

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

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Abstract The tapaculos (Rhinocryptidae) are tracheophone, suboscine birds restricted to South and Central America. Most tapaculos share a number of internal and external characteristics that have been used to define the family taxonomically. The genera *Melanopareia* and *Psiloramphus* do not fully fit this pattern and have caused considerable dispute among taxonomists since they were first described. In this paper we delimit the systematic boundaries of the tapaculos and assess their generic relationships by analysis of molecular sequence data. The results show that whereas *Psiloramphus* is nested well

within the Rhinocryptidae, *Melanopareia* falls far outside that clade. A new family is erected for *Melanopareia*.

Keywords *Melanopareia* · *Psiloramphus* · Rhinocryptidae · Tapaculos · Molecular systematics · Taxonomy · South America

Introduction

The impudently named tapaculos (Rhinocryptidae) are a small group of tracheophone, suboscine passerines whose greatest generic diversity is in southern South America. Most are large-footed, strong-legged ground birds reminiscent of some of the ground-dwelling antthrushes (Formicariidae), with which they were often associated. The family is generally well defined by the presence of operculate nostrils, a tracheophone syrinx, a somewhat curved humerus, and a four-notched sternum (Ames 1971; Feduccia and Olson 1982; Maurício et al. 2008). Thus, Krabbe and Schulenberg (2003), p. 748, considered that the “tapaculos constitute a well-knit group the members of which are united by several derived characters. Only the genera *Melanopareia* and *Psiloramphus* differ to such a degree that their systematic position as tapaculos could be disputed.” Furthermore, the phylogenetic relationships within the family Rhinocryptidae are poorly known, particularly regarding the placement of *Liosceles* and *Acropternis*, and the large austral species of *Pteroptochos* and *Scelorchilus*.

The early taxonomic history of the group was ably summarized by Sclater (1874). d’Orbigny (1837) first erected a family “Rhinomyidaeae” (sic., p. 192) for *Pteroptochos* and his *Rhinomya* (= *Rhinocrypta*) using the operculate nostril to separate them from the Formicariidae.

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However, there was no coherent understanding of the suboscine groups until their distinction from the oscines was established by the pioneering work of Müller (1847) on the syrinx. Müller showed that *Scytalopus* was a tracheophone suboscine and not a wren (Troglodytidae) and also that *Scytalopus* and *Pteroptochus* differed from other known passerines in having a four-notched sternum.

Sclater's (1874) "Pteroptochidae" comprised *Scytalopus* (including the type species of what later became *Myornis* Chapman 1915), *Merulaxis*, *Liosceles*, *Pteroptochos* (including the type species of what later became *Teledromas* Wetmore and Peters 1922, and *Scelorchilus* Oberholser 1923), *Rhinocrypta*, *Hylactes* (now included in *Pteroptochos*), *Acropternis*, and *Triptorhinus* (= *Eugralla*). Except for the problem genera *Psiloramphus* and *Melanopareia*, this composition of the group was essentially maintained until Peters (1951).

The three or four species of *Melanopareia* differ from other tapaculos by their rather slender build and boldly and attractively patterned plumage, and by sharing a semi-concealed white dorsal patch with various true antbirds (Thamnophilidae). They were originally described in the genus *Synallaxis* (Furnariidae), in which Sclater (1890) later submerged the genus. Salvin (1876) described a new species from Ecuador as *Formicivora speciosa*, duly recognized in that combination by Sclater (1890), p. 251, and others until Hellmayr (1906), p. 334, showed that this was a synonym of *Synallaxis elegans* Lesson, in which genus Hellmayr continued to place it while regarding Salvin's allocation of it to *Formicivora* with incredulity. Ridgway (1909) seems to have overlooked this when he created a new genus *Rhoporchilis* for *Formicivora speciosa*. It was Hellmayr (1921) who eventually established the modern concept of the genus in showing that *Synallaxis elegans*, *S. torquata*, and *S. maximiliani* were congeneric and would all fall under Reichenbach's earlier generic name *Melanopareia* and "find their natural place in the Formicariidae", where they stayed for only a few years (Cory and Hellmayr 1924). Next came the observation of W.D.W. Miller that the sternum of *Melanopareia* was four-notched—information that was conveyed to and presented by Wetmore (1926), p. 292. On this basis, Peters (1951) included *Melanopareia* in the Rhinocryptidae, where it has resided since.

