used to devise a phylogeny of the family (Zyskowski & Prum 1999). In this phylogeny, *Limnornis* and *Limnortites* were grouped with *Phleocryptes melanops* on the

basis of their supposedly building a domed nest with "a small awning over the nest entrance" (p. 899). The nest of *Limnornis curvirostris* is described by von Ihering (1902) and Belton (1984); that of *Limnortites rectirostris* by Daguerre (1933), Ricci & Ricci (1984) and Sick (1993); and those of both species in Vaurie (1980) and Narosky *et al.* (1983). Included here are all the references cited by Zyskowski & Prum (1999), plus some others, but none mentions an awning over the entrance of the nest of *Limnortites*. This error came about from misinterpretation (K. Zyskowski pers. com. to Olson, June 2004) of photographs of the nest of *Phylloscartes ventralis* in the article preceding the paper by Ricci & Ricci that were erroneously captioned as *Limnortites*. Zyskowski (pers. com. *ibid.*) has since found and photographed a nest of *L. rectirostris* in Uruguay and confirmed that it does not have an awning. Remsen (2003) took his descriptions of the nests of both reedhaunters as having awnings from Zyskowski & Prum (1999).

The first mention of an "awning" being constructed by *Limnornis curvirostris* appears to be that in one of two nests of described by Narosky (*in* Vaurie 1980: 213). Later, Narosky *et al.* (1983: 36) confirmed that the nest of *L. curvirostris* "possesses, like that of the junquero *Ph[leocryptes] melanops*, a 3 cm projection or eave above the mouth of the entrance" (our translation).

On the other hand, it does seem that the basic nest structure of *Limnornis* and *Phleocryptes* is similar, best exemplified by Narosky's descriptions in Vaurie (1980). *Phleocryptes* presents a presumably more derived condition in covering its nest with mud.

The vast majority of species of Furnariidae have pure white eggs, although the eggs in a few species of *Synallaxis* may have a light bluish, greenish or yellowish cast (Schönwetter & Meise 1967: 12, Sick 1993: 428). In contrast, the eggs of *Limnornis curvirostris* and

TABLE 1. Specimen data and Genbank accession numbers for samples used in the study. Family and subfamily designations are given according to two alternative classification schemes. Acronyms: AMNH = American Museum of Natural History, New York; NRM = Swedish Museum of Natural History; USNM = National Museum of Natural History, Smithsonian Institution; ZMUC = Zoological Museum of the University of Copenhagen.

