



Morphology-based phylogenetic analysis and classification of the family Rhinocryptidae (Aves: Passeriformes)

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Received 28 March 2012; accepted for publication 17 May 2012

The family Rhinocryptidae comprises an assemblage of 12 genera and 55 species confined to the Neotropical region. Here we present the first morphology-based phylogenetic study of the Rhinocryptidae, using 90 anatomical characters (62 osteological, 28 syringeal) scored for all genera of the family and representatives of all families of the infraorder Furnariides. Parsimony analysis of this dataset recovered 7428 equally most-parsimonious trees. The strict consensus of those trees was completely resolved at the genus level, with the topology (*Liosceles* (*Psilorhamphus* ((*Eleoscytalopus* + *Merulaxis*) (*Acropternis* ((*Teledromas* + *Rhinocrypta*) ((*Pteroptochos* + *Scelorchilus*) (*Eugralla* (*Myornis* + *Scytalopus*))))))). The monophyly of the Rhinocryptidae as presently understood was recovered with strong support [eight synapomorphies and Bremer support (BS) = 6]. Strongly supported internal arrangements included the basal position of the Amazonian genus *Liosceles* relative to the rest of the family (four synapomorphies, BS = 4), a clade containing *Acropternis* through *Scytalopus* (six synapomorphies, BS = 4), and other less inclusive nodes. The main points of congruence between the present morphological phylogeny and previous molecular phylogenetic work on the family were clades supported by six or more synapomorphies and Bremer values of 6–7: *Eleoscytalopus* + *Merulaxis* (eight synapomorphies, BS = 6), *Scelorchilus* + *Pteroptochos* (seven synapomorphies, BS = 7), *Rhinocrypta* + *Teledromas* (seven synapomorphies, BS = 7), and *Eugralla* + *Myornis* + *Scytalopus* (six synapomorphies, BS = 6). A classification derived from the morphological phylogeny is proposed, with new suprageneric taxa being named and diagnosed.

© 2012 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2012, 166, 377–432.
doi: 10.1111/j.1096-3642.2012.00847.x

ADDITIONAL KEYWORDS: biogeography – osteology – phylogenetic classification – syringeal anatomy.

INTRODUCTION

The family Rhinocryptidae comprises 12 genera and 55 species-level taxa that range in size from that of a wren to that of a thrush and are characterized by

terrestrial habits, extremely poor flying ability, and shy behaviour. Until recently it was poorly known taxonomically, and belongs to the infraorder Furnariides, a major division of the suborder Tyranni that contains nine family-level entities and hundreds of species, all exclusively Neotropical in distribution (del Hoyo, Elliott & Christie, 2003; Remsen *et al.*, 2011).

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Here we present a morphology-based phylogenetic analysis of the Rhinocryptidae involving representatives of all genera and almost all species of each genus, except for the very diverse *Scytalopus* whose sampled representatives, however, cover most of its morphological diversity.

HISTORY OF RHINOCRYPTIDAE SYSTEMATICS

Limits of the family

The large and membranous nasal operculae that hide the nares of the Rhinocryptidae and after which the family takes its name has intrigued ornithologists for a long time (e.g. Lesson, 1831 [1830]; Saint-Hilaire 1832) and has been used as a landmark for the diagnosis of the group. As a supra-generic entity, the Rhinocryptidae has its early taxonomic history rooted in contributions that appeared in the 1830s and 1840s. On the basis of the possession of the operculum covering the nostrils Ménériés (1835) recognized the close relationship between several taxa presently allocated in four rhinocryptid genera (*Merulaxis*, *Eleoscytalopus*, *Eugralla*, and *Scytalopus*) and placed them in the genus *Malacorhynchus*, within the family 'Myiotherinae' (an entity equivalent to the old sense Formicariidae). He also suggested a close relationship between his *Malacorhynchus* and the old sense *Pteroptochos* (including *Scelorchilus*). Lafresnaye & d'Orbigny (1837) erected the family Rhinomyidae (i.e. the present-day Rhinocryptidae) exclusively for the genera *Rhinomya* (= *Rhinocrypta*) and *Megalonyx* (= *Pteroptochos*, then including *Scelorchilus*) based on the possession of the diagnostic, prominent operculum covering the nostrils. When describing *Merulaxis senilis* (now *Myornis*; Chapman, 1915) Lafresnaye (1840) used the presence of the nasal operculum to suggest a close relationship between *Rhinomya*, *Megalonyx* (= *Pteroptochos*), and *Merulaxis* (including *Malacorhynchus sensu* Ménériés, [1835]), treating all within the family 'Myiotherinae'. Lesson's (1841 [1842]) inclusive version of *Megalonyx* included several subgenera containing the actual *Rhinocrypta*, *Pteroptochos*, *Scelorchilus*, *Eugralla*, and *Scytalopus*, which were united among other features by the possession of a 'naribus basalibus, membrane subtumennli pilisque per mediam longitudinem tectâ'. Surprisingly, he did not include *Merulaxis* among them, a genus that he himself had previously described as having the nasal operculum (Lesson, 1831 [1830]). A few years later, when describing *Merulaxis orthonyx* (now *Acropternis*; Cabanis & Heine, 1859), Lafresnaye (1843) explicitly united *Rhinomya*, *Megalonyx*, and *Merulaxis* under the subfamily Rhinomyinae, then included in the old sense Formicariidae. Shortly afterwards, Lafresnaye (1844) justified his treatment of the Rhinomyidae at the

subfamily level under Formicariidae [*sensu lato* (*s.l.*)] and tried to demonstrate the cohesion between the three genera admitted by him in this group, reaffirming and somewhat expanding his earlier conclusions. As the three-genera treatment of Lafresnaye (1843, 1844) embraced diverse taxa representing nine out of 12 genera now included in Rhinocryptidae (*Rhinomya* [= *Rhinocrypta*], *Megalonyx* [= *Pteroptochos* and *Scelorchilus*], and the enlarged *Merulaxis* [= *Merulaxis*, *Eleoscytalopus*, *Eugralla*, *Scytalopus*, *Myornis* and *Acropternis*]), the limits and the concept of the group were already well established in the first half of the 19th century, independently of its treatment at the family or subfamily level.

Gould & Darwin (1841) also recognized the affinities between some diverse rhinocryptid genera. In addition to their inclusion of *Eugralla*, *Scelorchilus*, and *Pteroptochos* in an expanded genus *Pteroptochos*, they placed *Scytalopus (magellanicus)* just below *P. paradoxus* (= *Eugralla paradoxa*) and regarded both genera as closely allied, remarking on their close relationship based on behaviour. The position of *Rhinomya* (= *Rhinocrypta*) was somewhat ambiguous: it was placed immediately above *Pteroptochos* and indicated to replace the Pacific *Pteroptochos* on the Atlantic side of the South American continent but was later said to be distantly allied to the furnariid *Eremobius phoenicurus*.

It is not clear how the preceding authors influenced each other in their attempt to define and classify the rhinocryptids, as there are no clear references to previous treatments or recognition of credits in these works. It appears that some sort of tacit synergy and convergent thoughts finally gave shape to the closely knitted group that we now refer to as Rhinocryptidae. It is also worthy of note that the family name Rhinomyidae was based on *Rhinomya* Geoffroy Saint-Hilaire, 1832, a generic name replaced by *Rhinocrypta* G. R. Gray, 1841 due to the fact that *Rhinomya* Robineau-Desvoidy, 1830, a genus of Diptera, had nomenclatural priority (Gray, 1841; Peters, 1951; Bock, 1994). Thus, Wetmore (1926) introduced the term Rhinocryptidae to replace Rhinomyidae, understanding that the family designation should be based on the generic name (i.e. *Rhinocrypta*) erected to substitute for *Rhinomya*, this latter being the first name used to form a family-group name having as basis a rhinocryptid taxon. Other names sometimes used to designate the family, such as Scytalopodidae, Megalonychidae, Hylactidae, and Pteroptochidae, the last-named being used for a long period until Wetmore's (1926) proposal, must be conditionally suppressed in favour of Rhinocryptidae (Bock, 1994).

The next sound contribution to the systematics and characterization of the rhinocryptids was the pioneering anatomical study of Johannes Müller (Müller, 1878 [1847]). This study on the syrinx and osteology

of Passeriformes and groups that were not considered to be closely related was first published in German in 1847 and translated into English in 1878. Based on a peculiar conformation of the syrinx, Müller (1878 [1847]) conceived and delimited the 'Tracheophone' division, a higher-level entity equivalent to the present-day infraorder Furnariides. He also proposed its division into three families, 'Scytalopidae' (= Rhinocryptidae), Anabatidae (= Furnariidae *s.l.*) and Myiotheridae (= Formicariidae *s.l.*). Müller (1878 [1847]) highlighted that the Scytalopidae was distinguished from the remaining Tracheophone based on the presence of four notches in the posterior margin of the sternum (two on each side), a condition previously described for *Pteroptochos* (= *Pteroptochos* + *Scelorchilus*) by Eyton (1841). Accordingly, he placed in his Scytalopidae only the few taxa whose sternum was known to him, namely *Scytalopus indigoticus* (= *Eleoscytalopus indigoticus*) and the old sense *Pteroptochos*.

Subsequently, although some authors did not recognize the group taxonomically (e.g. Cabanis, 1847; Bonaparte, 1850), others such as Chenu & Des Murs (1852; as Megalonychidae) and Sclater (1858a, b; as Pteroptochidae) did so. Although Sclater (1858a) regarded the rhinocryptids as a well-distinguished group, stating that 'their most essential character (. . .) consists in the covered nostril (. . .), which occurs in every species', he remotely admitted the possibility of considering them as a subfamily of Formicariidae. Shortly afterwards, however, he strongly defended that they 'form a division rather parallel than subordinate to the family Formicariidae' (Sclater, 1858b), citing the results of Müller (1878 [1847]) as the main basis for this treatment. Nevertheless, some doubts regarding the limits of the family remained as he later suspected that the genera *Psilorhamphus* and *Rhamphocaenus* (a polioptilid in the Passeri radiation) 'might perhaps be more naturally placed as a distinct subfamily of Pteroptochidae', although he left them in their traditional positions in the Formicariidae (*s.l.*) (Sclater, 1858c).

Still in the 19th century, representatives of two new genera were described: *Pteroptochus thoracicus*, described in the subgenus *Liosceles* (Sclater, 1864) but later elevated to the rank of genus (Sclater, 1874), and *Rhinocrypta fusca* (Sclater & Salvin, 1873), later placed in the monotypic genus *Teledromas* (Wetmore & Peters, 1922). The modern conformation of morphotypes in the family is almost the same as that in the taxonomic revision of the family by Sclater (1874), whose grouping included representatives of 11 out of 12 currently recognized genera, even though he only recognized eight genera (*Scytalopus*, *Merulaxis*, *Rhinocrypta*, *Liosceles*, *Pteroptochus* [= *Scelorchilus*], *Hylactes* [= *Pteroptochos*], *Acropternis*, and *Triptorhi-*

nus [= *Eugralla*]). Since then, the genera *Myornis* (Chapman, 1915), *Teledromas* (Wetmore & Peters, 1922), and *Eleoscytalopus* (Maurício *et al.*, 2008) were described and adopted for species allocated to the Rhinocryptidae since their descriptions, and the position of the two conflictive genera *Psilorhamphus* and *Melanopareia* in the family was debated. Wetmore (1926) transferred *Melanopareia* from the Formicariidae *s.l.* to the Rhinocryptidae, as it had a four-notched sternum, a feature considered to be exclusive of the Rhinocryptidae within the Passeriformes (Heimerdinger & Ames, 1967; Feduccia & Olson, 1982). By virtue of its peculiar external morphology, *Psilorhamphus* was transferred from the Formicariidae *s.l.* to the Sylviidae, jumping to the suborder Passeri (Peters, 1951), only to be placed again in the suborder Tyranni by Sick (1954; see also Sick, 1960). Sick (1954) suspected that *Psilorhamphus* could be a Rhinocryptidae, having even illustrated a nasal operculum covering the nares. However, it was only after the syrinx and the sternum (with four well-marked notches) were examined that *Psilorhamphus* was firmly allocated within the Rhinocryptidae (Plótnick, 1958). Despite this, the placement of *Psilorhamphus* and *Melanopareia* in the family was questioned, suggesting that their phylogenetic affinities may lay outside the Rhinocryptidae (Ridgely & Tudor, 1994; Krabbe & Schulenberg, 2003). Recent molecular studies support the inclusion of *Psilorhamphus* in the Rhinocryptidae, but strongly argue against the inclusion of *Melanopareia* (Irestedt *et al.*, 2002; Moyle *et al.*, 2009; Ericson *et al.*, 2010). In this way, the family Rhinocryptidae today comprises 12 genera (Remsen *et al.*, 2011).

Interfamilial relationships

Some early taxonomists considered the rhinocryptids to be related to oscine passerines such as wrens (Troglodytidae) and lyrebirds and allies (Menurae) (e.g. Kittlitz, 1830; Gray, 1841; Sclater, 1855; Cabanis & Heine, 1859), but most workers linked them exclusively to suboscine passerines such as antbirds, antthrushes, and allies, at that time collectively referred to as 'Myiotherinae' (or Myiotheridae), a paraphyletic assemblage containing the modern Thamnophilidae, Conopophagidae, Melanopareiidae, Formicariidae, and Grallariidae (see above). The hypothesis of a close relationship between rhinocryptids and the Menurae (families Menuridae and Atrichornithidae) was later revived by Feduccia & Olson (1982) on the basis of the discovery of osteological similarities. However, the concept of relationship they adopted includes paraphyletic arrangements (a characteristic of the evolutionary school of systematics; see Wiley, 1981) with the authors suggesting that the two groups might be 'basally related', i.e. they would lay close to each other

at the base of the passerine radiation, but also admitted that they might be related in the sense of 'the strict redefinition of monophyly advocated by cladists' (Feduccia & Olson, 1982: 17). In any event, a massive body of morphological (Bock & Clench, 1985; Clench, 1985; Raikow, 1985, 1987; Rich, McEvey & Baird, 1985) and molecular (Ericson *et al.*, 2002a; Barker *et al.*, 2004; Chesser & Have, 2007; Hackett *et al.*, 2008) data reject these hypotheses and show that the similarities between the two groups as described by Feduccia & Olson (1982) are the product of convergent evolution.

