

Circumscription of a monophyletic family for the tapaculos (Aves: Rhinocryptidae): in and out

Per G. P. Ericson, Storrs L. Olson, Martin Irestedt, Herculano Alvarenga, Jon Fjeldså

▶ To cite this version:

Per G. P. Ericson, Storrs L. Olson, Martin Irestedt, Herculano Alvarenga, Jon Fjeldså. Circumscription of a monophyletic family for the tapaculos (Aves: Rhinocryptidae): in and out. Journal für Ornithologie = Journal of Ornithology, 2009, 151 (2), pp.337-345. 10.1007/s10336-009-0460-9. hal-00568355

HAL Id: hal-00568355

https://hal.science/hal-00568355

Submitted on 23 Feb 2011

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1	
2	
3	
4	Circumscription of a monophyletic family for the tapaculos
5	(Aves: Rhinocryptidae): Psiloramphus in and Melanopareia out
6	
7	
8	Per G. P. Ericson ^{1, 6} , Storrs L. Olson ² , Martin Irestedt ³ , Herculano Alvarenga ⁴ ,
9	and Jon Fjeldså ⁵
10	
11	
12	
13	
14	
15	¹ Department of Vertebrate Zoology, Swedish Museum of Natural History, P.O. Box
16	50007, SE-10405 Stockholm, Sweden
17	
18	² Division of Birds, Department of Vertebrate Zoology, National Museum of Natural
19	History, P.O. Box 37012, Smithsonian Institution, Washington, D.C. 20013-7012,
20	USA
21	
22	³ Molecular Systematics Laboratorium, Swedish Museum of Natural History, P.O.
23	Box 50007, SE-10405 Stockholm, Sweden
24	
25	⁴ Museu de História Natural de Taubaté, Rua Juvenal Dias de Carvalho, 111, Taubaté
26	SP, CEP 12070–640, Brazil
27	
28	⁵ Zoological Museum, University of Copenhagen, Universitetsparken 15, DK–2100
29	Copenhagen, Denmark.
30	
	⁶ Corresponding author: <u>per.ericson@nrm.se</u> , phone: +46 8 51954117, fax: +46 8
	51954212

ABSTRACT

) [The tapaculos (Rinnocryptidae) are tracheophone, suboscine birds restricted to South
32	and Central America. Most tapaculos share a number of internal and external
33	characteristics that have been used to define the family taxonomically. The genera
34	Melanopareia and Psiloramphus do not fully fit this pattern and have caused
35	considerable dispute among taxonomists since they were first described. In this paper
36	we delimit the systematic boundaries of the tapaculos and assess their generic
37	relationships by an analysis of molecular sequence data. The results show that while
38	Psiloramphus is nested well within the Rhinocryptidae, Melanopareia falls far outside
39	that clade. A new family is erected for Melanopareia.
10	
11	INTRODUCTION
12	The impudently named tapaculos (Rhinocryptidae) are a small group of tracheophone
13	suboscine passerines whose greatest generic diversity is in southern South America.
14	Most are large-footed, strong-legged ground birds reminiscent of some of the ground-
15	dwelling antthrushes (Formicariidae), with which they were often associated. The
16	family is generally well defined by the presence of operculate nostrils, a tracheophone
17	syrinx, a somewhat curved humerus and a four-notched sternum (Ames 1971,
18	Feduccia and Olson 1982, Maurício et al. 2008). Thus, Krabbe and Schulenberg
19	(2003: 748) considered that the "tapaculos constitute a well-knit group the members
50	of which are united by several derived characters. Only the genera Melanopareia and
51	Psiloramphus differ to such a degree that their systematic position as tapaculos could
52	be disputed." Furthermore, the phylogenetic relationships within the family
53	Rhinocryptidae are poorly known, particularly regarding the placement of Liosceles
54	and Acropternis, and the large austral species of Pteroptochos and Scelorchilus.
55	The early taxonomic history of the group was ably summarized by Sclater
56	(1874). d'Orbigny (1837) first erected a family "Rhinomyidaeae" (sic., p. 192) for
57	Pteroptochos and his Rhinomya (= Rhinocrypta) using the operculate nostril to
58	separate them from the Formicariidae. However, there was no coherent understanding
59	of the suboscine groups until their distinction from the oscines was established by the
50	pioneering work of Müller (1847) on the syrinx, Müller showed that Scytalopus was a
51	tracheophone suboscine and not a wren (Troglodytidae) and also that Scytalopus and
52	Pteroptochus differed from other known passerines in having a 4-notched sternum.