Species	Classif. by Irestedt <i>et al.</i> (2002, in press)	Classif. by Remsen (2003)	Voucher no.	Cytochrome <i>b</i>	Myoglobin	G3PDH
<i>Cinclodes fuscus</i>	Furnariidae: Furnariinae	Furnariidae: Furnariinae	ZMUC S220	AY590044 ^d	AY590054 ^d	AY590065 ^d
<i>Furnarius cristatus</i>	Furnariidae: Furnariinae	Furnariidae: Furnariinae	NRM 966772	AY064279 ^c	AY064255 ^c	AY590066 ^d
<i>Furnarius leucopus</i>	Furnariidae: Furnariinae	Furnariidae: Furnariinae	ZMUC 125590			
<i>Upucerthia jelskii</i>	Furnariidae: Furnariinae	Furnariidae: Furnariinae	ZMUC S439	AY065700 ^a	AY065756 ^a	
<i>Automolus leucophthalmus</i>	Furnariidae: Furnariinae	Furnariidae: Philydorinae	NRM 937251	AY590048 ^d	AY590058 ^d	AY590078 ^d
<i>Lochmias nematura</i>	Furnariidae: Furnariinae	Furnariidae: Philydorinae	ZMUC S2577	AY065699 ^a	AY065755 ^a	AY590081 ^d
<i>Philydor atricapillus</i>	Furnariidae: Furnariinae	Furnariidae: Philydorinae	NRM 937334	AY065702 ^a	AY065758 ^a	AY590076 ^d
<i>Thripadectes flammulatus</i>	Furnariidae: Furnariinae	Furnariidae: Philydorinae	ZMUC S428	AY065701 ^a	AY065757 ^a	AY590077 ^d
<i>Anumbius annumbi</i> (*)	Furnariidae: Furnariinae	Furnariidae: Synallaxinae	NRM 966903	AY065709 ^a	AY065765 ^a	AY590072 ^d
<i>Asthenes cactorum</i>	Furnariidae: Furnariinae	Furnariidae: Synallaxinae	ZMUC S150	AY065705 ^a	AY065761 ^a	AY590070 ^d
<i>Coryphistera alaudina</i>	Furnariidae: Furnariinae	Furnariidae: Synallaxinae	NRM 966910	AY065710 ^a	AY065766 ^a	AY590073 ^d
<i>Cranioleuca albicapilla</i>	Furnariidae: Furnariinae	Furnariidae: Synallaxinae	ZMUC 124797			
<i>Cranioleuca pyrrhophia</i>	Furnariidae: Furnariinae	Furnariidae: Synallaxinae	NRM 966821	AY065708 ^a	AY065764 ^a	AY590069 ^d
<i>Cranioleuca sulphurifera</i>	Furnariidae: Furnariinae	Furnariidae: Synallaxinae	USNM B17199			
<i>Synallaxis ruficapilla</i>	Furnariidae: Furnariinae	Furnariidae: Synallaxinae	NRM 956643	AY065707 ^a	AY065763 ^a	AY590068 ^d
<i>Limnocites rectirostris</i>	Furnariidae: Furnariinae	Furnariidae: Synallaxinae	USNM B14895			
<i>Limnornis curvirostris</i>	Furnariidae: Furnariinae	Furnariidae: Synallaxinae	USNM B2735			
<i>Phleocryptes melanops</i>	Furnariidae: Furnariinae	Furnariidae: Synallaxinae	USNM B2734			
<i>Geositta tenuirostris</i>	Furnariidae: Sclerurinae	Furnariidae: Furnariinae	ZMUC S292	AY590043 ^d	AY590053 ^d	AY590063 ^d
<i>Sclerurus scansor</i>	Furnariidae: Sclerurinae	Furnariidae: Philydorinae	NRM 937258	AY065715 ^a	AY065772 ^a	AY590080 ^d
<i>Drymornis bridgesii</i>	Furnariidae: Dendrocolaptinae	Dendrocolaptidae	NRM 966930	AY065711 ^a	AY065768 ^a	AY590088 ^d
<i>Xiphocolaptes major</i>	Furnariidae: Dendrocolaptinae	Dendrocolaptidae	NRM 966847	AY065712 ^a	AY065769 ^a	AY590093 ^d
<i>Dendrocincla tyrannina</i>	Furnariidae: Dendrocolaptinae	Dendrocolaptidae	NRM 976662	AY065713 ^b	AY065770 ^b	AY590087 ^d
<i>Sittasomus griseicapillus</i>	Furnariidae: Dendrocolaptinae	Dendrocolaptidae	NRM 967031	AY065714 ^a	AY065771 ^a	AY590092 ^d
<i>Chamaeza meruloides</i>	Formicariidae	Formicariidae	ZMUC S2053	AY065718 ^a	AY065776 ^a	AY590095 ^d
<i>Pteroptochos tarnii</i>	Rhinocryptidae	Rhinocryptidae	AMNH RTC467	AY065717 ^a	AY065774 ^a	AY590096 ^d
<i>Scytalopus spillmanni</i>	Rhinocryptidae	Rhinocryptidae	ZMUC S540	AY065716 ^a	AY065773 ^a	AY590097

References: ^aIrestedt *et al.* (2001), ^bIrestedt *et al.* (in press), ^cEricson *et al.* (2002), ^dFjeldså *et al.* (2005).

Phleocryptes melanops are a deep greenish-blue (Schönwetter & Meise 1967: 12; Vaurie 1980). We reviewed the egg color of at least 32 genera of Furnariidae, mainly based on the collections of the British Museum (Michael Walters, pers. com. to Olson, June 2004) and scattered references in more recent literature and found no exceptions to the preceding observations. Thus, the decidedly greenish blue eggs of *Limnornis curvirostris* and *Phleocryptes* appear to be unique within the Furnariidae, a similarity noticed at least as early as Pereyra (1938).