That the Rhinocryptidae was part of a group composed exclusively by the presently recognized families Thamnophilidae, Conopophagidae, Melanopareiidae, Rhinocryptidae, Grallariidae, Formicariidae, Furnariidae, Dendrocolaptidae, and Scleruridae (i.e. the infraorder Furnariides) has been widely accepted since Müller (1878 [1847]), who showed that members of this assemblage are characterized by the possession of a tracheal syrinx, which is more complex than that of other members of the suborder Tyranni and is unique in the class Aves (Ames, 1971; Raikow, 1987; Krabbe & Schulenberg, 2003). Within Furnariides, the 'ground antbirds' [*sensu* Ames (1971), i.e. an assemblage composed by the actual families Formicariidae, Grallariidae, and Conopophagidae, excluding Thamnophilidae], the Furnariidae (including the actual Scleruridae), and Conopophagidae were alternately considered closely related to the Rhinocryptidae based on anatomical features, especially sternum and syrinx morphology (Garrod, 1877a; Forbes, 1881; Ames, 1971), whereas on the basis of DNA–DNA hybridization data the latter two families were found to be sisters (Sibley & Ahlquist, 1985, 1990). Even recent molecular phylogenetic analyses with fairly comprehensive taxon sampling were not congruent in defining the sister-taxon to the Rhinocryptidae, with possible alternatives being the Grallariidae (Moyle *et al.*, 2009), the Formicariidae (Irestedt *et al.*, 2002; Rice, 2005), or a clade formed by Scleruridae, Dendrocolaptidae, Furnariidae, and Formicariidae, with Grallariidae basal to them (Irestedt *et al.*, 2002; Chesser, 2004). The clade Grallariidae + Rhinocryptidae was given superfamily rank as Grallarioidea, despite its moderate statistical support, and was found to be sister to a clade including Scleruridae, Dendrocolaptidae, Furnariidae, and Formicariidae with high statistical support (Moyle *et al.*, 2009).

Intrafamilial relationships

Besides the simple grouping of species into distinct genera as reviewed above, a significant early attempt to organize the family Rhinocryptidae internally was that of Lafresnaye (1851). He divided his expanded genus *Merulaxis* (*sensu* Lafresnaye, 1843, 1844) into

four sections, the linear sequencing of which apparently being intended to reflect relationships: (1) 'Galeati' (rostri culmine in spatio frontali, horizontali limbo circumdato, modern *Eugralla* and *Acropternis*); (2) 'Rhinolophi' (rostri culmine basi elevato, compresso, plumulis frontalibus longiusculis erectis, modern *Merulaxis sensu stricto*); (3) 'Albiventris' (guttur, collo ântico pectoreque albis, rostro simplici, modern *Eleoscytalopus*); and (4) 'Concolores' (aut ferè concolores, collo ântico pectoreque non albis sed dorso fere concolore, modern *Scytalopus* and *Myornis*). Within this simple scheme, two aspects involve important systematic hypotheses. The 'Galeati' section groups two diverse genera that resemble each other only in the variably elevated base of the bill, an arrangement that was implemented a few years earlier by Cabanis (1847), who united *Eugralla* and *Acropternis* under his new genus *Triptorhinus*. The other important aspect is the recognition of the 'Albiventris' section for the white-bellied taxa, dissociating them from the generally grey 'Concolores', thus agreeing with the recently proposed genus *Eleoscytalopus*.

In his taxonomic revision of the family, Sclater (1874) recognized some relationships between the eight genera admitted by him in the Rhinocryptidae. He considered *Scytalopus* (then including *Myornis* and *Eleoscytalopus*) and *Merulaxis* as allied to each other and regarded *Rhinocrypta* (then including *Teledromas*) and *Liosceles* as allied to *Scelorchilus* (treated as *Pteroptochus*), with the present-day *Pteroptochos* (*Hylactes* at that time) being regarded as 'a strong form' of *Scelorchilus*. Although Sclater regarded *Eugralla* (as *Triptorhinus*) as being most similar to *Scytalopus*, he maintained it next to *Acropternis* based on the similarly shaped bill.

Relationships within the Rhinocryptidae were first studied using explicit methods by Sibley & Ahlquist (1985, 1990), whose classical DNA–DNA hybridization study recovered *Scytalopus* + *Liosceles* as sister to *Pteroptochos*. A study on the molecular phylogenetic relationships of *Pteroptochos* found it to be monophyletic and sister to *Scelorchilus*, even though only *Scytalopus* and *Rhinocrypta* were sampled as additional members of the family (Chesser, 1999). In a study investigating the molecular phylogenetic relationships of the Furnariides based on extensive sampling the included Rhinocryptidae formed a monophyletic clade, with *Scytalopus* + *Pteroptochos* as sister to *Rhinocrypta* (Irestedt *et al.*, 2002). *Melanopareia* (considered a member of the family at that time) was highly divergent and grouped either with the Conopophagidae or with the Thamnophilidae, or was recovered as being basal to the whole infraorder (Irestedt *et al.*, 2002). This result prompted the creation of the new family Melanopareiidae to host *Melanopareia* together with *Teledromas*, a relationship based on reported

behavioural and morphological similarities (despite *Teledromas* not being sampled for molecular characters) (Irestedt *et al.*, 2002). The same rhinocryptid genera were sampled for a wider molecular phylogenetic analysis including members of all the Tyranni, but in this case a clade *Pteroptochos* + *Rhinocrypta* was sister to *Scytalopus* (Chesser, 2004). In turn, *Melanopareia* was part of a polytomy together with Conopophagidae + Thamnophilidae, which was basal to the clade including Scleruridae, Dendrocolaptidae, Furnariidae, Formicariidae, Grallariidae, and Rhinocryptidae (Chesser, 2004). Some phylogenetic studies of other groups have also included members of the Rhinocryptidae. For example, *Scytalopus* was sister to a clade *Rhinocrypta* + *Liosceles* in a study on the molecular phylogenetic relationships of the Grallariidae (Rice, 2005), and *Rhinocrypta* was grouped with *Pteroptochos* in a study focused on the relationships of some species of Furnariidae (Claramunt & Rinderknecht, 2005), in the single morphological phylogenetic study including members of the Rhinocryptidae.

Only very recently have molecular phylogenetic studies included comprehensive taxon sampling of the family. In a study aimed at investigating the relationships of some genera, Maurício *et al.* (2008) sampled nine genera, recovering the topology (((*Myornis* (*Scytalopus* + *Eugralla*)) (*Eleoscytalopus* + *Merulaxis*)) (*Rhinocrypta* + *Psilorhamphus*)) (*Scelorchilus* + *Pteroptochos*)). In their study designed to elucidate relationships within the infraorder Furnariides, Moyle *et al.* (2009) also included nine genera and recovered a monophyletic Rhinocryptidae that was divided into two large clades, the subfamilies Scytalopodinae (*Myornis* (*Eugralla* + *Scytalopus*)) and Rhinocryptinae ((*Pteroptochos* + *Scelorchilus*) (*Liosceles* (*Acropternis* (*Rhinocrypta* + *Teledromas*))))). Ericson *et al.* (2010) also recovered a monophyletic Rhinocryptidae, in the only study to date that included all genera of the family. They found two major clades, one partially coinciding with the Rhinocryptinae of Moyle *et al.* (2009), with the topology ((*Teledromas* (*Acropternis* + *Rhinocrypta*)) (*Liosceles* + *Psilorhamphus*)), and another containing the Scytalopodinae of the latter authors plus the remaining genera, with the topology (((*Myornis* (*Eugralla* + *Scytalopus*)) (*Eleoscytalopus* + *Merulaxis*)) (*Pteroptochos* + *Scelorchilus*)).

At the species level, several studies focusing on particular groups of both Andean (Arctander & Fjeldså, 1994; Cuervo *et al.*, 2005; Krabbe *et al.*, 2005; Krabbe & Cadena, 2010) and Brazilian (Bornschein *et al.*, 2007; Mata *et al.*, 2009) members of the genus *Scytalopus* have been published, all of these including results of molecular phylogenetic analyses. Of these contributions, that of Mata *et al.* (2009) was the most taxonomically comprehensive and significant as it investigated the relationships of all Brazilian taxa, a

diversified assemblage frequently referred to as the *S. speluncae* group, whose monophyly was recovered with some confidence.

Additional hypotheses on the relationships within the Rhinocryptidae have been proposed albeit without any formal phylogenetic analysis. Krabbe & Schulenberg (1997, 2003) proposed, based on vocalizations, plumage and body proportions, that *Merulaxis*, *Myornis*, *Eugralla*, and *Scytalopus* (then including *Eleoscytalopus*) formed a more closely related group within the family, with the former two being hypothesized to be sister groups. Several hypotheses of relationship at the species level have been proposed on the basis of vocal and plumage characters (especially in *Scytalopus*) (Zimmer, 1939; Vielliard, 1990; Whitney, 1994; Krabbe & Schulenberg, 1997, 2003; Bornschein, Reinert & Pichorim, 1998; Maurício, 2005; Bornschein *et al.*, 2007), some of which have been corroborated by molecular analyses.

Higher-level classification adopted in the present study

We follow the classification of Moyle *et al.* (2009) and Tello *et al.* (2009), which divide the order Passeriformes into three suborders: Acanthisitti (a New Zealand relict), Passeri (the Oscine passerines, worldwide distribution), and Tyranni (the Suboscine passerines, mostly New World but with few Old World representatives). Ericson *et al.* (2002a, b) and Ericson, Irestedt & Johansson (2003) also delimited these same higher-level groups, but using different names and taxonomic subordinations. Within Tyranni, we recognize three infraorders: Eurylaimides (Old World suboscines), Tyrannides, and Furnariides (New World suboscines) (Moyle *et al.*, 2009; Tello *et al.*, 2009). The treatment of the Furnariides at the level of infraorder is in agreement with Cracraft (1981) and Raikow (1987), and contrasts with the traditional status of superfamily or suborder given to the group [see Sibley & Ahlquist (1990) for a revision of the topic]. The Tyrannides, sister-taxon to the Furnariides, are also given infraordinal level in the present study (Johansson *et al.*, 2001; Ericson *et al.*, 2002b; Barker *et al.*, 2004; Chesser, 2004; Irestedt *et al.*, 2009; Tello *et al.*, 2009). Following Moyle *et al.* (2009), we recognize nine family-level entities in the infraorder Furnariides, namely Thamnophilidae, Conopophagidae, Melanopareiidae, Grallariidae, Rhinocryptidae, Formicariidae, Scleruridae, Dendrocolaptidae, and Furnariidae.

Aims of the present study

This study aims to derive a phylogenetic hypotheses for the family Rhinocryptidae based on skeletal and syrinx features. Implicit in this main objective are the following empirical questions: (1) What is the potential of variation in internal morphological char-

acters to help elucidate phylogenetic relationships in the Rhinocryptidae? (2) Is the Rhinocryptidae a monophyletic group? (3) Do the disputed genera *Psilorhamphus* and *Melanopareia* belong to this family? (4) Are the genera *Merulaxis* and *Eleoscytalopus* sister taxa and closely related to *Scytalopus*, *Myornis*, and *Eugralla* as molecular phylogenetic studies proposed? (5) Is the highly speciose genus *Scytalopus* monophyletic?

METHODS

SYSTEMATIC METHODOLOGY AND ASSUMPTIONS

To investigate relationships within the family Rhinocryptidae, the character-based, cladistic methodology (Wiley, 1981) was employed. Within the framework of this methodology the principle of parsimony (strict or Wagner parsimony) was chosen as the essential criteria of optimality of character state transformations. It is recognized as intimately related to this principle that, in phylogenetic systematics, the concept of character contains an ideographic component where character-states constitute transformation events (i.e. steps), each of which constitutes a historical moment of a transformation series (Grant & Kluge, 2004). The fewer the transformation events (steps) a phylogenetic hypothesis requires to explain the character-states of the terminal taxa as hypotheses of homology, the greater its explanatory power, a circumstance that justifies the adoption of the principle of parsimony as the only philosophically robust approach in phylogenetic reconstruction, in contrast to model-based methods (Kluge & Grant, 2006; Grant & Kluge, 2008). In this context, the concept of homology is restricted to just those inherited features shared by species (Kluge & Grant, 2006).

CHARACTER SOURCES AND PRESENTATION

Among the several sources or systems of morphological characters traditionally used for the inference of bird phylogeny, the skeleton and the syrinx/trachea were those selected for this study. Both systems have proved to be informative for the reconstruction of passerine relationships in general (Lanyon, 1984, 1986, 1988a, b; Prum, 1992; James, 2004; Claramunt & Rinderknecht, 2005; Manegold, 2008) with some possible synapomorphies having been identified for the Rhinocryptidae in non-cladistic analyses (Feducia & Olson, 1982; Maurício *et al.*, 2008). However, the number of characters in single-system analyses of passeriform groups, e.g. those using only syringeal (Prum, 1992, 1993) or skeletal data alone (Claramunt & Rinderknecht, 2005; Manegold, 2008), is typically around 50 or fewer, and such a relatively low number of characters tends to increase limitations for the resolution of internal relationships. Therefore, the

present analysis focused on the use of the two different systems mentioned above in combination, in a total-evidence approach (see below), which resulted in a relatively large number of characters.