63 Sclater's (1874) "Pteroptochidae" comprised Scytalopus (including the type 64 species of what later became Myornis Chapman, 1915), Merulaxis, Liosceles, 65 Pteroptochos (including the type species of what later became Teledromas Wetmore 66 and Peters, 1922, and Scelorchilus Oberholser, 1923), Rhinocrypta, Hylactes (now 67 included in *Pteroptochos*), *Acropternis*, and *Triptorhinus* (=Eugralla). This 68 composition of the group was essentially maintained until Peters (1951), except for 69 the problem genera Psiloramphus and Melanopareia. 70 The three or four species of *Melanopareia* differ from other tapaculos by their 71 rather slender build and boldly and attractively patterned plumage, and by sharing a 72 semi-concealed white dorsal patch with various true antbirds (Thamnophilidae). They 73 were originally described in the genus Synallaxis (Furnariidae), in which Sclater 74 (1890) later submerged the genus. Salvin (1876) described a new species from 75 Ecuador as Formicivora speciosa, duly recognized in that combination by Sclater 76 (1890:251) and others until Hellmayr (1906:334) showed that this was a synonym of 77 Synallaxis elegans Lesson, in which genus Hellmayr continued to place it while 78 regarding Salvin's allocation of it to *Formicivora* with incredulity. Ridgway (1909) 79 appears to have overlooked this when he created a new genus Rhoporchilis for 80 Formicivora speciosa. It was Hellmayr (1921) who eventually established the modern 81 concept of the genus in showing that Synallaxis elegans, S. torquata, and S. 82 maximiliani were congeneric and would all fall under Reichenbach's earlier generic 83 name *Melanopareia* and "find their natural place in the Formicariidae", where they 84 stayed for only a few years (e.g. Cory and Hellmayr 1924). Next came the observation 85 of W.D.W. Miller that the sternum of *Melanopareia* was 4-notched – information that 86 was conveyed to and presented by Wetmore (1926: 292). On this basis, Peters (1951) 87 included *Melanopareia* in the Rhinocryptidae, where it has resided since. 88 The other problem species, the Bamboo-wren *Psilorhamphus guttatus*, is a 89 small bamboo specialist with a rather long, slender bill, a long tail and relatively weak 90 feet, so that it bears little resemblance to large-footed terrestrial tapaculos (Fig. 1). 91 From the beginning (Ménétriés 1835), it was placed with the antibreds in the 92 Myiotherinae (=Formicariidae). Sclater (1858:243) associated Psilorhamphus with 93 Ramphocaenus (which is now in the oscine family Polioptilidae) in the Formicariidae 94 with the comment that these genera "might perhaps be more naturally placed as a 95 distinct subfamily of Pteroptochidae [=Rhinocryptidae]" despite the fact that "there is

little external difference between the appearance of these birds and the true Wrens

97	[Troglodytidae]". We are not aware, however, of any instance in which
98	Psilorhamphus was placed in either the Troglodytidae or in a family with only
99	sylviid-like genera, as might be inferred from Krabbe and Schulenberg (2003).
100	Psilorhamphus continued to be associated with Ramphocaenus in the Formicariidae -
101	e.g. Sclater (1890) and Cory and Hellmayr (1924:205) – although in the latter
102	reference it was noted that W.D.W. Miller would show Psilorhamphus and
103	Ramphocaenus to "constitute a separate family" in "a paper shortly to be published."
104	Peters (1951: 213) later explained that Miller's death prevented publication of his
105	results but that Wetmore (1943:306) had shown Ramphocaenus to have an oscine
106	syrinx, and had told Peters that Microbates likewise was oscine and that he thought
107	based on external morphology that Psilorhamphus was also probably oscine.
108	Therefore, Peters postponed his treatment of those genera for a future volume treating
109	Sylviidae. Sick (1954) placed Ramphocaenus in the Sylviidae while provisionally
110	referring Psilorhamphus to the Formicariidae. Then, Plótnick (1958) revealed that
111	Psilorhamphus had a 4-notched sternum, a tracheophone syrinx, and had other
112	characters, including an operculate nostril, indicating that it should be placed in the
113	Rhinocryptidae. Thus, in Peters' Checklist Psilorhamphus appears as an addendum to
114	the Rhinocryptidae that appeared in the volume on Sylviidae (Paynter 1964).
115	Heimerdinger and Ames (1967) confirmed that the rhinocryptids they
116	examined all had a 4-notched sternum but also showed that this condition obtained in
117	at least two genera of grallarine Formicariidae, which was confirmed by Feduccia and
118	Olson (1982).
119	Ames (1971) made a thorough study of the anatomy of the syrinx in passerine
120	birds and examined Melanopareia first-hand but had to rely on the description of
121	Plótnick (1958) for <i>Psilorhamphus</i> . Although he noted that the cartilaginous elements
122	of Melanopareia differed from all other tapaculos examined, he found no grounds for
123	excluding either Melanopareia or Psilorhamphus from the Rhinocryptidae.
124	Feduccia and Olson (1982) made the much unexpected discovery that the
125	stapes in Melanopareia was of the primitive oscine type with a flattened footplate,
126	rather than having an expanded, bulbous, fenestrate footplate as in all other suboscine
127	birds. They went on to show other morphological similarities (which is all they ever
128	claimed they were) between some of the Rhinocryptidae and the oscine Menurae
129	(Menura and Atrichornis) of Australia. Although this observation was dismissed on
130	the grounds that the characters involved are either primitive or convergent (Krabbe