The other problem species, the Bamboo-wren *Psilorhamphus guttatus*, is a small bamboo specialist with a rather long, slender bill, a long tail, and relatively weak feet, so it bears little resemblance to large-footed terrestrial tapaculos (Fig. 1). From the beginning (Ménétriés 1835) it was placed with the antbirds in the Myiotherinae (= Formicariidae). Sclater (1858), p. 243, associated *Psilorhamphus* with *Ramphocaenus* (which is now in the oscine family Polioptilidae) in the Formicariidae with the



Fig. 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

comment that these genera "might perhaps be more naturally placed as a distinct subfamily of Pteroptochidae [= Rhinocryptidae]" despite the fact that "there is little external difference between the appearance of these birds and the true Wrens [Troglodytidae]". We are not aware, however, of any instance in which *Psilorhamphus* was placed in either the Troglodytidae or in a family with only sylviid-like genera, as might be inferred from Krabbe and Schulenberg (2003). *Psilorhamphus* continued to be associated with *Ramphocaenus* in the Formicariidae—e.g. Sclater (1890) and Cory and Hellmayr (1924), p. 205—although in the latter reference it was noted that W.D.W. Miller would show *Psilorhamphus* and *Ramphocaenus* to "constitute a separate family" in "a paper shortly to be published." Peters (1951), p. 213, later explained that Miller's death prevented publication of his results but that Wetmore (1943), p. 306, had shown *Ramphocaenus* to have an oscine syrinx, and had told Peters that *Microbates* likewise was oscine and that he believed, on the basis of external morphology, that *Psilorhamphus* was also probably oscine. Therefore, Peters postponed his treatment of

those genera for a future volume treating Sylviidae. Sick (1954) placed *Ramphocaenus* in the Sylviidae while provisionally referring *Psilorhamphus* to the Formicariidae. Then, Plótnick (1958) revealed that *Psilorhamphus* had a four-notched sternum, a tracheophone syrinx, and had other characters, including an operculate nostril, indicating that it should be placed in the Rhinocryptidae. Thus, in Peters' Checklist *Psilorhamphus* appears as an addendum to the Rhinocryptidae that appeared in the volume on Sylviidae (Paynter 1964).

Heimerdinger and Ames (1967) confirmed that the rhinocryptids they examined all had a four-notched sternum but also showed that this condition obtained in at least two genera of grallarine Formicariidae, which was confirmed by Feduccia and Olson (1982).

Ames (1971) made a thorough study of the anatomy of the syrinx in passerine birds and examined *Melanopareia* first-hand but had to rely on the description of Plótnick (1958) for *Psilorhamphus*. Although he noted that the cartilaginous elements of *Melanopareia* differed from those of all other tapaculos examined, he found no grounds for excluding either *Melanopareia* or *Psilorhamphus* from the Rhinocryptidae.

Feduccia and Olson (1982) made the much unexpected discovery that the stapes in *Melanopareia* was of the primitive oscine type with a flattened footplate, rather than having an expanded, bulbous, fenestrated footplate as in all other suboscine birds. They went on to show other morphological similarities (which is all they ever claimed they were) between some of the Rhinocryptidae and the oscine *Menurae* (*Menura* and *Atrichornis*) of Australia. Although this observation was dismissed on the grounds that the characters involved are either primitive or convergent (Krabbe and Schulenberg 2003), the fact remains that the oscines and suboscines had to share a common ancestor and that the ancestor was very likely to have looked like *Atrichornis*, *Melanopareia*, or one of the Rhinocryptidae, for example *Scelorhynchus*.

This paper aims to delimit the boundaries of the tapaculos and assess generic relationships within the group, supplementing the very detailed ongoing studies of relationships and speciation of small tapaculos (notably *Scytalopus*; Maurício et al. 2008, Cadena et al. unpublished) by providing a broader phylogenetic framework for the family.

Materials and methods

Taxon sampling, amplification and sequencing

This study includes representatives of all genera traditionally recognized in Rhinocryptidae (Ridgely and Tudor

1994; Krabbe and Schulenberg 2003), including representatives of the large genus *Scytalopus*, including one representative (*indigoticus*) of the “blue” species, which were recently placed in a separate genus *Eleoscytalopus* (Maurício et al. 2008). Three of the authors have significant field experience of the biology and vocalizations of tapaculos, and this was supplemented with comments and analyses of sound archives by Niels Krabbe (personal communication). Representatives of the main lineages within the tracheophone radiation serve as outgroups (Ridgely and Tudor 1994; Irestedt et al. 2002; Krabbe and Schulenberg 2003; Chesser 2004).

Three nuclear gene regions, myoglobin intron 2, ornithine decarboxylase (ODC) introns 6 to 7, and glyceraldehyde-3-phosphodehydrogenase (G3PDH) intron 11, were sequenced and used to estimate phylogenetic relationships. For each gene and taxon, multiple sequence fragments were obtained by sequencing with different primers. These sequences were assembled to complete sequences with SEQMAN II (DNASTAR). Positions where the nucleotide could not be determined with certainty were coded with the appropriate IUPAC code. GenBank accession numbers are given in Table 1. See Irestedt et al. (2002); Allen and Omland (2003); and Fjeldså et al. (2003) for extractions, amplifications, and sequencing procedures for fresh tissue/blood samples. Corresponding laboratory procedures for study skins are detailed in Irestedt et al. (2006).