Characters with clearly discrete states were defined after discovery operations consisting of visual inspection/comparisons of bones and syringes under binocular dissecting microscopes (45 and 60× magnification) and, in the case of larger structures, also by inspection using 10 and 20× magnifying hand-lenses. Characters were defined with all terminals simultaneously available for direct comparisons and under ideal conditions at the Museu de Ciências e Tecnologia of PUCRS, except for the skeleton of *Pteroptochos castaneus* and the skeleton and the syrinx of *Scytalopus meridanus* (the former examined through photographs and the latter during a visit at the institution where it was housed; see below). Most of the observed morphological variation was translated into binary characters, although some features with a more diverse presentation across taxa necessarily had to be accommodated into multi-state characters. Characters previously known from the literature were submitted to the same procedures, with some published multi-state characters having been reduced to binary ones.

Characters and character states are presented according to the logical structuring recommended by Sereno (2007). In this context, *character* is defined as an organismal feature expressed as an independent variable and *character states* as its variable conditions, with these two components forming what Sereno (2007) termed *character statement*. Sereno recognizes two patterns for character statements: *transformational* (i.e. those that consider the mutually exclusive conditions of a pre-existing attribute) and *neomorphic* (i.e. 'presence/absence' characters). For transformational character statements, we follow the example *Maxilla, anterior process, length relative to the posterior process: shorter (0); longer (1)* (Sereno, 2007: 573), in which there are four fundamental components: the *locators*, i.e. the terms pointing to general or particular features or structures (the more inclusive/general term first, followed by a more specific one: *Maxilla, anterior process*), a *variable*, i.e. the feature that varies (*length*), a *variable qualifier*, i.e. a phrase that establishes a comparative reference for the variable (*relative to the posterior process*), and the *character states* with their numeric codes. For neomorphic characters we follow the example *Maxilla, anterior process: present (0); absent (1)* (Sereno, 2007: 576), in which there are only two fundamental components: the *locators* and the *character states* with their numerical codes. Note that a single locator may be used in cases in which it is precise enough to place unequivocally the feature of interest. This form of structure stands to substantially reduce variation in presentation of morphology-based

phylogenetic characters, making them easier to evaluate and test (Serenó, 2007).

TAXON SAMPLING

Ingroup

Representatives of all 12 genera presently included in the Rhinocryptidae were sampled for this study. Seven of these are monotypic, and of the five polytypic genera two (*Merulaxis* and *Eleoscytalopus*) were represented in the analyses by their two constituent species whereas the remaining three were only partially covered. Of these three genera, *Scelorchilus*, with two species, was represented by its type species (*S. rubecula*) and *Pteroptochos* by two of its three species (*P. tarnii* and *P. castaneus*), being the only genus whose type species was not represented in this study. Finally, for the genus *Scytalopus*, which is exceptionally diverse (almost 40 named species, with additional taxa awaiting description), widely distributed and scarcely represented in museums by anatomical specimens, distinct and elaborated sampling criteria were established. The first and most important criterion was to obtain the type species to the genus, *S. magellanicus*. A second criterion was to obtain a wide geographical representation for the genus, including taxa from the southern, central and northern Andes and from the eastern section of South America (mainly eastern Brazil). The third criterion was the inclusion in the analyses of taxa pertaining to distinct vocal types, such as species having trilled songs and taxa with songs consisting of a slow repetition of the same note or phrase. A fourth criterion was the sampling of the two basic plumage patterns in the genus, i.e. taxa with plain plumage colours (uniformly black or grey), and species with brown and black barring on the head parts in adult plumage. The fifth criterion was to sample opposite ends of the size range in the genus, prioritarily taking as targets *S. magellanicus*, the smallest species, and *S. macropus*, by far the largest *Scytalopus*. A final criterion was the inclusion of *S. macropus*, as it has been suggested that it might be generically distinct from *Scytalopus* (Whitney, 1994). All the above criteria were fully satisfied by the sampling of *S. magellanicus*, *S. femoralis*, *S. spillmanni*, *S. meridanus*, *S. macropus*, *S. latrans*, *Scytalopus* sp., *S. speluncae*, *S. pachecoi*, and *S. iraiensis*. Therefore, because a comprehensive coverage of the genus *Scytalopus* was achieved and only one species of two polytypic genera could not be obtained, the taxonomic sampling for the ingroup in the present study was highly satisfactory.

Outgroup

Although there are competing hypotheses supporting some particular families as being the sister taxon of

the Rhinocryptidae (see above), both on morphological and on molecular grounds, the present study did not focus on these families to compose the outgroup. The focus of this study was to select the outgroup taxa based on the presence of more inclusive synapomorphies shared with the ingroup, an approach defended by Nixon & Carpenter (1993). The implementation of this logical approach implied the sampling of all other families included in the infraorder Furnariides, a higher-level taxon whose monophyly is supported by syringeal synapomorphies (Ames, 1971; Raikow, 1987; Raikow & Bledsoe, 2000) and several taxonomically comprehensive molecular studies (Sibley & Ahlquist, 1985, 1990; Irestedt *et al.*, 2002, 2009; Barker *et al.*, 2004; Chesser, 2004; Irestedt, Fjeldså & Ericson, 2006; Moyle *et al.*, 2009). The families containing only one or two genera (Melanopareiidae, Conopophagidae, Formicariidae, and Scleruridae) were represented in the analyses by one genus. The remaining four, more diversified families were represented by two or more genera, which were selected to represent to some extent the families' morphological diversity. The following taxa were selected in each family: Thamnophilidae: *Mackenziaena severa*, *Scatleria naevia*, and *Myrmotherula unicolor*; Conopophagidae: *Conopophaga lineata*; Melanopareiidae: *Melanopareia torquata*; Grallariidae: *Grallaria varia*, *Hylopezus macularius*, and *Hylopezus ochroleucus*; Formicariidae: *Formicarius colma*; Scleruridae: *Geositta cunicularia*; Dendrocolaptidae: *Sittasomus griseicapillus* and *Dendrocolaptes platyrostris*; Furnariidae: *Furnarius rufus*, *Cranioleuca sulphurifera*, *Phacellodomus striaticollis*, and *Syndactyla rufosuperciliata*. The sampling of the Furnariidae, moreover, includes representatives of the three subfamilies (Furnariinae, Synallaxinae, Philydorinae; *sensu* Vaurie, 1980) traditionally recognized in this highly diversified family, although these subfamilies' boundaries are not fully congruent with recent molecular phylogenies (Irestedt *et al.*, 2006, 2009; Moyle *et al.*, 2009). Additionally, a member of the sister taxon to the Furnariides (*Pitangus sulphuratus*, family Tyrannidae, infraorder Tyrannides) was sampled as a more distant outgroup, for rooting purposes.

ANATOMICAL TERMINOLOGY

Osteological terms follow Baumel & Witmer (1993) and are in English, with some strictly Latin terms being used when appropriate, in this case highlighted in italics. Terms related to the syrinx/trachea (both supporting elements and muscles) follow Ames (1971). The homology of A and B series of tracheal/bronchial elements (or rings) across taxa was established according to this author, except for the family Thamnophilidae, in which the distinction between A1

and B1 is not clear, a fact already recognized by Ames (1971). In members of this family the B1 element (in lateral view) was unequivocally identified because it is the widest point of the syrinx, and thus the remaining elements (from both A and B series) were determined taking this element as the starting point for the numbering of each series, the B2 element being that immediately caudal and the A1 that immediately cranial to B1 (see Gonzaga, 2001).

SPECIMEN IDENTIFICATION AND PREPARATION OF THE MATERIAL

Identification at the species level, in general, is difficult after preparation of the material for anatomical studies, and thus only after unequivocal determination of a whole specimen can dissecting and preparation techniques take place (Alvarenga, 1992). For the present study specimens representing all genera and almost all species (except *Pterotochos castaneus*) were examined as entire wet or fresh specimens, allowing species-level identification, being dissected only subsequently. In most cases the skin of these specimens was prepared as a shmoo, i.e. a 'traditional' dry study skin without bill and leg and wing from one side. This procedure allows future re-evaluation of species identification if necessary. Regarding the taxonomically complicated genus *Scytalopus*, particular care was employed in specimen identification, especially for those that were not tape-recorded (see Krabbe & Schulenberg, 1997, 2003). This concern is particularly justified for the Andean counterpart of the genus, as its taxonomy shows several problems and cryptic species (generally not separable by plumage and measurements) can occur at the same locality or within a small altitudinal interval (Krabbe & Schulenberg, 1997, 2003). With only one exception, all specimens of this genus included in this study were positively identified to the species level. The exception was a specimen (LSUMZ 89465) from Cordillera Colán, north-eastern Peru, whose original label reads '*Scytalopus unicolor*'. However, the database of the LSUMZ collection presently identifies it as *Scytalopus* sp. In fact, *S. unicolor* was recently circumscribed to a population restricted to the western Andes of northern Peru, with its former subspecies (including *intermedius*, the form expected for the Cordillera Colán) being lumped under *S. latrans* (Coopmans, Krabbe & Schulenberg, 2001). Analyses of the plumage, measurements, and distribution indicate that LSUMZ 89465 could be attributed to both *S. latrans intermedius* and to a taxon related to *S. parvirostris* (N. Krabbe, in litt., 2009). Although vocal data would probably be decisive in species identification, there is no tape-recording of any *Scytalopus* from Cordillera Colán (T. Schulenberg, in litt., 2009). Given

that *intermedius* appears to be fully diagnosable from *S. latrans* based on plumage and possibly also vocally (Coopmans *et al.*, 2001), and that the specimen in question could also be referable to the *S. parvirostris* complex, that specimen is included here as *Scytalopus* sp., an uncertainty also expressed in the database of the LSUMZ collection. All specimens used in this study are listed in Appendix 1.

Skeletons were prepared with dermestid beetles, by manual dissection and by maceration in distilled water at 50 °C (see Alvarenga, 1992). The syringes were extracted from carcasses (except a few previously extracted by museum personnel) after determination of the point of origin of the *Musculus sternotrachealis* (i.e. if originating on the costal process of the sternum or on the medial surface of the second rib) and then prepared according to the following protocol. First, each syrinx was fixed in 10% formalin for several days (usually 3–7 days) and then transferred to 70% ethyl alcohol. Posteriorly, the syringes were stained with Alizarin Red S diluted in 75% ethyl alcohol over 24–48 h. This solution stains calcified tissue deep red and, in being alcohol-based, does not macerate muscles as do traditional (e.g. Cannell, 1988) solutions with KOH, having also the advantage of staining muscular fibres with a reddish tone (Springer & Johnson, 2000). Subsequently, the material was stained with alcian blue over 24–48 h to highlight cartilaginous tissue (see Cannell, 1988). After the study and dissection of the syringeal musculature each dissected syrinx was cleared in enzymatic solution with trypsin (see Taylor & Van Dyke, 1985; Cannell, 1988) to highlight the previously stained supporting elements. Finally, after being examined and drawn, the syringes were stored in 70% glycerin (cleared) or in 70% ethyl alcohol (non-cleared). Drawings were produced with a camera lucida adapted to binocular dissecting microscopes (45 and 60× magnification).

PHYLOGENETIC ANALYSES

Character states of the terminal taxa were entered into a taxon/character matrix in the program Mesquite, version 2.71 (Maddison & Maddison, 2009) (Appendix 2), whereas the parsimony analysis of this dataset was run with Nona (Goloboff, 1999) via WinClada, version 1.00.08 (Nixon, 2002). All multi-state characters were treated as unordered unless ontogenetic evidence supporting additivity of states was available. Characters were given equal weight and the polymorphic characters were treated as such in the analysis.

Heuristic searches for the most parsimonious cladograms consisted of 10 000 replications with random addition sequence (RAS) of taxa followed by branch swapping using the tree bisection-reconnection algo-

rithm (TBR), with an additional TBR by the end. The maximum number of trees to be held in the program's memory was adjusted to 100 000, which is the maximum allowed by the program. All maximally parsimonious trees obtained in the cladistic analysis were summarized in a strict consensus diagram, in which only the clades that were recovered in all optimal trees are maintained. Only those characters with unambiguous optimization are presented in the resulting trees (i.e. either ACCTRAN or DELTRAN were not favoured in this study). An analysis using these same parameters was performed without the four incomplete terminals (*Eleoscytalopus psychopomus*, *Merulaxis stresemanni*, *Scytalopus speluncae* and *S. iraiensis*, for which only partial skeletons were available) to check their effect on the outcome of the parsimony analysis.

Inferences about polarity of the transformation series were derived a posteriori from the rooting of the tree in a more distant outgroup (see below). Relationships of both ingroup and outgroup taxa were resolved simultaneously in a single analysis of global parsimony, as explained and recommended by Nixon & Carpenter (1993). However, contrary to what has been suggested by those authors, the root was not placed in the internode between ingroup and outgroup, which would result in both being monophyletic (de Pinna, Ferraris & Vari, 2007). Therefore, the root was fixed in *Pitangus sulphuratus* (Tyrannidae), a representative of a more distant outgroup, the infraorder Tyrannides, which is widely accepted as being the sister taxon to the Furnariides (see above). Clade support was evaluated with Bremer support index, which is expressed, for a given clade, as the difference between the length (i.e. the number of transformation events or steps) of the globally most parsimonious tree(s) and the length of the optimal tree(s) where that clade has disappeared (Bremer, 1994; Grant & Kluge, 2008). Bremer support was calculated by using the program Nona (Goloboff, 1999), with searches for trees up to 12 steps longer than the optimal ones.

The two character systems considered in this study (skeleton and syrinx) were analysed in combination, following the claim of Kluge (1989) in favour of a total-evidence approach, which postulates that the best, more robust hypothesis is that taking into consideration the greater amount of evidence. Furthermore, the sensibility of this approach has been recognized by several authors (see Chu, 1998; Griffiths, 1999).