131 and Schulenberg 2003), the fact remains that the oscines and suboscines had to share a 132 common ancestor and that the ancestor very likely looked like Atrichornis, 133 *Melanopareia*, or one of the Rhinocryptidae such as *Scelorchilus*. 134 This paper aims to delimit the boundaries of the tapaculos and assess generic 135 relationships within the group, supplementing the very detailed ongoing studies of relationships and speciation of small tapaculos (notably Scytalopus; Maurício et al. 136 137 2008, Cadena et al. unpublished) by providing a broader phylogenetic framework for 138 the family. 139 140 MATERIALS AND METHODS 141 Taxon sampling, amplification and sequencing 142 This study includes representatives of all genera traditionally recognized in 143 Rhinocryptidae (e.g. Ridgely and Tudor 1994, Krabbe and Schulenberg 2003), 144 including representatives of the large genus Scytalopus, including one representative 145 (indigoticus) of the "blue" species, which were recently placed in a separate genus 146 Eleoscytalopus (Maurício et al. 2008). Three of the authors have significant field 147 experience concerning the biology and vocalizations of tapaculos, and this was 148 supplemented with comments and analyses of sound archives by Niels Krabbe (pers. 149 comm.). Representatives of the main lineages within the tracheophone radiation serve 150 as outgroups (Ridgely and Tudor 1994, Irestedt et al. 2002, Krabbe and Schulenberg 151 2003, Chesser 2004). 152 Three nuclear gene regions, myoglobin intron 2, ornithine decarboxylase 153 (ODC) introns 6 to 7, and glyceraldehyde-3-phosphodehydrogenase (G3PDH) intron 154 11, were sequenced and used to estimate phylogenetic relationships. For each gene 155 and taxon, multiple sequence fragments were obtained by sequencing with different 156 primers. These sequences were assembled to complete sequences with SEOMAN IITM 157 (DNASTAR Inc.). Positions where the nucleotide could not be determined with 158 certainty were coded with the appropriate IUPAC code. GenBank accession numbers 159 are given in Table 1. See Irestedt et al. (2002), Allen and Omland (2003), and Fjeldså 160 et al. (2003) for extractions, amplifications, and sequencing procedures for fresh 161 tissue/blood samples. Corresponding laboratory procedures for study skins are 162 detailed in Irestedt et al. (2006). 163 164 Phylogenetic inference and model selection

Due to the rather low number of insertions in the introns, the combined sequences could easily be aligned by eye. All gaps have been treated as missing data in the analyses. Bayesian inference (see, e.g., Holder and Lewis 2003; Huelsenbeck et al. 2001) was used to estimate the phylogenetic relationships. The models for nucleotide substitutions used in the analyses were selected for each gene individually by applying the Akaike Information Criterion (AIC, Akaike 1973) and the program MrModeltest 2.2 (Nylander 2005) in conjunction with PAUP* (Swofford 1998).

Posterior probabilities of trees and parameters in the substitution models were approximated with MCMC and Metropolis coupling using the program MrBayes 3.1.1 (Ronquist and Huelsenbeck 2003). Analyses were performed for both the individual gene partitions and the combined data set. In the analysis of the combined data set, the models selected for the individual gene partition were used. The chains for the individual gene partitions were run for 5 million generations while the chains for the combined data set were run for 10 million generations. Trees were sampled every 100th generations, and the trees sampled during the burn-in phase (i.e., before the chain had reached its apparent target distribution) were then discarded after checking for convergence, final inference was made from the concatenated outputs.

Sequence lengths and alignments

We were able to sequence all three gene regions almost completely for all included taxa (a few sequences miss some base pairs in the 3′ or 5′ends in the myoglobin or the ODC regions, and in the ODC region all sequences obtained from study skins lack a short fragment of 22 bp in the exon 7). Taking into account the missing base pairs, the sequences obtained varied in length between 667–701 bp for the myoglobin intron 2, and between 313–363 bp for the G3PDH intron 11, except for the two antthrushes *Chamaeza* and *Formicarius* which contains two large deletions in the G3PDH intron 11 which makes these sequences 251–252 bp long. In the ODC region all Rhinocryptidae and Furnariidae taxa have a large deletion in intron 7 and the sequences from these taxa range between 403 and 500 bp, while the sequences for all other taxa range between 586 and 624 bp.

Most indels observed in the introns were autapomorphic and mainly found in certain variable regions. Some indels vary in length between taxa, which makes it difficult to know if these indels are homologous or represent independent evolutionary events. Several apparently synapomorphic indels were also observed when mapping