Phylogenetic inference and model selection

Because of 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 (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 software 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 software 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 five million generations while the chains for the combined data set were run for ten million generations. Trees were sampled every 100th generation, and the trees

Table 1 Specimen data and GenBank accession numbers for samples used in the study

Species	Family: Subfamily	Voucher/Sample No.	Myoglobin	G3PDH	ODC
<i>Acropternis orthonyx</i>	Rhinocryptidae	ZMUC 125695*	GQ925894	GQ925879	GQ925860
<i>Merulaxis ater</i>	Rhinocryptidae	ZMUC 128820	GQ925895	GQ925880	GQ925861
<i>Pteroptochos tarnii</i>	Rhinocryptidae	AMNH RTC467*	AY065774 ^a	AY590096 ^c	GQ925862
<i>Rhinocrypta lanceolata</i>	Rhinocryptidae	NRM 966793	AY065775 ^a	DQ438953 ^f	DQ435499 ^f
<i>Teledromas fuscus</i>	Rhinocryptidae	USNM BKS3703*	GQ925896	GQ925881	GQ925863
<i>Psilorhamphus guttatus</i>	Rhinocryptidae	MHNT-4812	GQ925897	GQ925882	GQ925864
<i>Myornis senilis</i>	Rhinocryptidae	ZMUC 134967*	GQ925898	GQ925883	GQ925865
<i>Scytalopus parvirostris</i>	Rhinocryptidae	ZMUC 128441	GQ925899	GQ925884	GQ925866
<i>Scytalopus speluncae</i>	Rhinocryptidae	ZMUC 128818	GQ925900	GQ925885	GQ925867
<i>Scytalopus spillmannii</i>	Rhinocryptidae	ZMUC 125091*	AY065773 ^a	AY590097 ^c	GQ925868
<i>Scytalopus zimmeri</i>	Rhinocryptidae	ZMUC 126278*	GQ925901	GQ925886	GQ925869
<i>Scytalopus superciliaris</i>	Rhinocryptidae	USNM BKS 3592*	GQ925902	GQ925887	GQ925870
<i>Eugralla paradoxa</i>	Rhinocryptidae	NRM 570026*, TP	GQ925903	GQ925888	GQ925871
<i>Scelorchilus rubecula</i>	Rhinocryptidae	NRM 570029*, TP	GQ925904	GQ925889	GQ925872
<i>Liosceles thoracicus</i>	Rhinocryptidae	NRM 570027*, TP	GQ925905	GQ925890	GQ925873
<i>Eleoscytalopus indigoticus</i>	Rhinocryptidae	NRM 570028*, TP	GQ925906	GQ925891	GQ925874
<i>Melanopareia maximiliani</i>	Rhinocryptidae	ZMUC 125045*	AY065785 ^a	GQ925892	GQ925875
<i>Furnarius cristatus</i>	Furnariidae: Furnariinae	NRM 966772*	AY064255 ^b	AY590066 ^c	DQ435482 ^f
<i>Philydor atricapillus</i>	Furnariidae: Furnariinae	NRM 937334*	AY065758 ^a	AY590076 ^c	EF212110 ^h
<i>Synallaxis ruficapilla</i>	Furnariidae: Furnariinae	NRM 956643*	AY065763 ^a	AY590068 ^c	EF212119 ^h
<i>Lepidocolaptes angoustirostris</i>	Furnariidae: Dendrocolaptinae	NRM 937184*	AY065767 ^a	AY336576 ^e	DQ435486 ^f
<i>Dendrocicla tyrannina</i>	Furnariidae: Dendrocolaptinae	ZMUC 125661*	AY442959 ^c	AY590087 ^c	EF212098 ^h
<i>Chamaeza meruloides</i>	Formicariidae	ZMUC 126604*	AY065776 ^a	AY590095 ^c	GQ140036 ⁱ
<i>Formicarius nigricapillus</i>	Formicariidae	ZMUC 125987*	AY065777 ^a	GQ925893	GQ925876
<i>Grallaria squamigera</i>	Grallariidae	ZMUC 124629*	AY065778 ^a	AY677078 ^c	GQ140073 ⁱ
<i>Dysithamnus mentalis</i>	Thamnophilidae	NRM 956629*	AY676995 ^c	AY677042 ^c	GQ925877
<i>Terenura humeralis</i>	Thamnophilidae	FMNH 389941	AY677004 ^c	AY677051 ^c	GQ925878
<i>Thamnophilus caeruleus</i>	Thamnophilidae	NRM 967007*	AY065783 ^a	AY336587 ^e	DQ435504 ^f
<i>Conopophaga aurita</i>	Conopophagidae	ZMUC 125796*	AY065784 ^a		DQ435478 ^f
<i>Conopophaga lineata</i>	Conopophagidae	NRM 956653*		AY336577 ^e	
<i>Pipra fasciicauda</i>	Pipridae	NRM 947271*	AY065787 ^a	AY336583 ^e	DQ435495 ^f
<i>Corythopsis delalandi</i>	Tyrannidae	NRM 937282*	AY065788 ^a	DQ435463 ^f	DQ435479 ^f
<i>Elaenia flavogaster</i>	Tyrannidae	NRM 966970*	AY228295 ^d	DQ435464 ^f	DQ435480 ^f