RESULTS

CHARACTER ANALYSIS

Here we describe the 90 morphological characters used in this study. These are arranged according to

the two major systems considered here: the skeleton (characters 1–62) and the syrinx/trachea (characters 63–90). The former is further divided into skull (1–39) and postcranium (40–62), and the latter into supporting elements (63–82) and musculature (83–90).

Each character statement is followed by a brief text in which some complementary information is given, including previous mentions of the character in the literature regarding the infraorder Furnariides. Authors who have described similar characters in groups of birds other than the Furnariides are not mentioned. For instance, an open or closed bottom of the fossa pneumatica of the humerus, a variation described as occurring among the Furnariides for the first time in this paper, is also found in other groups such as anatids (Livezey, 1986) and finches (James, 2004), but these papers are not mentioned in the character's account assuming that the occurrence of the relevant conditions in such diverse groups is the result of homoplasy.

Skeleton – skull

1. Premaxilla, rostrum, length relative to the maxilla: longer (0); shorter (1); Figure 1. For this character, the length of the rostrum is taken as the distance between its tip and the anterior margin of the nasal opening and that of the maxilla as being the distance from the latter to the caudal margin of the maxillary process of the nasal. In the Melanopareiidae and the Rhinocryptidae, except *Liosceles* and *Psilorhamphus*, the premaxillary rostrum is short.
2. Premaxilla, nasal process, form: not arched (0); smoothly arched (1); strongly arched (2); developed into a high crest (3); Figure 1. In most rhinocryptid genera the nasal process of the premaxilla is arched to some degree. Feduccia & Olson (1982) noted the existence of a distinctly arched culmen in skulls of the rhinocryptid genera *Liosceles*, *Myornis*, and, to an extreme degree, in *Acropternis*, also noting that from skins it would appear that *Merulaxis* and *Eugralla* also have such a condition, especially developed in the former. See also Claramunt & Rinderknecht (2005; character 4) and Claramunt *et al.* (2010; character 2).
3. Premaxilla, nasal process (mesorhinum), width relative to the width of the rostral portion of the maxilla plus the adjacent rostral portion of the maxillary process of the palatine: wider (0); narrower (1). In most rhinocryptids and some outgroup taxa the nasal process of the premaxilla is narrow.
4. Maxilla, pneumatization: fully pneumatized (0); non-pneumatized (1). In most rhinocryptids and Melanopareiidae the maxilla is not pneumatized.
5. Nasal septum, ossification: unossified (0); largely ossified (1). In some outgroup taxa examined (most

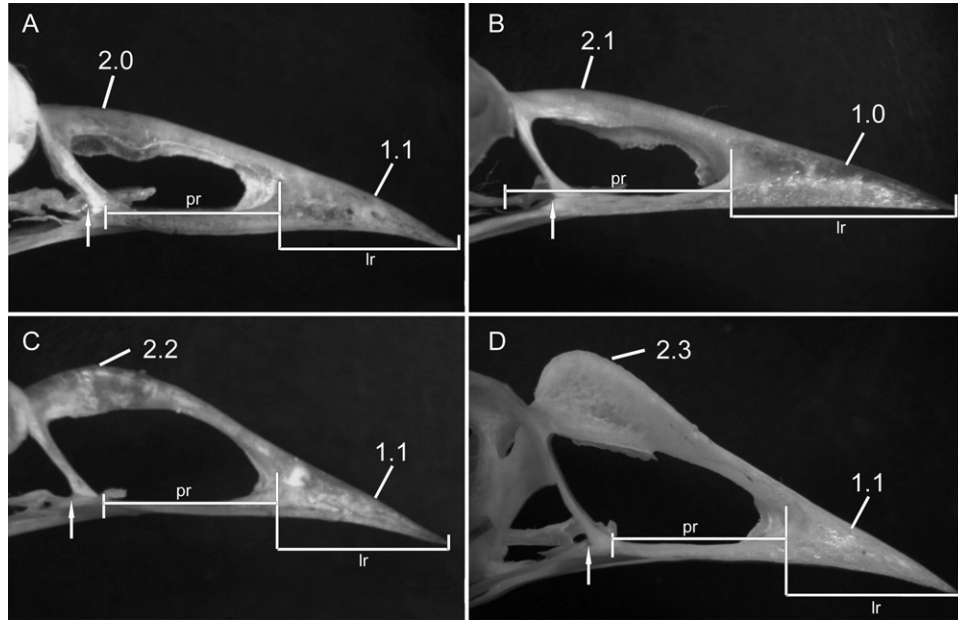


Figure 1. Characters 1 and 2 and their postulated states. Char. 1. Premaxilla, rostrum, length relative to the maxilla: B, longer – 1.0; A, C, D, shorter – 1.1. Lr is the length of the rostrum and pr is its caudal projection over the maxilla; an arrow marks the caudal margin of the maxillary process of the nasal (see text). Char. 2. Premaxilla, nasal process, form: A, not arched – 2.0; B, smoothly arched – 2.1; C, strongly arched – 2.2; D, developed into a high crest – 2.3. Rostrum of (A) *Rhinocrypta lanceolata* (MCP 2395), (B) *Liosceles thoracicus* (MPEG O-3953), (C) *Eugralla paradoxa* (MCP 2398) and (D) *Acropternis orthonyx* (QCAZ 3723) in lateral view. Not to scale.

furnariids and Tyrannidae) the nasal septum is composed by a large ossified wall that covers most of the septal space medially. Claramunt & Rinderknecht (2005; character 9) found an extensively ossified nasal septum in several genera of the Furnariidae and Dendrocolaptidae. See also Claramunt *et al.* (2010; character 4).

6. Nasal septum, recurrent lamina, length relative to the width at base: longer (0); shorter (1). According to Claramunt & Rinderknecht (2005; character 10), the recurrent lamina is the distal end of the nasal septum which bends ventrally and then caudally. The long condition occurs in most Furnariidae, Scleruridae, Dendrocolaptidae, Rhinocryptidae, Conopophagidae, and *Pitangus* (Tyrannidae).
7. Nasal and alinasal walls, ossification: unossified (0); ossified (1). The ossification of the nasal and alinasal laminae produces a sheet of bone that covers the external nares of some birds (the 'amphirhinal' condition; Ihering, 1915; Feduccia, 1967), a condition that is typical of the Thamnophilidae and Conopophagidae. See Claramunt & Rinderknecht (2005; characters 11 and 12) and Claramunt *et al.* (2010; characters 5 and 6).
8. Nares, caudal margin, extension relative to the culmen level: ventral (0); dorsal (1). In some outgroup families examined (Scleruridae, Dendrocolaptidae and Furnariidae) the caudal margin of

the nasal opening extends dorsal to the level of the culmen. See Tonni & Noriega (2001; character 12), Claramunt & Rinderknecht (2005; character 13), and Claramunt *et al.* (2010; character 7), who compared the position of the caudal extension of the nares with the position of the craniofacial hinge.

9. Nasal, premaxillary process, lateral border, shape: concave (0); convex (1). In the outgroup family Furnariidae the lateral border of the premaxillary process of the nasals is convex (see Claramunt & Rinderknecht, 2005; character 14).
10. Maxillopalatine, shape: shaft or pedicel wide, not contrasting in width with the plate (0); shaft or pedicel very narrow, contrasting in width with a wide plate (1); Figure 2. Two rhinocryptid genera (*Teledromas* and *Rhinocrypta*) have the maxillopalatine shaft contrastingly narrow in comparison with the plate. See Claramunt & Rinderknecht (2005; characters 15 and 16) and Claramunt *et al.* (2010; characters 8 and 9), who considered the width of the shaft and that of the plate as separate characters.
11. Transpalatine process, length relative to the width of the palatine plate: shorter (0); as long as or longer (1). See Claramunt & Rinderknecht (2005; character 19) and Claramunt *et al.* (2010; character 10).

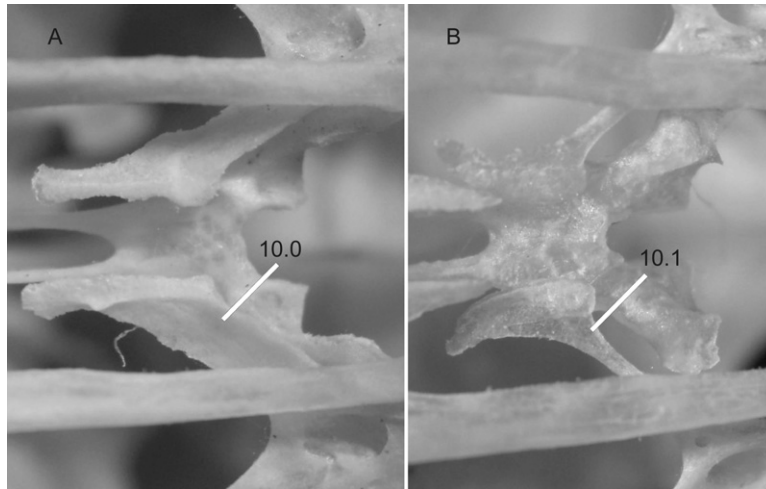


Figure 2. Character 10 and its postulated states. Maxillopalatine, shape: A, shaft or pedicel wide, not contrasting in width with the plate – 10.0; B, shaft or pedicel very narrow, contrasting in width with a wide plate – 10.1. Palatum of (A) *Pteroptochos tarnii* (MCP 2397) and (B) *Teledromas fuscus* (MCP 2396) in ventral view. Not to scale.

12. Jugal bar, shape: straight or slightly curved (0); sinusoidal (1); Figure 3. In half of the Rhinocryptidae genera and some outgroup taxa the jugal bar is clearly sinusoidal.
13. Jugal bar, rostral portion, lateral margin: not emarginated (0); emarginated (1); Figure 4. In *Scytalopus* (Rhinocryptidae) the lateral margin of the rostral portion of the jugal bar is enlarged and emarginated.
14. Vomer and alinasal turbinals, configuration: unfused or unossified alinasal turbinals (0); alinasal turbinals ossified and fused to the vomer (1); Figure 5. In Rhinocryptidae, Furnariidae, Dendrocolaptidae, and Scleruridae the alinasal turbinals are ossified and fused to the rostral margin of the vomer, one on each side, forming a compound, forked vomer. See Claramunt & Rinderknecht (2005; character 21) and Claramunt *et al.* (2010; character 11).

Remarks: Claramunt & Rinderknecht (2005) observed ossified alinasal turbinals fused to the vomer only in Rhinocryptidae and several, but not all, genera of Furnariidae examined by them. In the present study this condition was observed in Scleruridae, Dendrocolaptidae, Rhinocryptidae, and all Furnariidae taxa examined, although it was observed that the alinasal turbinals of the compound vomer, even if fully ossified, may be lost during the process of preparation of the skeletons due to excessive exposure to the dermestid beetles. For instance, in a specimen of *Phacellodomus striaticollis* (MCP 2639) only one of the two ossified alinasal turbinals remained attached to the vomer, with the point of attachment being very thin; this very limited area of fusion between the two bony structures

plus long exposure to the dermestid beetles probably led to loss of the alinasal turbinal from the other side. In a control inspection during preparation of a specimen of *Teledromas fuscus* (MCP 2396) the two ossified alinasal turbinals were present and well fused to the vomer but next day one of them had been removed by the dermestids. Previously prepared skeletons of furnariid genera not included in the cladistic analysis (*Limnornis* and *Phleocryptes*) showed ossified alinasal turbinals that were firmly fused to the vomer. Although an exhaustive examination of specimens of Furnariidae has not been conducted for this study, it is suggested here that the compound vomer has a generalized occurrence in this family and that its absence in many museum specimens may be the result of an exceedingly long exposure to the dermestid beetles in combination with a very limited surface of fusion between the vomer and the turbinals.

On the other hand, these findings raised the suspicion that the apparent absence of a compound vomer in families such as Grallariidae, Formicariidae, and Conopophagidae might be, at least in part, the result of inadequate preparation of the skeletal specimens via the beetles. Thus, we dissected alcohol-stored specimens of taxa pertaining to families typically without a compound vomer to provide better appreciation of this character. Careful dissection of the nasal cavity of specimens of Conopophagidae (*Conopophaga lineata*, MCP 2490), Thamnophilidae (*Mackenziaena severa*, MCP 2505; *Sclateria naevia*, MCP 2508), Grallariidae (*Hyllopezus macularius*, MPEG A-6921), and Formicariidae (*Formicarius analis*, MPEG A-4632) revealed soft, completely cartilaginous alinasal turbinals firmly attached not only to the distal end of the vomer but also to adjoining surfaces. As the turbinals are not ossified

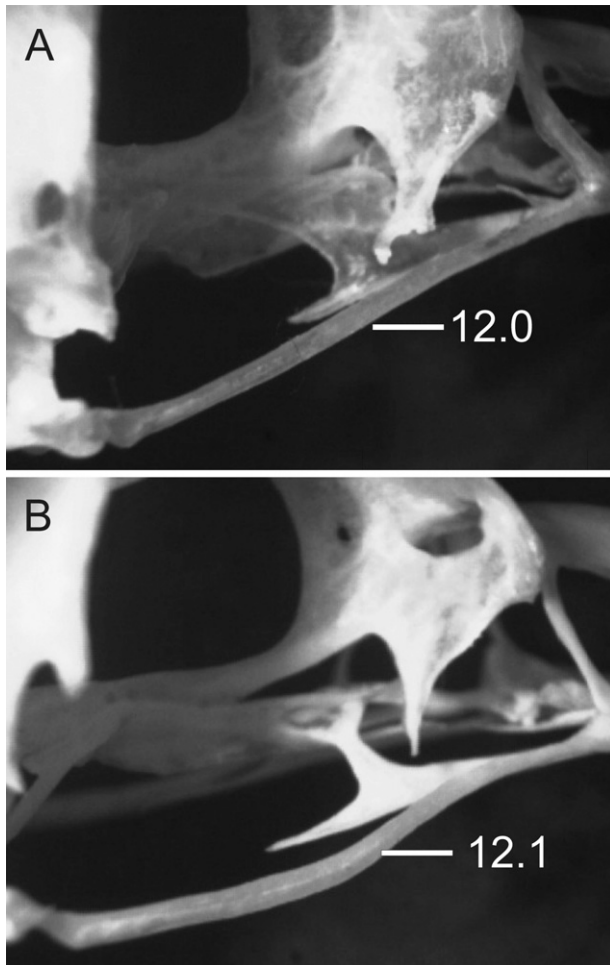


Figure 3. Character 12 and its postulated states. Jugal bar, shape: A, straight or slightly curved – 12.0; B, sinuoidal – 12.1. Skulls of (A) *Rhinocrypta lanceolata* (MCP 2395) and (B) *Liosceles thoracicus* (MPEG O-3953) in caudolateral view. Not to scale.

in these families, they may be easily eliminated by the dermestids. Therefore, the validity of this character regarding its postulated variation among Furnariides was corroborated by our data.