199 the data onto the tree topology obtained from the Bayesian analyses of the combined 200 data set. A few indels were also found to be incongruent with the phylogenetic tree 201 obtained from the analysis of the combined data set. These were generally found in 202 the most variable regions and some of the single base pair insertions actually consist 203 of different bases. For more details of indel length and positions see the alignments of 204 the individual gene regions deposited at Genbank, accession numbers XX 205 (myoglobin), XX (G3PDH), and XX (ODC). 206 207 Models for nucleotide substitutions 208 The priori selection of nucleotide substitution models suggested that the GTR + Γ 209 model had the best fit for all three gene regions, but as the nucleotide state frequencies 210 and gamma distribution differed between the partitions we applied a partitioned 211 analysis of the combined data set. After discarding the burn-in phase the inference for 212 myoglobin and G3PDH were based on a total of 45,000 samples from the posterior, 213 the inference for ODC were based on a total of 40,000 samples, while the inference 214 for the combined data set were based on a total of 95,000 samples. The posterior 215 distribution of topologies is presented as a majority-rule consensus tree from the 216 combined analysis in Figure 2. 217 218 **RESULTS** 219 The trees obtained from the Bayesian analyses of the individual gene partitions (Fig. 220 3) are overall topologically congruent. *Melanopareia* clusters with Thamnophilidae 221 and Conopophagidae and we can therefore reject it as a member of the family 222 Rhinocryptidae with high confidence. Apart from this, all traditional tapaculo genera 223 form a monophyletic clade within a broader group which also contains Formicariidae 224 sensu stricto and Furnariidae, in agreement with previous molecular studies of 225 tracheophone suboscines (Irestedt et al. 2002, Chesser 2004). 226 Within the radiation of tapaculos there is also good support for two major 227 clades. Clade 1 includes Teledromas, Acropternis, Rhinocrypta, Liosceles and 228 Psilorhamphus and Clade 2 includes Scytalopus, Eugralla, Myornis, Merulaxis and 229 *Eleoscytalopus*. The only conflict within the rhinocryptid radiation supported by 230 posterior probabilities above 0.95 involves determining to which of the previous two clades *Pteroptochos* and *Scelorchilus* belong. In the ODC tree they group with Clade 231 232 1 (0.97), whereas the myoglobin tree indicates that these two taxa are sister to the

Clade 2 (1.00). In the G3PDH tree this relationship is unresolved. Based on the overall congruence of the individual gene trees we believe that the tree obtained from the combined analysis (Fig. 2) represents the best estimate of the phylogenetic relationship of the tapaculos and in this *Pteroptochos* and *Scelorchilus* fall out as sister to Clade 2. This tree is fully congruent with the results of studies using other genetic markers, but with focus on detailed relationships within Clade 2 (Maurício et al. 2008 and Cadena et al., unpublished).

DISCUSSION

Melanopareia resembles members of the Rhinocryptidae in having the lacrimal bones partly fused with the ectethmoid (but the lacrimals are lacking in Conopophagidae, Thamnophilidae, Grallaridae and Formicariidae) and in having a 4-notched sternum. The significance of these characters is uncertain because of the weak cranial ossification in these groups and a considerable flexibility (including varying degrees of developmental asymmetry) in the degree of ossification of the membranes serving as attachment of pectoral muscles (Heimerdinger and Ames 1967). The molecular data reject a close relationship of Melanopareia to the Rhinocryptidae. With four closely related extant species, Melanopareia represents a long, unbroken phylogenetic branch, and it may be difficult to tell with confidence whether this clade is nested within the Conopophagidae-Thamnophilidae complex or represents a relictual, basal tracheophone type of bird.

Irestedt et al. (2002) associated *Teledromas* with *Melanopareia* primarily because their vocalizations are confusingly similar, and *Teledromas* was considered to resemble a robust and pale version of *Melanopareia*. Both genera are reported to share a peculiarity of the pterylography of the flank region, and details of the nasal operculum and tarsal scutellation, and an X-ray photo suggested almost straight humeri (approaching those of *Melanopareia*; Irestedt et al. 2002). However, our DNA data and further examination of skeletal characters reject a closer relationship between them and places *Teledromas* centrally in Clade 1 of the Rhinocryptidae.

Psilorhamphus was placed with Polioptiline oscines based on the acutiplantar tarsus, but a similar tarsal scalation is also found in some antbirds, and osteology and syringeal morphology suggested placement with Rhinocryptidae. We were able to confirm from examination of skeletal specimens that *Psilorhamphus* – as well as

Teledromas – have the expanded footplate of the stapes typical of other suboscines (except *Melanopareia*).

The distinctive appearance of *Psilorhamphus* may result from its divergent habits (albeit shared with *Myornis*, N. Krabbe pers. comm.), as it generally feeds by climbing in tangles of vine-like bamboo, occasionally up to 7 m, and it rarely feeds on the ground. This species is also known for its unbelievably loud and low-pitched vocalizations (for its small size, 13.5 cm): A fast series of hollow whistles at 0.9–1 kHz. Its sister taxon in Figure 2, *Liosceles*, also gives hollow whistles, but they are higher pitched (1.3 kHz) and are given at a slower pace; the pace and quality of the song notes of *Psilorhamphus* is most like the songs of larger species of *Pteroptochos*, which are even lower pitched (0.5–0.6 kHz). Interestingly, *Psilorhamphus* shares with *Liosceles* barred posterior underparts and distinctive whitish subterminal spots with a black outline on the middle and greater wing-coverts. Apart from this, it is difficult to see any external features supporting the suggested relationships within Clade 1.