In contrast, the nest and eggs of *Limnornis rectirostris* have been likened to that of *Craniolenca*. “The [white] eggs and nest more closely resemble those of *C. sulphurifera* than those of *L. curvirostris*, whose eggs are bluish green and the nest [of *L. curvirostris*], although spherical with a lateral entrance, is more conspicuous for being constructed at considerable height (up to 1.6 m), and is without much differentiation between the external material and the lining” (translated from López-Lanús *et al.* 1999: 63).

Within the Furnariidae the white eggs and less elaborate nest of *L. rectirostris* are probably plesiomorphic states, or relatively so in the case of the nest, the apparently unique awninged nest and blue-green eggs of *L. curvirostris* and *Phleocryptes* are derived conditions that argue for a sister-group relationship for these two taxa.

MOLECULAR SYSTEMATICS

Materials and methods. Twenty species of ovenbirds and four woodcreepers were selected for the molecular analysis. In addition to *Limnornis* and *Limnornites*, we included representatives of all major clades of furnariids identified by Fjeldså *et al.* (2005), as well as the genera *Sclerurus* and *Geositta*, which form the sister group to a clade consisting of all the other ovenbirds (called “core ovenbirds”

herein) and the woodcreepers (Irestedt *et al.* 2002, Chesser 2004, Fjeldså *et al.* 2005). Serving as outgroups are three representatives of the proposed sister clade of Furnariidae (Irestedt *et al.*, 2002, Chesser 2004): *Pteroptochos tarnii* and *Scytalopus spillmanni* (family Rhinocryptidae) and *Chamaeza meruloides* (family Formicariidae). Sample identifications and GenBank accession numbers are given in Table 1.

We sequenced the complete myoglobin intron 2 (along with 13 bp and 10 bp of the flanking regions of exons 2 and 3, respectively), the complete glyceraldehydes-3-phosphodehydrogenase (G3PDH) intron 11 (along with 36 bp and 18 bp of exons 11 and 12, respectively), and 999 bp from the cytochrome *b* gene (see Ericson *et al.* 2002, Irestedt *et al.* 2002, and Fjeldså *et al.* 2003, 2004, for primer sequences and procedures). Positions where the nucleotide could not be determined with certainty were coded with the appropriate IUPAC code. Due to the low number of insertions in the introns, the combined sequences could easily be aligned by eye. All gaps in the myoglobin and the G3PDH sequences were treated as missing data in the analyses. No insertions, deletions, stop or nonsense codons were observed in any of the cytochrome *b* sequences.

ModelTest 3.06 (Posada & Crandall 1998) in conjunction with PAUP* (Swofford 1998) was used to evaluate the fit of the data to different models for nucleotide substitutions. The GTR+I+ Γ model has the best fit for the combined data set and for the cytochrome *b* partition, while GTR+G was selected for both the myoglobin intron 2 and the G3PDH intron 11 partitions. These models were used in the analyses of the individual genes, as well in the analysis of the combined data set. The posterior probabilities of trees and parameters in the substitution models were approximated with Markov chain

TABLE 2. Descriptive statistics for the observed pairwise, uncorrected sequence divergencies (p-distances) between selected groups of taxa. Larger distances suggest higher rates of nucleotide substitutions.

	Cytochrome <i>b</i>			Myoglobin intron 2			G3PDH intron 11		
	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
Within core ovenbirds	12.63	2.4	15.62	2.3	0.29	3.62	5.16	0.76	7.73
Core ovenbirds vs woodcreepers	14.53	12.21	17.12	4.17	2.96	5.16	6.84	4.59	8.83
Core ovenbirds vs <i>Sclerurus</i> / <i>Geositta</i> -clade	15.57	13.51	18.12	3.77	2.8	4.92	7.71	4.53	9.63
Core ovenbirds vs Outgroups	17.7	15.84	20.32	7.09	5.67	8.6	9.31	6.68	11.54

Monte Carlo and Metropolis coupling using the program MrBayes (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003).