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, Chicago, USA; MHNT, Museu de História Natural de Taubaté, Sao Paulo, Brazil; NRM, Swedish Museum of Natural History; USNM, National Museum of Natural History, Washington, USA; ZMUC Zoological Museum, University of Copenhagen, Denmark

^a Irestedt et al. (2002)

^b Ericson et al. (2002)

^c Irestedt et al. (2004)

^d Ericson and Johansson (2003)

^e Fjeldså et al. (2005)

^f Ericson et al. (2006)

^g Fjeldså et al. (2003)

^h Fjeldså et al. (2007)

ⁱ Irestedt et al. (in press)

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 exon 7). Taking into account the missing base pairs, the sequences obtained varied in length between 667 and 701 bp for the myoglobin intron 2, and between 313 and 363 bp for the G3PDH intron 11, except for the two ant-thrushes *Chamaeza* and *Formicarius* which contain 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 the data on to the tree topology obtained from the Bayesian analyses of the combined data set. A few indels were also found to be incongruent with the phylogenetic tree obtained from analysis of the combined data set. These were generally found in the most variable regions and some of the single base pair insertions actually consist of different bases.

Models for nucleotide substitutions

The prior selection of nucleotide substitution models suggested that the GTR + Γ model had the best fit for all three gene regions, but as the nucleotide state frequencies and gamma distribution differed between the partitions we applied a partitioned analysis of the combined data set. After discarding the burn-in phase the inferences for myoglobin and G3PDH were based on a total of 45,000 samples from the posterior, the inferences for ODC were based on a total of 40,000 samples, and the inferences for the combined data set were based on a total of 95,000 samples. The posterior distribution of topologies is presented as a majority-rule consensus tree from the combined analysis in Fig. 2.

Results

The trees obtained from the Bayesian analyses of the individual gene partitions (Fig. 3) are overall topologically congruent. *Melanopareia* clusters with Thamnophilidae and Conopophagidae and we can therefore reject it as a member of the family Rhinocryptidae with high confidence. Apart from this, all traditional tapaculo genera form a monophyletic clade within a broader group which also

contains Formicariidae *sensu stricto* and Furnariidae, in agreement with previous molecular studies of tracheophone suboscines (Irestedt et al. 2002; Chesser 2004).

Within the radiation of tapaculos there is also good support for two major clades. Clade 1 includes *Teledromas*, *Acropternis*, *Rhinocrypta*, *Liosceles*, and *Psilorhamphus* and Clade 2 includes *Scytalopus*, *Eugralla*, *Myornis*, *Merulaxis*, and *Eleoscytalopus*. The only conflict within the rhinocryptid radiation supported by 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 1 (0.97), whereas the myoglobin tree indicates that these two taxa are sister to Clade 2 (1.00). In the G3PDH tree this relationship is unresolved. On the basis of 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 four-notched sternum. The significance of these characters is uncertain because of the weak cranial ossification in these groups and substantial 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 are not suggestive of a close relationship of *Melanopareia* to the Rhinocryptidae. With four closely related extant species, *Melanopareia* is 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 is 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