The possible association of the large Chilean tapaculos (*Pteroptochos*, *Scelorchilus*) with Clade 2 receives some morphological support, as *Pteroptochos* has 14 rectrices, something that is also found in some species or individuals of *Scytalopus*, although other representatives of this genus have a reduced number of rectrices or asymmetrical tails (Krabbe and Schulenberg 2003). Other suboscine birds typically have 12 rectrices, although there are many cases of reduction. Molecular relationships within *Pteroptochos* have been analyzed by Chesser (1999).

Within Clade 2, the *Myornis-Eugralla-Scytalopus* group is particularly well defined morphologically by small size and sooty-grey to blackish plumage and atrophied clavicles, which do not form a fused furcula (Maurício et al. 2008). This may reflect reduced flying ability of these specialized birds, which tunnel through the densest parts of the forest understorey. *Myornis* bears some resemblance to *Merulaxis*, in shape and juvenile plumage (Krabbe and Schulenberg 2003), but our result does not support such an association. On the other hand, *Myiornis* and *Eugralla* clearly fall outside the group of species of *Scytalopus* that we studied (except with G3PDH) and we therefore support keeping them in separate monotypic genera.

Under "Incertae sedis", Irestedt et al. (2002) introduced a family "Melanopareiidae (new family, incl. *Melanopareia* and *Teledromas*)" and this family name has been accepted by SACC (Proposal #239, 2006). These sources, however, did not meet the requirements of the International Code of Zoological Nomenclature

300	(ICZN 1999) as it lacked any description purporting to differentiate the taxon from
301	other taxa, so the name was invalid at that point. The need still remains for separate
302	family status for the genus, which we re-propose here:
303	
304	Melanopareiidae, new family
305	Type and only included genus: Melanopareia Reichenbach, 1853.
306	Diagnosis: Tracheophone suboscine passeriformes differing from other
307	Tracheophonae except Rhinocryptidae (and a few other taxa: Myrmothera, Hylopezus,
308	Pittasoma, Conopophaga) in having a 4-notched sternum and differing from the
309	Rhinocryptidae and all other suboscines in retaining the primitive morphology of the
310	stapes, with a flat, rather than inflated footplate.
311	
312	Zusammenfassung
313	
314	Umschreibung einer monophyletischen Familie für die Bürzelstelzer (Aves:
315	Rhinocryptidae): Psiloramphus rein und Melanopareia raus
316	
317	Die Bürzelstelzer (Rhinocryptidae) sind tracheophone, suboscine Vögel, deren
318	Vorkommen auf Süd- und Mittelamerika beschränkt ist. Die meisten Bürzelstelzer
319	haben eine Reihe innerer und äußerer Merkmale gemeinsam, die benutzt worden sind,
320	um die Familie taxonomisch zu definieren. Die Gattungen Melanopareia and
321	Psiloramphus passen nicht vollständig in dieses Schema und haben zu beträchtlichen
322	Disputen unter Taxonomen geführt, seit sie erstmals beschrieben worden sind. In
323	diesem Artikel stecken wir die systematischen Grenzen der Bürzelstelzer ab und
324	bewerten ihre Gattungsbeziehungen mit Hilfe einer Analyse molekularer
325	Sequenzdaten. Die Ergebnisse zeigen, dass Melanopareia weit aus dieser Klade
326	herausfällt, während Psiloramphus gut in die Rhinocryptidae hineinpasst. Eine neue
327	Familie wird für Melanopareia eingerichtet.
328	
329	
330	Acknowledgements
331	Our thanks go especially to those researchers who, for years, and often with very
332	small economic means, have collected the specimens and tissue samples without
333	which studies like this could not be made. N. Krabbe is thanked for comments to the

334	manuscript. E. Endrigo kindly provided the photo of <i>Psilorhamphus</i> . The following
335	institutions provided samples that have been included in the study: Zoological
336	Museum of Copenhagen University, Swedish Museum of Natural History, National
337	Museum of Natural History, American Museum of Natural History and Field Museum
338	of Natural History. The Swedish Research Council provided financial support for the
339	laboratory work (grant no. 621–2007–5280 to PE).
340	
341	REFERENCES
342	Akaike H (1973) Information theory as an extension of the maximum likelihood
343	principle. In: Petrov BN, Csaki F (eds) Second international symposium on
344	information theory. Akademini Kiado, Budapest, pp 267-281
345	Allen ES, Omland KE (2003) Novel intron phylogeny (ODC) supports plumage
346	convergence in orioles (Icterus). Auk 120:961-969
347	Ames PL (1971) The morphology of the syrinx in passerine birds. Bull Peabody Mus
348	Nat Hist 37:1–194
349	Chapman FL (1915) The more northern species of the genus Scytalopus Gould. Auk
350	32:406–423
351	Chesser RT (1999) Molecular systematics of the rhinocryptid genus <i>Pteroptochus</i> .
352	Condor 101:439–446
353	Chesser RT (2004) Molecular systematics of New World Suboscine birds. Mol Phyl
354	Evol 32:11–24
355	Cory CB, Hellmayr CE (1924) Catalogue of birds of the Americas and adjacent
356	islands. Part III. Field Mus Natural Hist Zool Ser 13:1–369
357	Ericson PGP, Christidis L, Irestedt M, Norman JA (2002) Systematic affinities of the
358	lyrebirds (Passeriformes: Menura), with a novel classification of the major
359	groups of passerine birds. Mol Phyl Evol 25:53-62
360	Ericson PGP, Johansson US (2003) Phylogeny of Passerida (Aves: Passeriformes)
361	based on nuclear and mitochondrial sequence data. Mol Phyl Evol 29:126–138
362	Ericson PGP, Zuccon D, Ohlson JI, Johansson US, Alvarenga H, Prum RO (2006)
363	Higher level phylogeny and morphological evolution of tyrant flycatchers,
364	cotingas, manakins and their allies (Aves: Tyrannida). Mol Phyl Evol 40:471-
365	483