We ran two analyses of 500,000 generations for each gene with trees sampled every 100 generation. The parameter estimates from the two separate MCMC runs for each data set were compared and found to be very similar, thus allowing an inference from the concatenated output. Posterior probabilities for the individual genes were based on a total of 9000 trees saved after discarding the trees saved during the “burnin phase” (as estimated graphically) in each analysis. The analysis of the combined data set was conducted in the same manner as for the individual genes except that the number of generations in each run was two millions. The 50% majority-rule consensus trees were identical in the runs and the posterior probabilities are based on a total of 390,000 saved trees.

Results. The concatenated sequences became 2164 basepairs long after alignment. Within the ingroup (all ovenbirds and woodcreepers) the lengths of the myoglobin sequences range from 677 in *Philydor* to 701 bp in *Geositta*, and the lengths of the G3PDH sequences range from 349 in *Dendrocincla* to 401 bp in *Xiphocolaptes*. The myoglobin intron is the least variable among the three genetic markers studied herein (Table 2). The observed substitution rate is larger in the mitochondrial cytochrome *b* gene, in accordance with previous studies (Irestedt *et al.* 2004). The alignment of the

myoglobin intron 2 and G3PDH intron 11 sequences requires postulation of a few insertions and deletion events (indels) among the core ovenbirds, most of which involve only a single basepair (singletons) and/or are found only in a single taxon (autapomorphic).

The phylogenetic trees obtained from the Bayesian analyses of the individual genetic markers, as well as of the combined data set, are generally similar (Figs 1A-C and 2). The analyses also agree well on the systematic positions of *Limmornis* and *Limnoctites*, which clearly are not sister taxa. Most major groupings of ingroup taxa are recovered by all data partitions and receive generally high supports (Table 3). Monophyly of the ingroup is strongly corroborated, as is the basal position of *Geositta* and *Sclerurus* relative to the core ovenbirds and woodcreepers, which in turn are recovered as sister groups. All data partitions except cytochrome *b* also support a basal position among the core ovenbirds of a clade consisting of *Automolus*, *Thripadectes* and *Philydor*. Although the cytochrome *b* data set also recognizes monophyly of this clade, it leaves the group unresolved in relation to the other core ovenbirds. The remaining core ovenbirds are divided into two clades that receive strong support in the analyses of most data partitions. *Limmornis* groups with *Phleocryptes* with 100% posterior probabilities in the analyses of both myoglobin and the genes combined. The analyses of cytochrome *b* and G3PDH also suggest a *Limmornis*-*Phleocryptes* clade, albeit with weaker support.