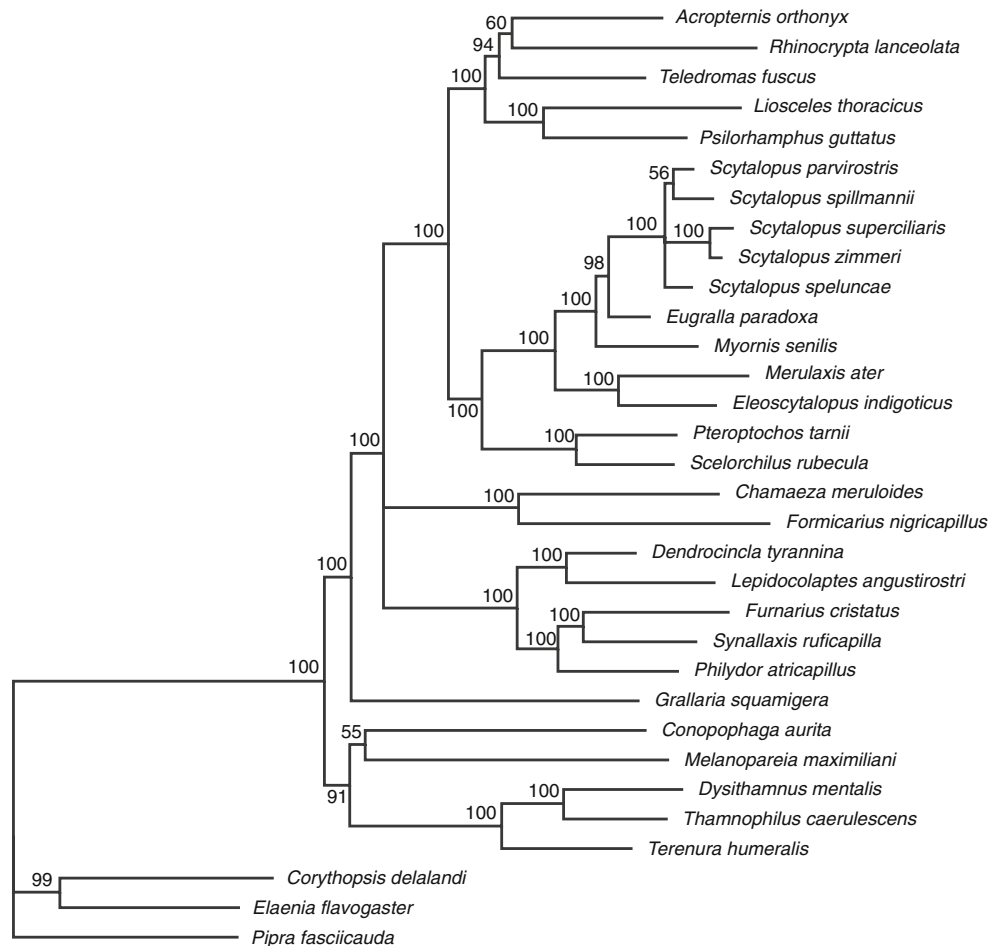


Fig. 2 Majority rule consensus tree obtained from Bayesian analyses of the combined data set (myoglobin intron 2, ODC introns 6 and 7, and G3PDH intron 11). Posterior probability values are indicated at the node

further examination of skeletal characters suggest rejection of 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 sculation 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*—and *Teledromas*—have the expanded footplate of the stapes typical of other subsoscines (except *Melanopareia*).

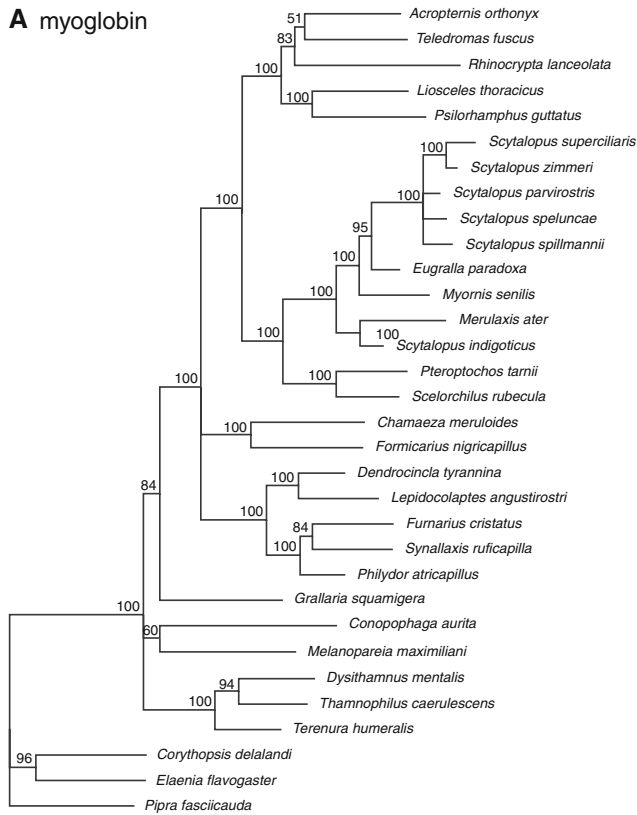
The distinctive appearance of *Psilorhamphus* may result from its divergent habits (albeit shared with *Myornis*, N. Krabbe personal communication), because it generally feeds by climbing in tangles of vine-like bamboo, occasionally up to 7 m, and it rarely feeds on the ground. This species is also known 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 Fig. 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* are 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.