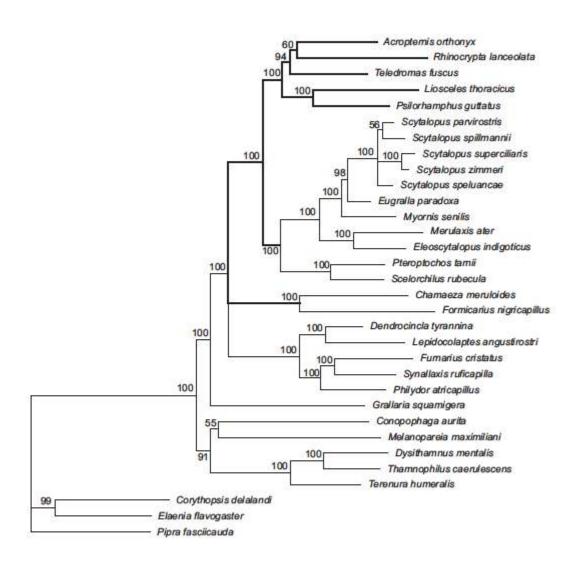
300	Feduccia A, Olson, SL (1982) Morphological similarities between the Menurae and
367	the Rhinocryptidae, relict passerine birds of the Southern Hemisphere.
368	Smithson Contr Zool 366:1–22
369	Fjeldså J, Irestedt M, Ericson PGP (2005) Molecular data reveal some major
370	adaptational shifts in the early evolution of the most diverse avian family, the
371	Furnariidae. J Ornith 146:1–13
372	Fjeldså J, Irestedt M, Jönsson KA, Ohlson JI, Ericson PGP (2007) Phylogeny of the
373	ovenbird genus Upucerthia: a case of independent adaptations for terrestrial
374	life. Zool Scr 36:133–141
375	Fjeldså J, Zuccon D, Irestedt M, Johansson US, Ericson PG (2003) Sapayoa aenigma:
376	a New World representative of 'Old World suboscines'. Proc R Soc Lond B.
377	[Suppl] 270:238–241
378	Heimerdinger MA, Ames PL (1967) Variation in the sternal notches of suboscine
379	passeriform birds. Postilla 105:1–44
380	Hellmayr CE (1906) Critical notes on the types of little-known species of Neotropical
381	birds. Novitates Zoologicae 13:305–352
382	Hellmayr CE (1921) Review of the birds collected by Alcide d'Orbigny. Novitates
383	Zoologicae 28:230–276
384	Holder M., Lewis PO (2003) Phylogeny estimation: Traditional and Bayesian
385	approaches. Nat Gen 4:275–284
386	Huelsenbeck J P, Ronquist F, Nielsen R, Bollback JP (2001) Bayesian inference of
387	phylogeny and its impact on evolutionary biology. Science 294:2310-2314
388	International Commission on Zoological Nomenclature (1999) International Code of
389	Zoological Nomenclature, 4th edn. International Trust for Zoological
390	Nomenclature, British Museum (Natural History), and University of California
391	Press.
392	Irestedt M, Fjeldså J, Johansson US, Ericson PGP (2002) Systematic relationships and
393	biogeography of the tracheophone suboscines (Aves: Passeriformes). Mol Phyl
394	Evol 23:499–512
395	Irestedt M, Fjeldså J, Ericson PGP (2004) Phylogeny and morphological plasticity in
396	woodcreepers (Dendrocolaptinae). J Avian Biol 35:280-288
397	Irestedt M, Ohlson JI, Zuccon D, Källersjö M, Ericson PGP (2006) Nuclear DNA
398	from old collections of avian study skins reveals the evolutionary history of
399	the Old World suboscines (Aves, Passeriformes). Zool Scr 35:567-580