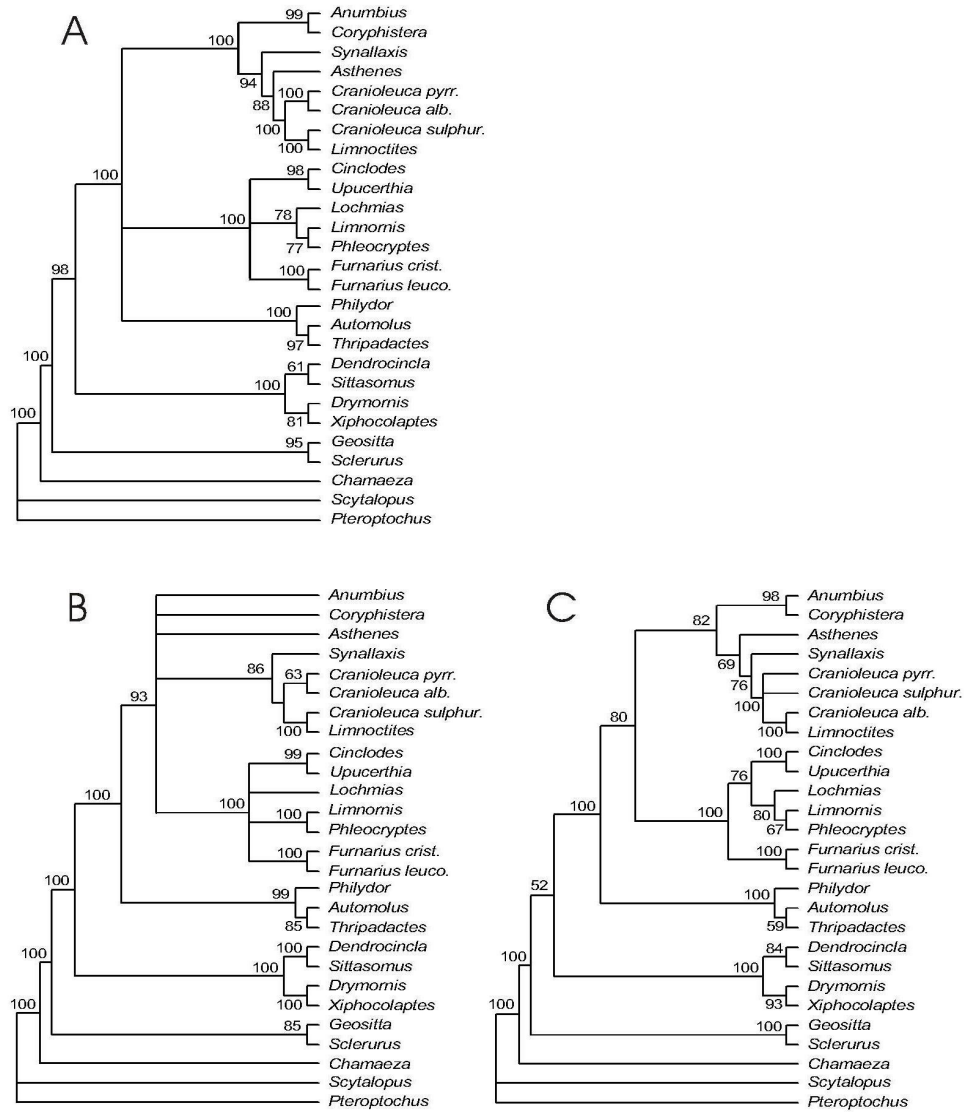


FIG. 1. Majority-rule consensus trees obtained from Bayesian analyses of three genetic markers: A. cytochrome *b*, B. myoglobin intron 2, C. glyceraldehydes-3-phosphodehydrogenase (G3PDH) intron 11. Posterior probabilities are indicated at the nodes.

Cinclodes, *Lochmias*, *Upucerthia* and the two species of *Furnarius* are the other members of this larger group of core ovenbirds. The other group consists of the three species of *Cranioleuca*, *Limnocites*, *Synallaxis*,

Asthenes, *Anumbius* and *Coryphistera*. *Limnocites* falls well within the *Cranioleuca* clade, but it groups with different species of *Cranioleuca* depending on which genetic marker is studied.