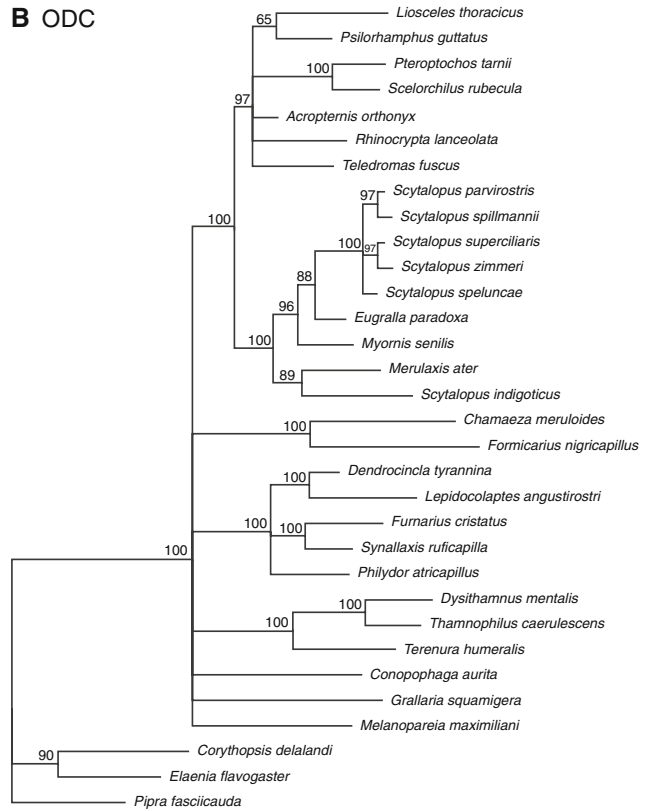
The possible association of the large Chilean tapaculos (*Pteroptochos*, *Scelorchilus*) with Clade 2 receives some morphological support, as *Pteroptochos* has 14 rectrices, something that is also found in some species or individuals of *Scytalopus*, although other representatives of this genus have a reduced number of rectrices or asymmetrical tails (Krabbe and Schulenberg 2003). Other subsoscine 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

A myoglobin



B ODC



C G3PDH

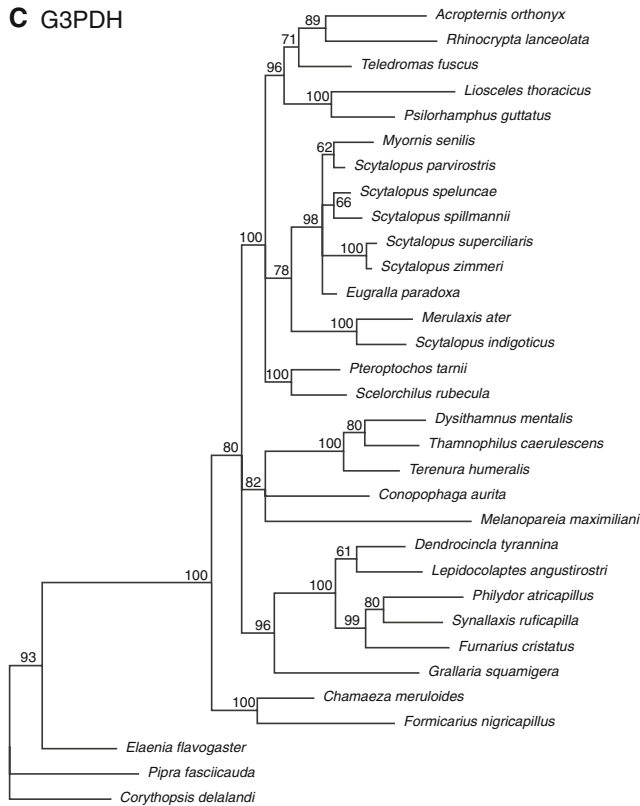


Fig. 3 The majority rule consensus trees obtained from the Bayesian analyses of the individual genes. **a** myoglobin intron 2; **b** ornithine decarboxylase introns 6 to 7; and **c** glyceraldehyde-3-phosphodehydrogenase intron 11. Posterior probability values are indicated at the node

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, *Myornis* 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 “Melanopareidae (new family, incl. *Melanopareia* and *Teledromas*)”, which, however, was invalid because it did not meet the requirements of the International Code of Zoological Nomenclature (ICZN 1999) in lacking any description purporting to differentiate the taxon from other taxa. The need still remains for separate family status for the genus, which we re-propose here:

Melanopareidae, new family

Type and only included genus: *Melanopareia* Reichenbach 1853.

Diagnosis: Tracheophone suboscine passeriformes differing from other Tracheophonae except Rhinocryptidae (and a few other taxa: *Myrmothera*, *Hylopezus*, *Pittasoma*, *Conopophaga*) in having a four-notched sternum and differing from the Rhinocryptidae and all other suboscines in retaining the primitive morphology of the stapes, with a flat, rather than inflated, footplate.