400	Krabbe NK, Schulenberg TS (2003) Family Rhinocryptidae (Tapaculos). In: del Hoyo
401	J, Elliott A, Christie DA (eds) Handbook of Birds of the World, vol. 8. Lynx
402	Edicions, Barcelona, pp 748–787
403	Maurício GN, Mata H, Bornschein MR, Cadena CD, Alvarenga H, Bonatto SL (2008)
404	Hidden genetic diversity in Neotropical birds: molecular and anatomical data
405	support a new genus for the "Scytalopus" indigoticus species-group (Aves:
406	Rhinocryptidae). Mol Phyl Evol 49:125-135
407	Ménétriés E (1835) Monographie de la famille des Myiotherinae où sont décrites les
408	espèces qui ornent le Musée de l'Académie Impériale des Sciences. Mémoires
409	de l'Académie Impériale des Sciences de Saint-Petersbourg. Ser. 6, 3 (pt
410	2):443–543
411	Müller J (1847) Über die bisher unbekannten typischen Verschiedenheiten der
412	Stimmorgane der Passerini. Konnig. Akad. Wiss. Berline Abhandl. 71 pp
413	Nylander JAA (2005) MrModeltest v.2.2. Program distributed by the author.
414	Department of Systematic Zoology, Uppsala University, Uppsala
415	Oberholser HC (1923) Note on the generic name Pteroptochos Kittlitz. Auk 40:326-
416	327
417	d'Orbigny AD (1837) Voyage dans l'Amérique Séptentrionale. Vol. 4, part 3,
418	Oiseaux, Strasbourgh: V ^e . Levrault
419	Paynter RA Jr (1964) Family Rhinocryptidae (part). In: Mayr E, Paynter RA Jr (eds)
420	Check-list of Birds of the World. Museum of Comparative Zoology,
421	Cambridge, Massachusetts. p 456
422	Peters JL (1951) Check-list of birds of the world, vol. VII. Museum of Comparative
423	Zoology: Cambridge, Massachusetts.
424	Plótnick R (1958) Posicion [sic] sistemática del género "Psiloramphus"
425	(Rhinocryptidae, Passeriformes). Physis 21:130-136
426	Reichenbach HGL (1853) Handbuch der speciellen Ornithologie, Die Vögel, part 3.
427	Dresden
428	Ridgely RS, Tudor G (1994) The Birds of South America, vol II. Oxford University
429	Press, Oxford
430	Ridgway R (1909) New genera, species, and subspecies of Formicariidae,
431	Furnariidae, and Dendrocolaptidae. Proc Biol Soc Washington 22:69-74
432	Ronquist F, Huelsenbeck JP (2003) MrBAYES 3: Bayesian phylogenetic inference
433	under mixed models. Bioinformatics 19:1572–1574

434	Salvin O (1876) On some new species of birds from western Ecuador. Ibis 6:493-496
435	Sclater PL (1858) Synopsis of the American ant-birds (Formicariidae). Proc Zool Soc
436	Lond 1858:232-254
437	Sclater PL (1874) On the Neotropical species of the family Pteroptochidae. Ibis
438	4:189–206
139	Sclater PL (1890) Catalogue of the birds in the British Museum, vol 15. British
440	Museum, London
441	Sick H (1954) Zur Kenntnis von Ramphocaenus (Sylviidae) und Psilorhamphus
142	(Formicariidae). Bonner Zool. Beitr. 5:179–190
143	Swofford DL (1998) Paup*. Phylogenetic analysis using parsimony (* and other
144	methods), v.4. Sinauer, Sunderland, Mass.
145	Wetmore A (1926) Observations on the birds of Argentina, Paraguay, Uruguay, and
146	Chile. Bull United States Nat Mus 133:1-448
147	Wetmore A (1943) The birds of southern Veracruz, Mexico. Proc United States Nat
148	Mus 93:215–340
149	Wetmore A, Peters JL (1922) A new genus and four new subspecies of American
450	birds. Proc Biol Soc Washington 35:41-46
451	
452	
453	
454	

Figure 1. The bamboo-wren *Psilorhamphus guttatus* bears little external resemblance to typical members of the tapaculo family. With its grey iris, facial expression, bill shape, and wing-coverts with white dots *Psilorhamphus* instead resembles some antbirds (Dysithamnus, Myrmotherula) with which early ornithologists consequently placed it. Unlike other tapaculos *Psilorhamphus* spends most of the time above the ground. Photo: Edson Endrigo. Figure 2. Majority rule consensus tree obtained from the Bayesian analyses of the combined data set (myoglobin intron 2, ODC introns 6 and 7, and G3PDH intron 11). Posterior probability values are indicated at the node. Figure 3. The majority rule consensus trees obtained from the Bayesian analyses of the individual genes. A) myoglobin intron 2; B) ornithine decarboxylase introns 6 to 7; and C) glyceraldehyde-3-phosphodehydrogenase intron 11. Posterior probability values are indicated at the node. **Table 1:** Specimen data and GenBank accession numbers for samples used in the study. Samples vouchered with a study skin are indicated by an asterisk. "TP" indicates that the sample is obtained from toe-pads of an old study skin. Acronyms are AMNH, American Museum of Natural History, FMNH, Field Museum of Natural History, Chigaco, USA; NRM, Swedish Museum of Natural History; USNM, University States National Museum, Washington, USA; ZMUC Zoological Museum of Copenhagen. References: A, Irestedt et al. (2002); B: Ericson et al. (2002); C: Irestedt et al. (2004); D: Ericson & Johansson (2003); E: Fjeldså et al. (2005); F: Ericson et al. (2006); G: Fjeldså et al. (2003); H: Fjeldså et al. (2007).