15. Compound vomer, alinasal turbinals, disposition: parallel (0); approaching distally (1); Figure 6. In *Teledromas* and *Rhinocrypta* (Rhinocryptidae), the alinasal turbinals of the compound vomer converge distally.
16. Compound vomer, alinasal turbinals, configuration: untwisted (0); twisted (1); Figure 7. In *Teledromas* and *Rhinocrypta* (Rhinocryptidae), the distal half of the alinasal turbinals of the compound vomer are twisted dorsally, i.e. the lateral portion of each turbinal is turned up.
17. Quadrate, mandibular process, lateral condyle, width relative to the caudal end of the jugal bar: nearly as narrow (0); wider (1). In *Teledromas* and *Rhinocrypta* (Rhinocryptidae), the lateral condyle of the mandibular process of the quadrate is very wide, contrasting with the narrow caudal end of the jugal bar, with which it articulates.
18. Ectethmoid, dorsal portion, extension relative to the culmen level: at the same level or below (0); well above (1); Figure 8. In *Pteroptochos* and *Scelorchilus* (Rhinocryptidae), the ectethmoid plate extends dorsally well above the level of the culmen.
19. Ectethmoid, pneumatization: fully pneumatized (0); non-pneumatized (1). In the Rhinocryptidae the ectethmoid is almost completely non-pneumatized, comprising a single, very thin wall with one or two restricted points of pneumatization, whereas in the outgroup taxa and birds in general the bone is composed of two walls, a rostral and a caudal one between which all space is highly pneumatized.
20. Ectethmoid, jugal projection, ventral portion, width relative to the distance between the lateral margin of the palatine and the jugal bar: nearly as wide or wider (0); narrower (1). In Rhinocryptidae and Furnariidae the jugal projection of the ectethmoid is narrow. In this character, the lacrimal, either fused or unfused to the ectethmoid, is taken into consideration together with the jugal projection of the latter. See Ames, Heimerdinger & Warter (1968), Claramunt & Rinderknecht (2005; character 24), and Claramunt *et al.* (2010; character 14).
21. Ectethmoid and the jugal bar, distance between the bones: in contact (0); largely separated (1). In the Rhinocryptidae and some outgroups the jugal projection of the ectethmoid is separated by a considerable distance from the jugal bar. In this character, the lacrimal, either fused or unfused to the ectethmoid, is taken in consideration together with the jugal projection of the latter. Ames *et al.* (1968) illustrated the contact between the ectethmoid/lacrimal with the jugal bar in Conopophagidae, Thamnophilidae, and Tyrannidae.
22. Ectethmoid, rostral surface, lateral portion, projection: absent (0); present (1); Figure 9. In *Scelorchilus* and *Pteroptochos* (Rhinocryptidae), there is a wide rostral projection, directed rostro-medially, in the lateral portion of the ectethmoid.
23. Ectethmoid, rostral surface, medial portion, projection: absent (0); present (1); Figure 9. In *Scelorchilus* and *Pteroptochos* (Rhinocryptidae), the rostral surface of the ectethmoid has a large, rostrally directed projection in its medial portion.
24. Ectethmoid, medial opening: absent (0); present (1); Figure 10. In *Pteroptochos* and some *Scytalo-*

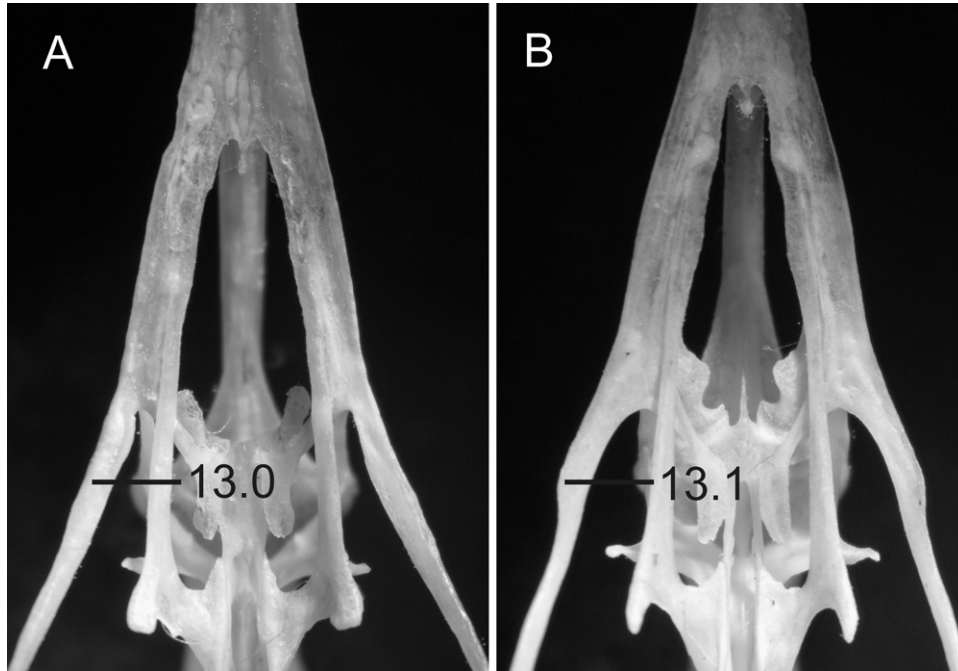


Figure 4. Character 13 and its postulated states. Jugal bar, rostral portion, lateral margin: A, not emarginated – 13.0; B, emarginated – 13.1. Skulls of (A) *Myornis senilis* (QCAZ 3724) and (B) *Scytalopus spillmanni* (QCAZ 3536) in ventral view. Not to scale.

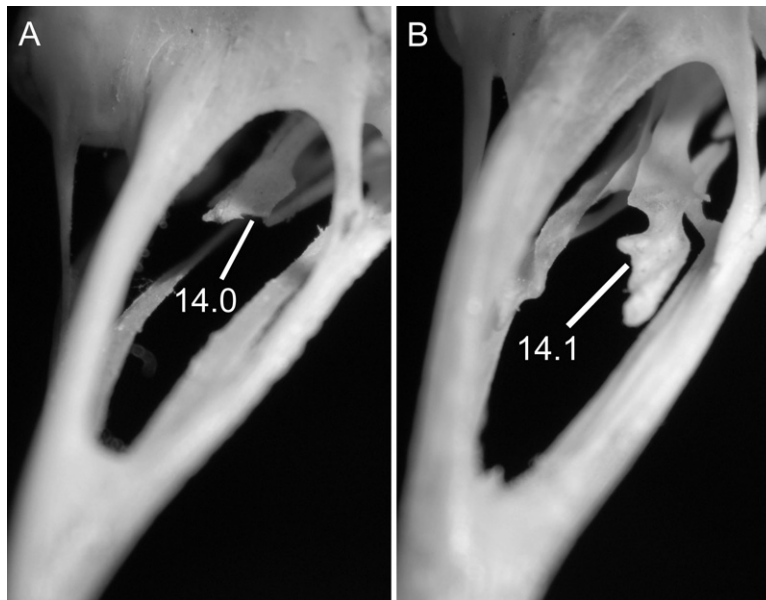


Figure 5. Character 14 and its postulated states. Vomer and alinasal turbinals, configuration: A, unfused or unossified alinasal turbinals – 14.0; B, alinasal turbinals ossified and fused to the vomer – 14.1. Rostrum of (A) *Melanopareia torquata* (MCP 2271) and (B) *Merulaxis ater* (MCP uncatalogued) in craniodorsolateral view. Not to scale.

pus taxa (Rhinocryptidae), there is a semi-circular opening in the medial portion of the ectethmoid.
25. Ectethmoid, lateral portion, orientation: laterally or rostromedially directed (0); rostrally directed

(1); Figure 11. In *Scytalopus* and *Psilorhamphus* (Rhinocryptidae), the lateral portion of the ectethmoid is rostrally directed due to a strong arching of the bone.

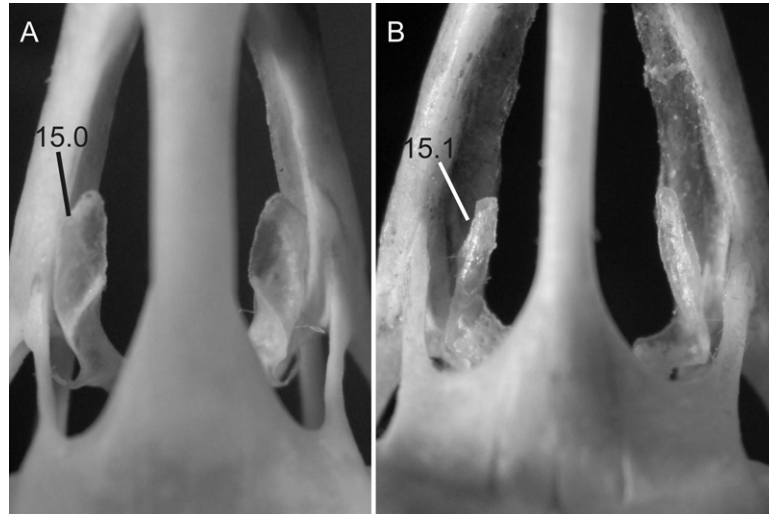


Figure 6. Character 15 and its postulated states. Compound vomer, alinasal turbinals, disposition: A, parallel – 15.0; B, approaching distally – 15.1. Rostrum of (A) *Liosceles thoracicus* (MPEG O-3953) and (B) *Rhinocrypta lanceolata* (MCP 2395) in dorsal view. Not to scale.

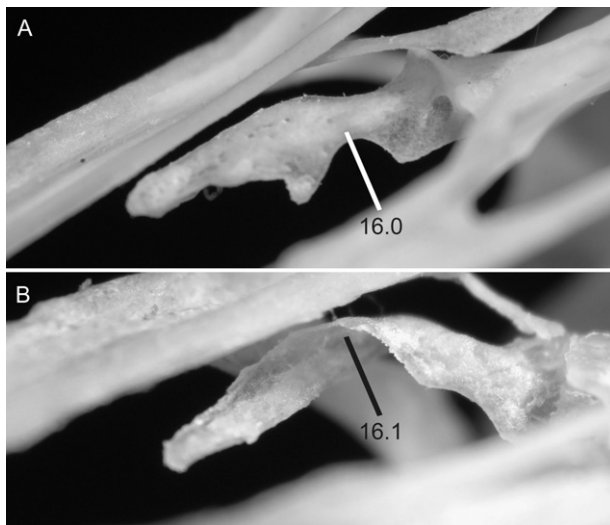


Figure 7. Character 16 and its postulated states. Compound vomer, alinasal turbinals, configuration: A, untwisted – 16.0; B, twisted – 16.1. Palatum of (A) *Merulaxis ater* (MCP uncatalogued) and (B) *Rhinocrypta lanceolata* (MCP 2395) in ventrolateral view. Not to scale.

26. Lacrimal, configuration: free, only adhered (unfused) to the ectethmoid (0); partially fused to the ectethmoid, with the suture between the bones being discernible (1); completely fused to the ectethmoid, with no points of suture being discernible between the bones (2); Figure 12. It is well known that in the Furnariides the lacrimal is absent or totally incorporated (fused) to the ectethmoid, whereas in the infraorder Tyrannides and Old World suboscines the lacrimal is present

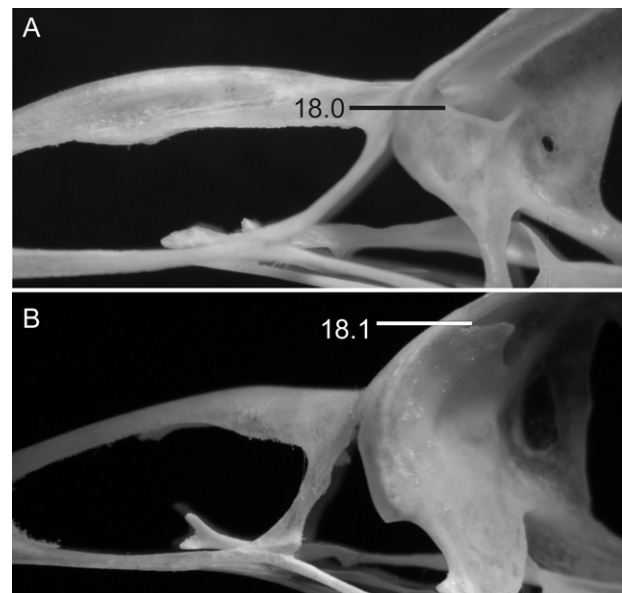


Figure 8. Character 18 and its postulated states. Ectethmoid, dorsal portion, extension relative to the culmen level: A, at the same level or below – 18.0; B, well above – 18.1. Skulls of (A) *Merulaxis ater* (MCP uncatalogued) and (B) *Pteroptochos tarnii* (MCP 2397) in lateral view. Not to scale.

and free, unfused to the ectethmoid (Ames *et al.*, 1968; Feduccia & Olson, 1982; McKittrick, 1985; Prum & Lanyon, 1989). However, Ames *et al.* (1968) and Feduccia & Olson (1982) highlighted that in the Rhinocryptidae the lacrimal is only partially fused, with a suture discernible between it and the ectethmoid, and suggested that in the

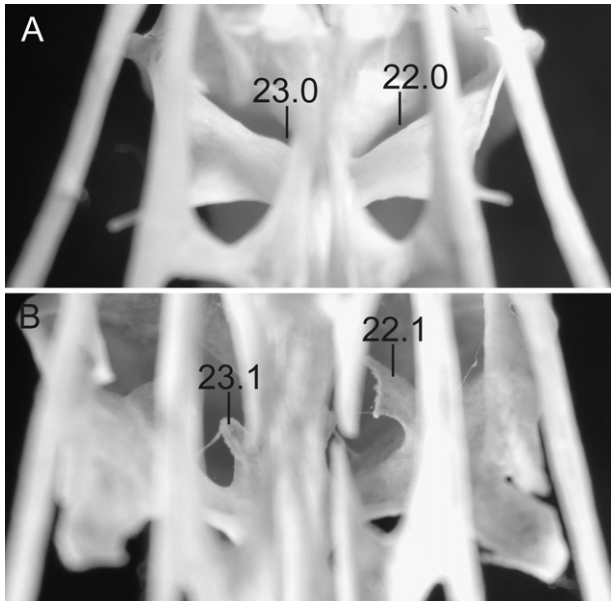


Figure 9. Characters 22 and 23 and their postulated states. Char. 22. Ectethmoid, rostral surface, lateral portion, projection: A, absent – 22.0; B, present – 22.1. Char. 23. Ectethmoid, rostral surface, medial portion, projection: A, absent – 23.0; B, present – 23.1. Skulls of (A) *Liosceles thoracicus* (MPEG O-3953) and (B) *Pteroptochos tarnii* (MCP 2397) in ventral view. Not to scale.