Zusammenfassung

Umschreibung einer monophyletischen Familie für die Bürzelstelzer (Aves: Rhinocryptidae): *Psiloramphus* rein und *Melanopareia* raus

Die Bürzelstelzer (Rhinocryptidae) sind tracheophone, suboscine Vögel, deren Vorkommen auf Süd- und Mittelamerika beschränkt ist. Die meisten Bürzelstelzer haben eine Reihe innerer und äußerer Merkmale gemeinsam, die benutzt worden sind, um die Familie taxonomisch zu definieren. Die Gattungen *Melanopareia* und *Psiloramphus* passen nicht vollständig in dieses Schema und haben zu beträchtlichen Disputen unter Taxonomen geführt, seit sie erstmals beschrieben worden sind. In diesem Artikel stecken wir die systematischen Grenzen der Bürzelstelzer ab und bewerten ihre Gattungsbeziehungen mit Hilfe einer Analyse molekularer Sequenzdaten. Die Ergebnisse zeigen, dass *Melanopareia* weit aus dieser Klade herausfällt, während *Psiloramphus* gut in die Rhinocryptidae hineinpasst. Eine neue Familie wird für *Melanopareia* eingerichtet.

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References

- Akaike H (1973) Information theory as an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (eds) Second international symposium on information theory. Akademi Kiado, Budapest, pp 267–281
- Allen ES, Omland KE (2003) Novel intron phylogeny (ODC) supports plumage convergence in orioles (*Icterus*). *Auk* 120: 961–969
- Ames PL (1971) The morphology of the syrinx in passerine birds. *Bull Peabody Mus Nat Hist* 37:1–194
- Chapman FL (1915) The more northern species of the genus *Scytalopus* Gould. *Auk* 32:406–423
- Chesser RT (1999) Molecular systematics of the rhinocryptid genus *Pteroptochus*. *Condor* 101:439–446
- Chesser RT (2004) Molecular systematics of New World Suboscine birds. *Mol Phyl Evol* 32:11–24
- Cory CB, Hellmayr CE (1924) Catalogue of birds of the Americas and adjacent islands. Part III. *Field Mus Nat Hist Zool Ser* 13:1–369
- d’Orbigny AD (1837) Voyage dans l’Amérique Séptentrionale. vol 4. part 3, Ve. Levrault, Oiseaux, Strasbourg
- Ericson PGP, Johansson US (2003) Phylogeny of Passerida (Aves: Passeriformes) based on nuclear and mitochondrial sequence data. *Mol Phyl Evol* 29:126–138
- Ericson PGP, Christidis L, Irestedt M, Norman JA (2002) Systematic affinities of the lyrebirds (Passeriformes: *Menura*), with a novel classification of the major groups of passerine birds. *Mol Phyl Evol* 25:53–62
- Ericson PGP, Zuccon D, Ohlson JI, Johansson US, Alvarenga H, Prum RO (2006) Higher level phylogeny and morphological evolution of tyrant flycatchers, cotingas, manakins and their allies (Aves: Tyrannida). *Mol Phyl Evol* 40:471–483
- Feduccia A, Olson SL (1982) Morphological similarities between the *Menurae* and the Rhinocryptidae, relict passerine birds of the Southern Hemisphere. *Smithson Contr Zool* 366:1–22
- Fjeldså J, Zuccon D, Irestedt M, Johansson US, Ericson PG (2003) *Sapayoa aenigma*: a New World representative of ‘Old World suboscines’. *Proc R Soc Lond B [Suppl]* 270:238–241
- Fjeldså J, Irestedt M, Ericson PGP (2005) Molecular data reveal some major adaptational shifts in the early evolution of the most diverse avian family, the Furnariidae. *J Ornithol* 146:1–13
- Fjeldså J, Irestedt M, Jönsson KA, Ohlson JI, Ericson PGP (2007) Phylogeny of the ovenbird genus *Upucerthia*: a case of independent adaptations for terrestrial life. *Zool Scr* 36:133–141
- Heimerdinger MA, Ames PL (1967) Variation in the sternal notches of suboscine passeriform birds. *Postilla* 105:1–44
- Hellmayr CE (1906) Critical notes on the types of little-known species of Neotropical birds. *Novitates Zoologicae* 13:305–352
- Hellmayr CE (1921) Review of the birds collected by Alcide d’Orbigny. *Novitates Zoologicae* 28:230–276
- Holder M, Lewis PO (2003) Phylogeny estimation: traditional and Bayesian approaches. *Nat Gen* 4:275–284