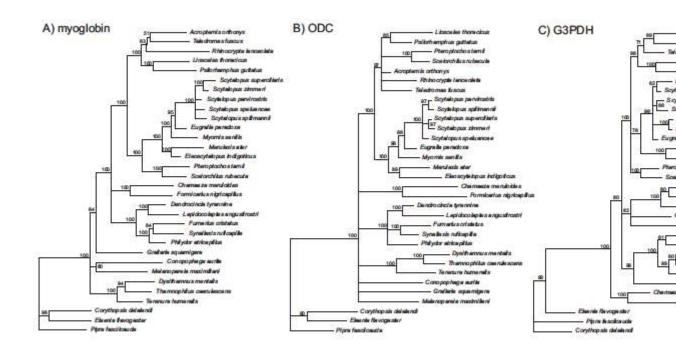


Table 1

Species	Family: Subfamily	Voucher / Sample No.	Myoglobin	G3PDH	ODC
Acropternis orthonyx	Rhinocryptidae	ZMUC 125695 *	new	new	new
Merulaxis ater	Rhinocryptidae	ZMUC 128820	new	new	new
Pteroptochos tarnii	Rhinocryptidae	AMNH RTC467 *	AY065774 A)	AY590096 E)	new
Rhinocrypta lanceolata	Rhinocryptidae	NRM 966793	AY065775 A)	DQ438953 F)	DQ435499 F)
Teledromas fuscus	Rhinocryptidae	USNM BKS3703 *	new	new	new
Psilorhamphus guttatus	Rhinocryptidae	ZMCU? Olson 2005	new	new	new
Myornis senilis	Rhinocryptidae	ZMUC 134967 *	new	new	new
Scytalopus parvirostris	Rhinocryptidae	ZMCU 128441	new	new	new
Scytalopus speluancae	Rhinocryptidae	ZMCU 128818	new	new	new
Scytalopus spillmannii	Rhinocryptidae	ZMUC 125091 *	AY065773 A)	AY590097 E)	new
Scytalopus zimmeri	Rhinocryptidae	ZMUC 126278 *	new	new	new
Scytalopus superciliaris	Rhinocryptidae	USNM BKS 3592 *	new	new	new
Eugralla paradoxa	Rhinocryptidae	NRM 570026 *, TP	new	new	new
Scelorchilus rubecula	Rhinocryptidae	NRM 570029 *, TP	new	new	new
Liosceles thoracicus	Rhinocryptidae	NRM 570027 *, TP	new	new	new
Eleoscytalopus indigoticus	Rhinocryptidae	NRM 570028 *, TP	new	new	new
Melanopareia maximiliani	Rhinocryptidae	ZMUC 125045 *	AY065785 A)	new	new
Furnarius cristatus	Furnariidae: Furnariinae	NRM 966772 *	AY064255 B)	AY590066 E)	DQ435482 F)
Philydor atricapillus	Furnariidae: Furnariinae	NRM 937334 *	AY065758 A)	AY590076 E)	EF212110 H)
Synallaxis ruficapilla	Furnariidae: Furnariinae	NRM 956643 *	AY065763 A)	AY590068 E)	EF212119 H)
Lepidocolaptes angoustirostris	Furnariidae: Dendrocolaptinae	NRM 937184 *	AY065767 A)	AY336576 G)	DQ435486 F)
Dendrocincla tyrannina	Furnariidae: Dendrocolaptinae	ZMUC 125661 *	AY442959 C)	AY590087 E)	EF212098 H)
Chamaeza meruloides	Formicariidae	ZMUC 126604 *	AY065776 A)	AY590095 E)	new
Formicarius nigricapillus	Formicariidae	ZMUC 125987 *	AY065777 A)	new	new
Grallaria squamigera	Grallariidae	ZMUC 124629 *	AY065778 A)	AY677078 C)	new
Dysithamnus mentalis	Thamnophilidae	NRM 956629 *	AY676995 C)	AY677042 C)	new
Terenura humeralis	Thamnophilidae	FMNH 389941	AY677004 C)	AY677051 ^{C)}	new
Thamnophilus caerulescens	Thamnophilidae	NRM 967007 *	AY065783 A)	AY336587 G)	DQ435504 F)
Conopophaga aurita	Conopophagidae	ZMUC 125796 *	AY065784 A)		DQ435478 F)
Conopophaga lineata	Conopophagidae	NRM 956653 *		AY336577 G)	
Pipra fasciicauda	Pipridae	NRM 947271 *	AY065787 A)	AY336583 ^G)	DQ435495 F)
Corythopsis delalandi	Tyrannidae	NRM 937282 *	AY065788 A)	DQ435463 ^{F)}	DQ435479 F)
Elaenia flavogaster	Tyrannidae	NRM 966970 *	AY228295 ^{D)}		
Elaerila liavuyastei	ı yranında e	INKINI 900970	V1770739	new	new