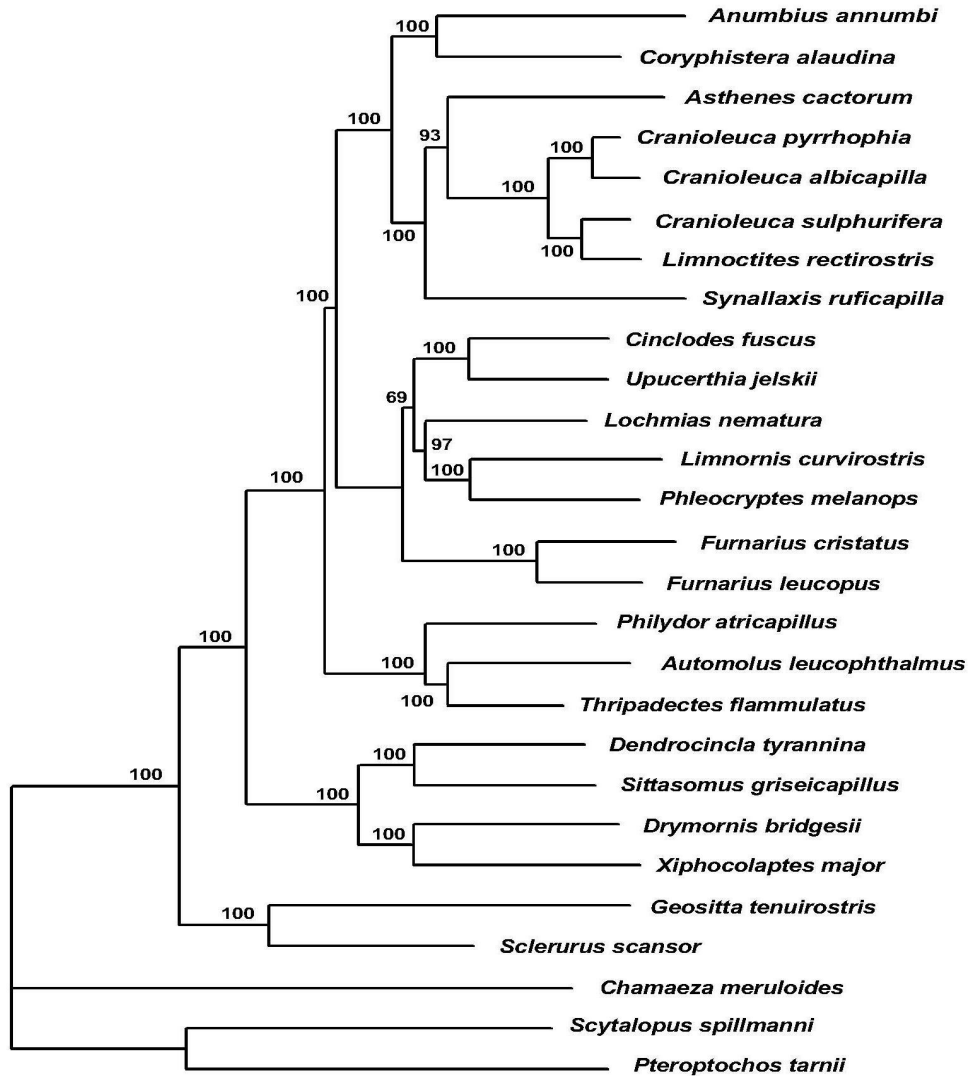


FIG. 2. Maximum-likelihood tree calculated from the combined data set (cytochrome *b*, myoglobin intron 2 and glyceraldehydes-3-phosphodehydrogenase intron 11). Posterior probabilities from the Bayesian analysis are indicated at the nodes.

DISCUSSION

DNA sequence data unambiguously show that *Limnornis curvirostris* and *Limnocites rectirostris* are not particularly closely related. *Limnocites* falls out among the species of *Cranioleuca*

and within the sample we tested was closest to the Sulphur-throated Spinetail *C. sulphurifera*. This is another marsh-inhabiting species with a distribution similar to the two reedhaunters, except that it also occurs farther inland and to the south in Argentina (Remsen 2003). As

TABLE 3. Posterior probabilities for selected nodes obtained in analyses of different data partitions.

	Combined data set	Cytochrome <i>b</i>	Myoglobin intron 2	G3PDH 11
Monophyly of Furnariidae (ovenbirds and woodcreepers)	100%	100%	100%	100%
Basal position of a <i>Sclerurus</i> / <i>Geositta</i> -clade	100%	98%	100%	90%
Monophyly of core-ovenbirds	100%	100%	100%	100%
Basal position of <i>Automolus</i> , <i>Tbripadectes</i> and <i>Philydor</i> among core-ovenbirds	100%	No support, but no contradiction	92%	93%
Monophyly of a <i>Cranioleuca</i> spp. and <i>Limnoscites</i> clade	100%	99%	100%	100%
Sister group relationship between <i>Limnoscites</i> and <i>Cranioleuca sulphurifera</i>	100%	100%	100%	Alternative tree topology suggested
Sister group relationship of <i>Limnornis</i> and <i>Phleocryptes</i>	100%	76%	100%	61%

recounted above, Esteban (1949) advocated putting *Limnoscites* in the Synallaxinae. Gerzenstein & Acheval (1967), followed by Ricci & Ricci (1984), noted its general similarity in appearance to *Cranioleuca sulphurifera*. López-Lanús *et al.* (1999) concurred and also considered that the vocalizations, nest, and eggs of *Limnoscites* were more similar to *C. sulphurifera* than to *Limnornis curvirostris*.