- Huelsenbeck JP, Ronquist F, Nielsen R, Bollback JP (2001) Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* 294:2310–2314
- International Commission on Zoological Nomenclature (1999) International Code of Zoological Nomenclature, 4th edn. International Trust for Zoological Nomenclature, British Museum (Natural History), University of California Press
- Irestedt M, Fjeldså J, Dalén L, Ericson PGP (in press) Convergent evolution, habitat shifts and variable diversification rates in the ovenbird-woodcreeper family (Furnariidae). *BMC Evol Biol*
- Irestedt M, Fjeldså J, Johansson US, Ericson PGP (2002) Systematic relationships and biogeography of the tracheophone suboscines (Aves: Passeriformes). *Mol Phyl Evol* 23:499–512
- Irestedt M, Fjeldså J, Ericson PGP (2004) Phylogeny and morphological plasticity in woodcreepers (Dendrocolaptinae). *J Avian Biol* 35:280–288
- Irestedt M, Ohlson JI, Zuccon D, Källersjö M, Ericson PGP (2006) Nuclear DNA from old collections of avian study skins reveals the evolutionary history of the Old World suboscines (Aves, Passeriformes). *Zool Scr* 35:567–580
- Krabbe NK, Schulenberg TS (2003) Family Rhinocryptidae (Tapaculos). In: del Hoyo J, Elliott A, Christie DA (eds) *Handbook of birds of the world*, vol 8. Lynx Edicions, Barcelona, pp 748–787
- Maurício GN, Mata H, Bornschein MR, Cadena CD, Alvarenga H, Bonatto SL (2008) Hidden genetic diversity in Neotropical birds: molecular and anatomical data support a new genus for the “*Scytalopus*” *indigoticus* species-group (Aves: Rhinocryptidae). *Mol Phyl Evol* 49:125–135
- Ménétriés E (1835) *Monographie de la famille des Myiotherinae où sont décrites les espèces qui ornent le Musée de l’Académie Impériale des Sciences. Mémoires de l’Académie Impériale des Sciences de Saint-Petersburg. Ser. 6, 3 (pt 2):443–543*
- Müller J (1847) Über die bisher unbekanntenen typischen Verschiedenheiten der Stimmorgane der Passerinen. *Abhandlung der Königlichen Akademie Wissenschaft zu Berlin*, pp 321–391, 405–406
- Nylander JAA (2005) MrModeltest v.2.2. Program distributed by the author. Department of Systematic Zoology, Uppsala University, Uppsala
- Oberholser HC (1923) Note on the generic name *Pteroptochos* Kittlitz. *Auk* 40:326–327
- Paynter RA Jr (1964) Family Rhinocryptidae (part). In: Mayr E, Paynter RA Jr (eds) *Check-list of Birds of the World*. Museum of Comparative Zoology, Cambridge, Massachusetts, p 456
- Peters JL (1951) *Check-list of birds of the world*, vol VII. Museum of Comparative Zoology, Cambridge, Massachusetts
- Plótnick R (1958) Posición [sic] sistemática del género “*Psiloramphus*” (Rhinocryptidae, Passeriformes). *Physis* 21:130–136
- Reichenbach HGL (1853) *Handbuch der speciellen Ornithologie, Die Vögel*, part 3. Dresden
- Ridgely RS, Tudor G (1994) *The birds of South America*, vol II. Oxford University Press, Oxford
- Ridgway R (1909) New genera, species, and subspecies of Formicariidae, Furnariidae, and Dendrocolaptidae. *Proc Biol Soc Washington* 22:69–74
- Ronquist F, Huelsenbeck JP (2003) MrBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574
- Salvin O (1876) On some new species of birds from western Ecuador. *Ibis* 6:493–496
- Sclater PL (1858) Synopsis of the American ant-birds (Formicariidae). *Proc Zool Soc Lond* 1858:232–254
- Sclater PL (1874) On the Neotropical species of the family Pteroptochidae. *Ibis* 4:189–206
- Sclater PL (1890) *Catalogue of the birds in the British Museum*, vol 15. British Museum, London
- Sick H (1954) Zur Kenntnis von *Ramphocaenus* (Sylviidae) und *Psilorhamphus* (Formicariidae). *Bonner Zool Beitr* 5:179–190
- Swofford DL (1998) Paup*. Phylogenetic analysis using parsimony (* and other methods), v.4. Sinauer, Sunderland
- Wetmore A (1926) Observations on the birds of Argentina, Paraguay, Uruguay, and Chile. *Bull United States Nat Mus* 133:1–448
- Wetmore A (1943) The birds of southern Veracruz, Mexico. *Proc United States Nat Mus* 93:215–340
- Wetmore A, Peters JL (1922) A new genus and four new subspecies of American birds. *Proc Biol Soc Washington* 35:41–46