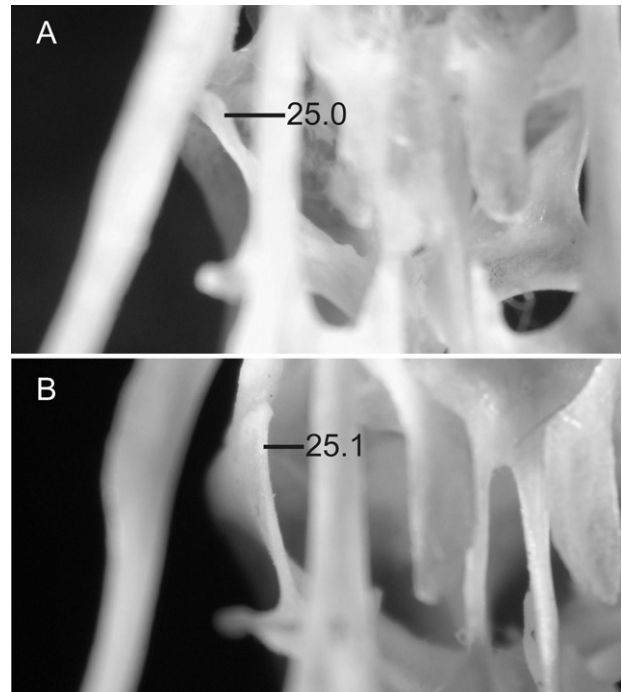


Figure 11. Character 25 and its postulated states. Ectethmoid, lateral portion, orientation: A, laterally or rostrolaterally directed – 25.0; B, rostrally directed – 25.1. Skulls of (A) *Myornis senilis* (QCAZ 3724) and (B) *Scytalopus spillmanni* (QCAZ 3536) in ventral view. Not to scale.

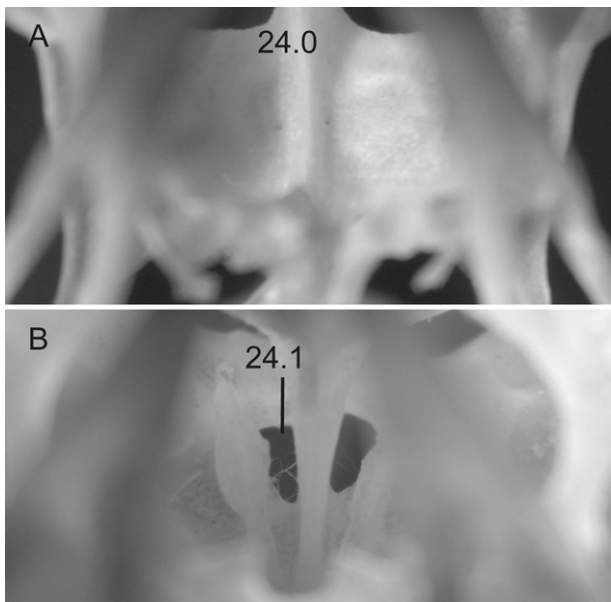


Figure 10. Character 24 and its postulated states. Ectethmoid, medial opening: A, absent – 24.0; B, present – 24.1. Ectethmoid of (A) *Liosceles thoracicus* (MPEG O-3953) and (B) *Pteroptochos tarnii* (MCP 2397) in rostral view. Not to scale.

other Furnariides the lacrimal might be present and completely incorporated (i.e. with no suture discernible) to the former bone.

Remarks: The ornithological literature, taken as a whole, is not decisive regarding the status of the lacrimal in most families of Furnariides, i.e. if it is present and completely incorporated into the ectethmoid, with no suture between the bones, or if it is absent, but when this question is critically evaluated there is an apparent tendency to accept the former hypothesis (e.g. Feduccia & Olson, 1982). It was observed that in the genus *Chamaeza* (Formicariidae), not included in the present phylogenetic analysis, the lacrimal is present, large, and only adhered (unfused) to the ectethmoid, exactly the same condition found in the infraorder Tyrannides. It was further observed that the lacrimal in this genus easily disarticulates from the ectethmoid, a fact that probably has been responsible for the omission of its presence in this genus in the literature. With the loss of the lacrimal, the resulting configuration of the ectethmoid when compared with other taxa (e.g. *Formicarius*, *Grallaria*) is that of a laterally limited bone, being barely visible in frontal view. Given that in

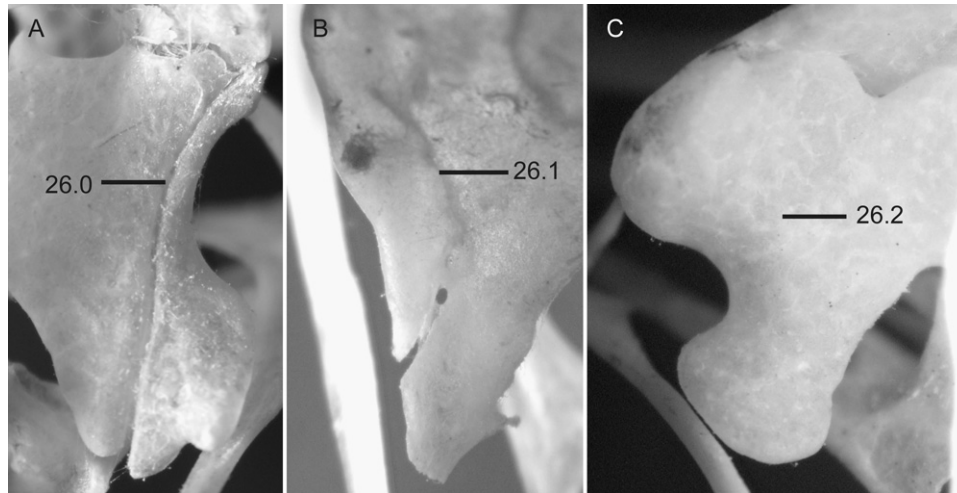


Figure 12. Character 26 and its postulated states. Lacrimal, configuration: A, free, only adhered (unfused) to the ectethmoid – 26.0; B, partially fused to the ectethmoid, with suture being discernible – 26.1; C, completely fused to the ectethmoid, with no points of suture being discernible – 26.2. Ectethmoid/lacrimal complex of (A) *Pitangus sulphuratus* (MCP 2288), (B) *Scelorchilus rubecula* (MCP 2400), and (C) *Melanopareia torquata* (MCP 2271) in caudolateral view. Not to scale.

Formicarius, *Grallaria*, *Furnarius*, and several other genera the lateral portion of the ectethmoid is well exposed in frontal view, as is the case when the lacrimal is present and discernible (as in rhinocryptids and tyrannids), it is suggested here that this 'lateral portion of the ectethmoid' actually represents part or the whole lacrimal completely fused to the ectethmoid plate. Therefore, it is assumed here that the lacrimal is present in all members of Furnariides, be it free (as in *Chamaeza*), partially or entirely fused to the ectethmoid, with no suture between the bones. Material of the genus *Chamaeza* examined for this character (not mentioned in the Appendix) includes specimens of *C. campanisona*, *C. meruloides*, and *C. ruficauda* from MHNT, MCP, and MZUSP.

27. Lacrimal, general configuration: narrow dorsally and wide ventrally (0); wide dorsally, narrower ventrally (1); wide dorsally, being not discernible (possibly missing) ventrally (2); vestigial, very narrow dorsally and absent ventrally (3); Figure 13. In the Rhinocryptidae the lacrimal bone is distinctly divisible into three types, with the largest one (state 1) of large genera (e.g. *Rhinocrypta* and *Pteroptochos*) at one end and the vestigial condition (state 3) of smaller genera (e.g. in *Scytalopus* and *Psilorhamphus*) at the other.
28. Lacrimal, rostral surface, foramen: present (0); absent (1); Figure 14. In *Scelorchilus* and *Pteroptochos* (Rhinocryptidae), the lacrimal bears a conspicuous, rounded foramen in its rostral surface.

29. Interorbital septum, configuration: comprises an extensive ossified wall covering most of the orbit and a short osseous beam caudally (0); comprises an ossified wall that covers the rostral half of the orbit and an osseous beam in the caudal half (1); comprises a short, ossified rostral wall (covering between about one-third and one-quarter of the interorbital space) and a long osseous beam in the remaining caudal portion (2); comprises a short, ossified rostral wall (covering about one-quarter of the interorbital space), but only vestiges of an osseous beam in the caudal portion (3); Figure 15. As highlighted by Feduccia & Olson (1982), in most rhinocryptids the interorbital septum is almost completely unossified (state 3). See Claramunt & Rinderknecht (2005; characters 25 and 26) and Claramunt *et al.* (2010; character 15).
30. Frontal, ridges: present (0); absent (1). A ridge in the midline of the frontal is present in some outgroup taxa. See Claramunt & Rinderknecht (2005; character 28) and Claramunt *et al.* (2010; character 17).
31. Region of the parietal and frontal bones, pneumatization: fully pneumatized (0); largely non-pneumatized (1). In the Rhinocryptidae (except *Rhinocrypta* and *Teledromas*) and some furnariids almost all the region dorsal to the temporal fossae (i.e. corresponding mainly to the parietal bone) and the adjacent portion of the frontals are non-pneumatized. Feduccia & Olson (1982) observed that several rhinocryptid genera had poorly pneumatized parietals, a condition also

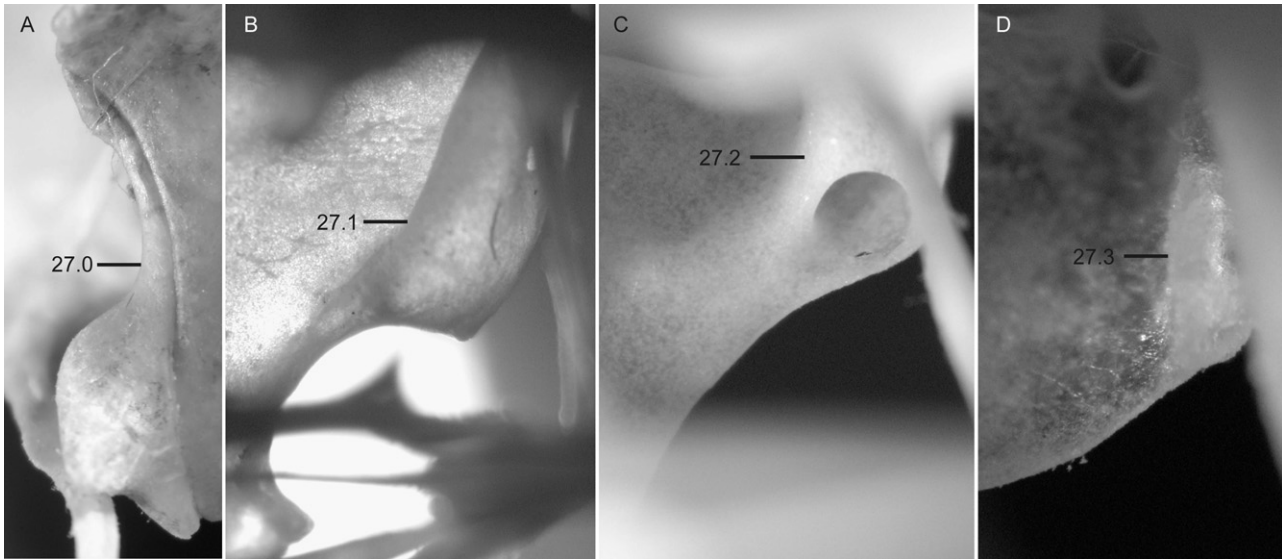


Figure 13. Character 27 and its postulated states. Lacrimal, general configuration: A, narrow dorsally and wide ventrally – 27.0; B, wide dorsally, narrower ventrally – 27.1; C, wide dorsally, missing ventrally – 27.2; D, vestigial – 27.3. Ectethmoid/lacrimal complex of (A) *Pitangus sulphuratus* (MCP 2288) in caudal view and of (B) *Pteroptochos tarnii* (MCP 2397), (C) *Eleoscytalopus indigoticus* (MCP 2201) and (D) *Eugralla paradoxa* (MCP 2398) in medial view. Not to scale.