In the straight bill and in tail and rectrix shape, *Limnoscites* agrees better with *Cranioleuca* than with *Limnornis*. The juvenal plumage of *C. sulphurifera*, which lacks the breast streaks and yellow throat of the adult, is like that of *Limnoscites* in every respect except for its rufous and black pattern in the wing.

Similarities extend to vocalizations as well. “*L. rectirostris* gives a hissing trill Ti-ti-ti-tititritriiiii, accelerating at the end. This is maintained at a stable frequency of between 4 and 6.5 kHz, lasting about 2.5 and 3.5 s, composed of 14 to 18 elements, varying up to 22 The territorial advertising vocalization of this species is well differentiated from that of *L. curvirostris*, whose song sounds rough and faltering. On the other hand, it could be confounded by an untrained ear with that of *C.*

sulphurifera, which gives a vocalization of similar length (between 2.5 and 3.5 s) but with a wider frequency range (between 1 and 6.5 kHz) and a greater and more complex quantity of elements” (translated from López-Lanús *et al.* 1999: 62).

In our molecular phylogeny *Limnornis* is well separated from *Limnoscites* and its closest relative among the taxa we sampled is the Wren-like Rushbird *Phleocryptes melanops*, with the Sharp-tailed Streamcreeper *Lochmias nematura* as the closest outlying sister group. There is nothing in the external morphology of these three genera that suggests a particularly close relationship. An obligate inhabitant of streams in dense forests (Remsen 2003), *Lochmias* differs strikingly from the other two in its habits.

Phleocryptes, like *Limnornis*, inhabits marshy reedbeds and the two may occur together in the same marsh, although *Phleocryptes* is much more widely distributed, from Pacific Ecuador to Chile and east across parts of Bolivia, Paraguay, most of Argentina, Uruguay and southern Brazil (Remsen 2003). It is a smaller bird with a much more variegated plumage than *Limnornis*. Apart from DNA sequences,

the best evidence for a relationship between these two genera comes from the nests and eggs, as outlined above.

CONCLUSIONS

The available molecular, morphological, and behavioral data all indicate that *Limnoides rectirostris* belongs among the species currently included in the genus *Craniolenca*, within which it appears to be most closely related to another marsh-dwelling species, *C. sulphurifera*. Thus it appears possible that *Limnoides rectirostris* may be a large, paedomorphic (in plumage) derivative of *C. sulphurifera* that moved out of reedbeds and became adapted to marshes of *Eryngium*, where its long, straight bill is possibly an adaptation for extracting prey from the spiny rosettes of that plant, as suggested by Ricci & Ricci (1984).

It would be premature, however, to make any taxonomic or nomenclatural recommendations until the systematics of the entire genus *Craniolenca* has been undertaken. Zyskowski & Prum (1999) indicate that there are two distinct groups within *Craniolenca* based on nest structure, which they designate as the *albiceps* group and the *pyrrhophia* group. *Limnoides* and *C. sulphurifera* belong to the *pyrrhophia* group. The type species of *Craniolenca* is *C. albiceps* and there does not seem to be any previously recognized generic name available for the *pyrrhophia* group (Hellmayr 1925). Thus, if this group were to be separated generically from *Craniolenca*, the 8 species now in it would presumably have to take the name *Limnoides*, which would certainly be an ironic turn of events. Another possibility is that *L. rectirostris* and *C. sulphurifera* may be sufficiently distinct as to be separated in *Limnoides*, so that the rest of the *pyrrhophia* group would require a new name.

Our molecular evidence indicates that the previous intimation of a relationship between *Limnornis* and *Pheocryptes* is correct. This

hypothesis is corroborated by the similar nest structure, egg coloration, and to some extent by the similarity in microhabitat. These two taxa otherwise appear to be sufficiently distinct from one another morphologically and molecularly to justify the recognition of separate monotypic genera.

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