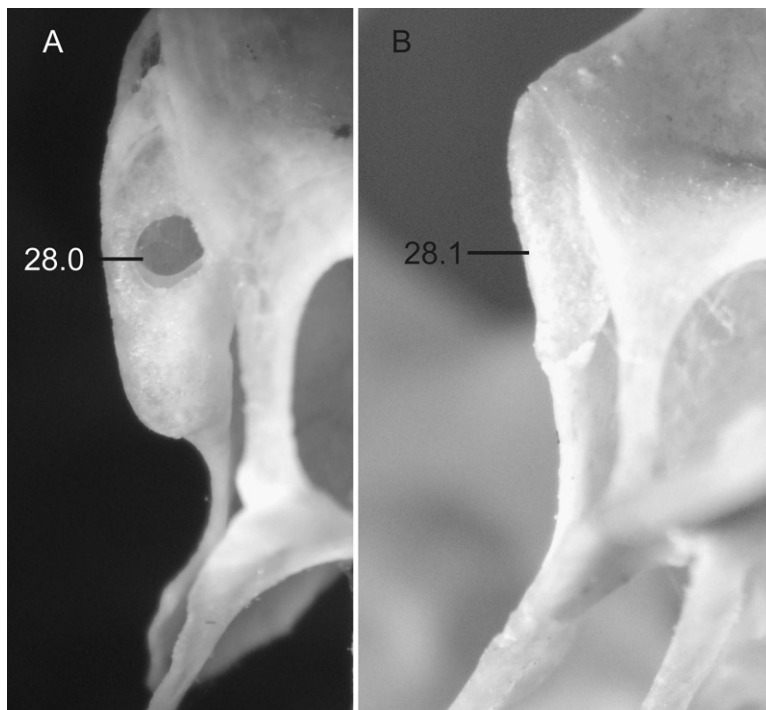


Figure 14. Character 28 and its postulated states. Lacrimal, rostral surface, foramen: A, present – 28.0; B, absent – 28.1. Lacrimal of (A) *Pteroptochos tarnii* (MCP 2397) and (B) *Rhinocrypta lanceolata* (MCP 2395) in frontal view. Not to scale.

reported for *Merulaxis* by Sick (1960), for *Scytalopus* by Krabbe & Schulenberg (1997), and for the latter genus and *Eleoscytalopus* by Bornschein *et al.* (1998).

32. Postorbital and zygomatic processes, fusion: unfused (0); fused (1); Figure 16. In *Rhinocrypta* and *Teledromas* (Rhinocryptidae) and some out-group taxa the postorbital process reaches the

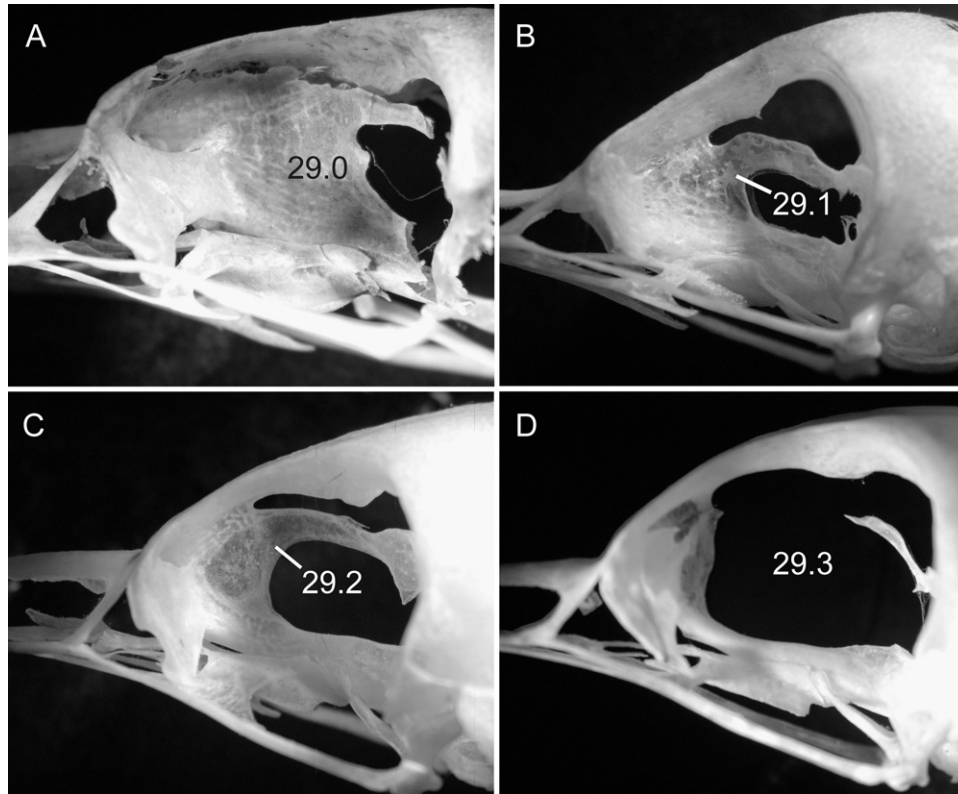


Figure 15. Character 29 and its postulated states. Interorbital septum, configuration: A, large ossified wall with a short osseous beam caudally – 29.0; B, ossified wall covering the rostral half of the orbit with an osseous beam in the caudal half – 29.1; C, short ossified rostral wall and a long osseous beam in the remaining caudal portion – 29.2; D, short ossified rostral wall with vestigial osseous beam in the caudal portion – 29.3. Skulls of (A) *Pitangus sulphuratus* (MCP 2288), (B) *Geositta cunicularia* (MCP 2632), (C) *Teledromas fuscus* (MCP 2396), and (D) *Scelorchilus rubecula* (MCP 2400) in lateral view. Not to scale.

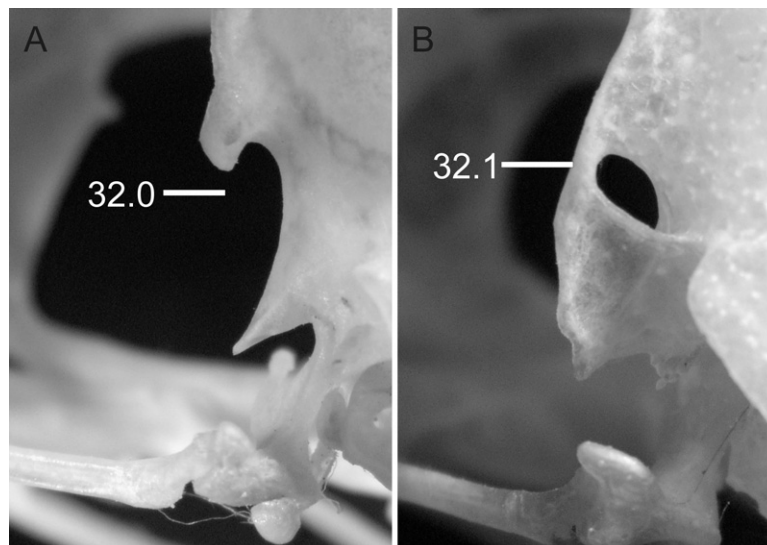


Figure 16. Character 32 and its postulated states. Postorbital and zygomatic processes, fusion: A, unfused – 32.0; B, fused – 32.1. Postorbital region of skulls of (A) *Merulaxis ater* (MCP uncatalogued) and (B) *Teledromas fuscus* (MCP 2396) in caudolateral view. Not to scale.

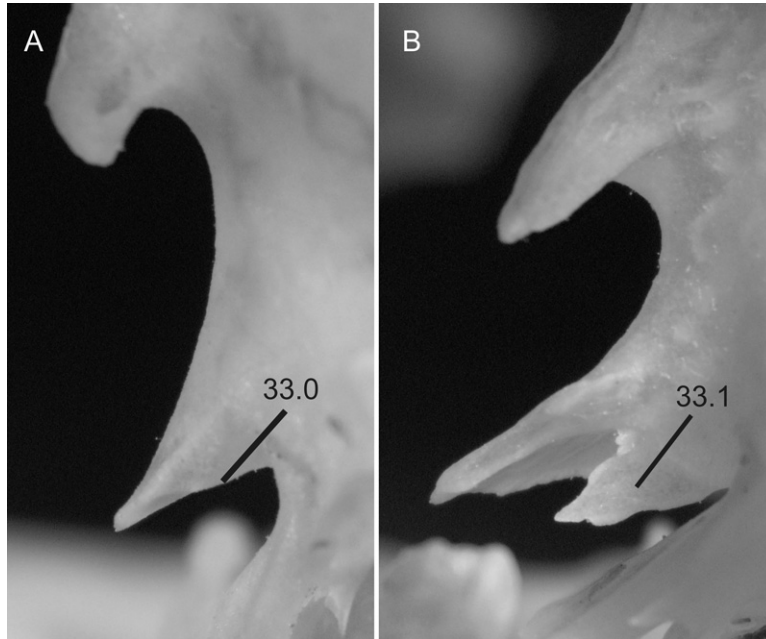


Figure 17. Character 33 and its postulated states. Zygomatic process, ventral surface, configuration: A, plain or with a small crest – 33.0; B, with a conspicuous lamina – 33.1. Postorbital region of skulls of (A) *Merulaxis ater* (MCP uncatalogued) and (B) *Acropternis orthonyx* (QCAZ 3723) in lateroventral view. Not to scale.

zygomatic process and fuses firmly with it. See Claramunt & Rinderknecht (2005; character 31).

33. Zygomatic process, ventral surface, configuration: plain or with a small crest (0); with a conspicuous lamina (1); Figure 17. In most Rhinocryptidae the ventral surface of the zygomatic process has a ventromedially projected lamina of thin bone which, although variable in size between taxa, is characteristically prominent.
34. Parasphenoidal sheet, rostral margin, small projection on each side of the parasphenoidal rostrum: absent (0); present (1). In the outgroup families Dendrocolaptidae and Furnariidae there is a small rostral projection on each side of the parasphenoidal rostrum. See Claramunt & Rinderknecht (2005; character 33).
35. Temporal fossa, length: long, reaches the nuchal (caudal) region of the skull (0); short, ending at the lateral region of the skull (1); Figure 18. In some rhinocryptid genera the temporal fossa ends abruptly at the lateral region of the skull due to a dorsally oriented inflection of the *Crista nuchalis transversa*.
36. Paraoccipital process, dorsal projection: absent (0); present (1); Figure 19. In some rhinocryptid genera the dorsal end of the paraoccipital process presents a pointed, dorsally oriented projection.
37. Mandible, lateral margin, caudal end in dorsal view, configuration: relatively plain, with no protuberance (0); with a small protuberance (1); with

a well-developed protuberance (2); Figure 20. With the exception of *Liosceles*, *Psilorhamphus*, and *Scytalopus*, all rhinocryptid genera have a prominent protuberance at the lateral margin of the caudal end of the mandible.

38. Mandible, medial process, foramen: present (0); absent (1); Figure 20. All rhinocryptids lack a pneumatic foramen at the dorsal surface of the medial (internal) process of the mandible. See Feduccia & Olson (1982).
39. Mandibular ramus, pneumatization: fully pneumatized (0); only the caudal end is pneumatized (1). In the Rhinocryptidae and some outgroup families (Formicariidae, Scleruridae, Dendrocolaptidae and Furnariidae) the mandibular rami are almost entirely non-pneumatized, except in the region caudal to the mandibular fenestra (*Fenestra caudalis mandibulae*).

Skeleton – postcranium

40. Manubrium, external spine, processes, configuration: prominent (0); short or vestigial (1); Figure 21. In most rhinocryptids the processes (i.e. the *Alae spinae externae*) of the manubrium are very short or vestigial.
41. Manubrium, foramen: absent (0); present (1). Some outgroup taxa have a foramen in the cranial surface of the manubrium. See Claramunt & Rinderknecht (2005; character 35) and Claramunt *et al.* (2010; character 23).

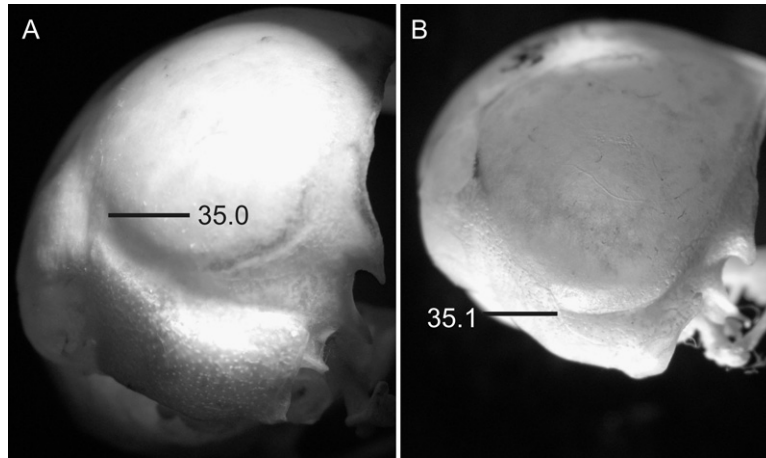


Figure 18. Character 35 and its postulated states. Temporal fossa, length: A, long, reaching the nuchal (caudal) region of the skull – 35.0; B, short, ending at the lateral region of the skull – 35.1. Skulls of (A) *Pteroptochos tarnii* (MCP 2397) and (B) *Eugralla paradoxa* (MCP 2398) in caudolateral view. Not to scale.

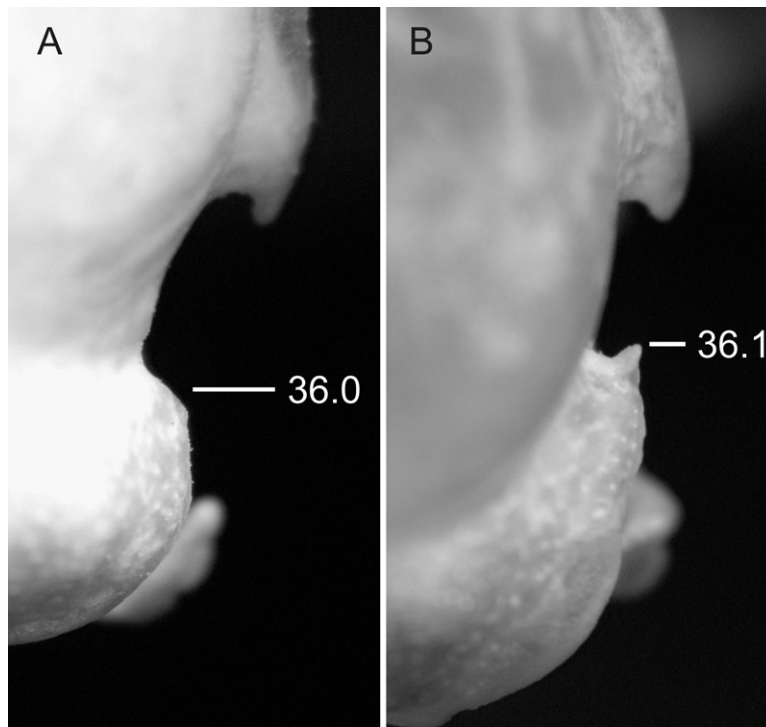


Figure 19. Character 36 and its postulated states. Paraoccipital process, dorsal projection: A, absent – 36.0; B, present – 36.1. Skulls of (A) *Pteroptochos tarnii* (MCP 2397) and (B) *Eugralla paradoxa* (MCP 2398) in caudal view. Not to scale.

42. Sternum, caudal margin, configuration: one pair of lateral notches (0); one pair of lateral notches and a pair of medial fenestrae (1); two pairs of notches, a lateral and a medial one (2). It is well known that the caudal margin (or metasternum) of the sternum of the Rhinocryptidae is four-notched, although this condition occurs in a few other members of the infraorder Furnariides

(Heimerdinger & Ames, 1967; Ames *et al.*, 1968; Lowery & O'Neill, 1969; Feduccia & Olson, 1982). See Bornschein *et al.* (1998), Claramunt & Rinderknecht (2005; character 37) and Claramunt *et al.* (2010; character 25).

43. Coracoid, brachial tuberosity, medial face, foramen: absent (0); present (1). All rhinocryptids lack a foramen in the medial surface of the

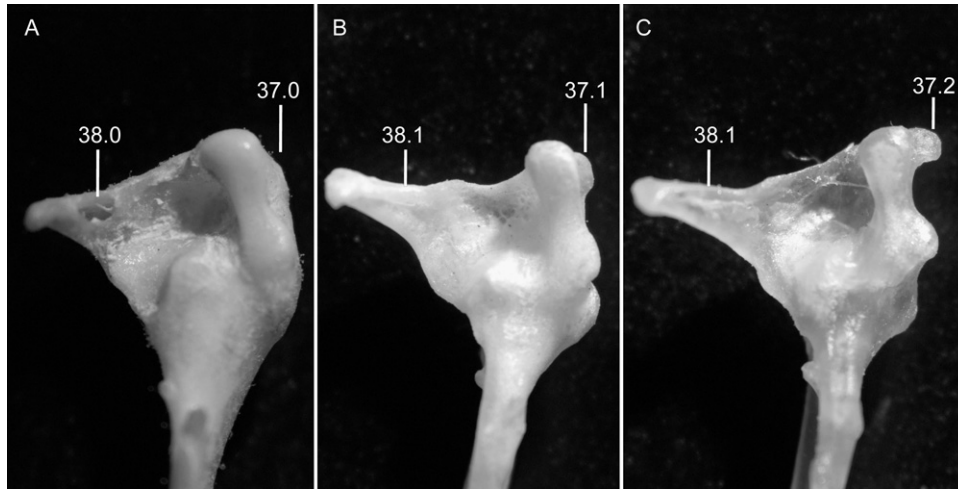


Figure 20. Characters 37 and 38 and their postulated states. Char. 37. Mandible, lateral margin, caudal end in dorsal view, configuration: A, relatively plain, with no protuberance – 37.0; B, with a small protuberance – 37.1; C, with a well-developed protuberance – 37.2. Char. 38. Mandible, medial process, foramen: A, present – 38.0; B, C, absent – 38.1. Caudal end of the mandible of (A) *Melanopareia torquata* (MCP 2271), (B) *Liosceles thoracicus* (MPEG O-3953), and (C) *Teledromas fuscus* (MCP 2396) in dorsal view. Not to scale.

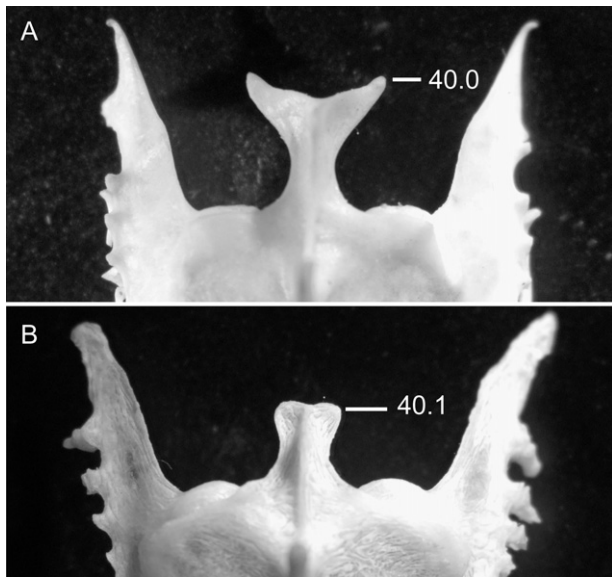


Figure 21. Character 40 and its postulated states. Manubrium, external spine, processes, configuration: A, prominent – 40.0; B, short or vestigial – 40.1. Cranial portion of the sternum of (A) *Liosceles thoracicus* (MPEG O-3953) and (B) *Acropternis orthonyx* (QCAZ 3723) in ventral view. Not to scale.

brachial tuberosity of the coracoid, which is present in most outgroup families. See Clararunt & Rinderknecht (2005; character 38).

44. Clavicles, sternal extremity, medial portion, configuration: fused, hypocleideum present (0); unfused, no hypocleideum (1); Figure 22. In some

rhinocryptids the clavicles show a strong atrophy, terminating distally as a weak spine (Feduccia & Olson, 1982; Maurício *et al.*, 2008). Some specimens of *Scytalopus* present a weak fusion between the flexible (apparently not fully ossified) distal ends of the clavicles, but no hypocleideum was present, a reason upon which these cases were coded as state (1).

45. Hypocleideum, configuration: without cranial extension (0); with a cranial extension (1); Figure 23. In *Scelorhynchus* and *Pteroptochos* (Rhinocryptidae) the hypocleideum extends cranially to the point of fusion of the clavicles.
46. Scapula, acromion, configuration: not prominent, being mostly or completely covered by the *extremitas omalis* of clavicle in medial view (0); prominent, exposed in medial view (1); Figure 24. Almost all rhinocryptids (except *Liosceles*) and one outgroup family (Conopophagidae) have a prominent acromion.
47. Humerus, fossa pneumotricipitalis, internal osseous wall: absent (0); present (1); Figure 25. In all outgroup taxa and *Liosceles* (Rhinocryptidae) the bottom of the fossa pneumotricipitalis is totally open, in a continuous and wide passage to the hollow interior of the humerus, whereas in the remaining rhinocryptids the fossa is completely closed by an osseous wall, with no opening to the interior of the bone. In their analysis of neornithine relationships, Mayr & Clarke (2003) described the character 'Humerus, foramina pneumatica at bottom of fossa pneumotricipitalis (. . .): absent (0), present (1)' and scored the state

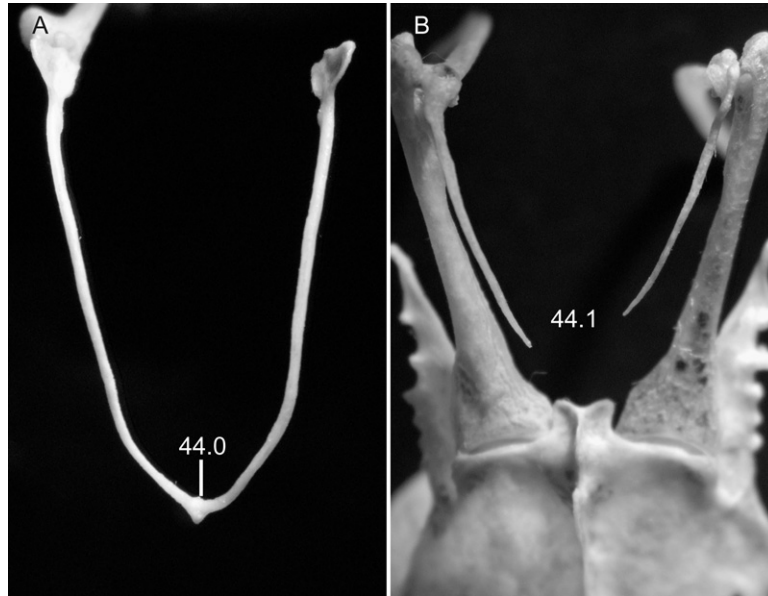


Figure 22. Character 44 and its postulated states. Clavicles, sternal extremity, medial portion, configuration: A, fused, hypocleideum present – 44.0; B, unfused, no hypocleideum – 44.1. Clavicles of (A) *Psilorhamphus guttatus* (MCP 2699) and (B) *Myornis senilis* (QCAZ 3724) in cranial aspect. Not to scale.

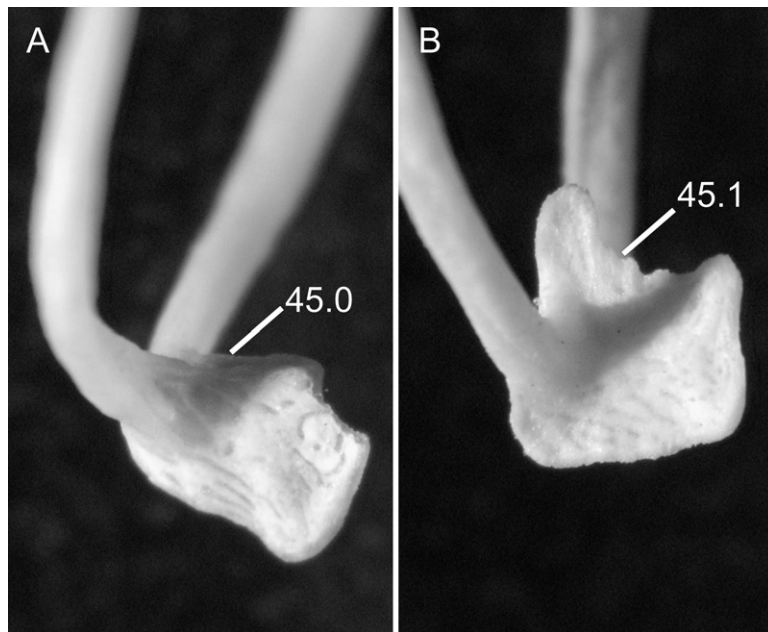


Figure 23. Character 45 and its postulated states. Hypopleideum, configuration: A, without cranial extension – 45.0; B, with a cranial extension – 45.1. Clavicles of (A) *Acropternis orthonyx* (QCAZ 3723) and (B) *Pterotochos tarnii* (MCP 2397) in caudolateral view. Not to scale.

1 for the Passeriformes based on analysis of representatives of seven families, including the Furnariidae (genus *Furnarius*), Thamnophilidae (genus *Thamnophilus*), and Tyrannidae (genus *Pitangus*). However, in all representatives of these three families included in the present study the

bottom of the fossa pneumotricipitalis showed a single, very large opening, a condition clearly distinct from a fossa having multiple foramina. The single, large opening condition of the fossa pneumotricipitalis was also observed in all additional genera of Furnariides examined

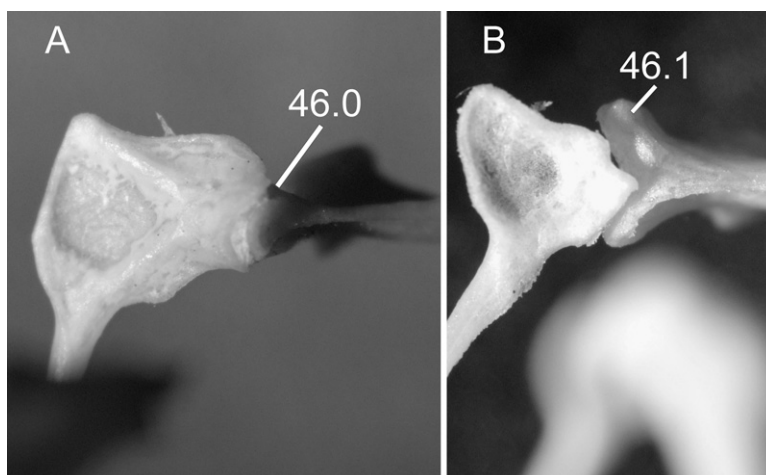


Figure 24. Character 46 and its postulated states. Scapula, acromion, configuration: A, not prominent, being mostly or completely covered by the *extremitas omalis* of the clavicle in medial view – 46.0; B, prominent, exposed in medial view – 46.1. *Extremitas omalis* of clavicle and cranial extremity of scapula of (A) *Liosceles thoracicus* (MPEG O-3953) and (B) *Psilorhamphus guttatus* (MCP 2699) in medial view. Not to scale.

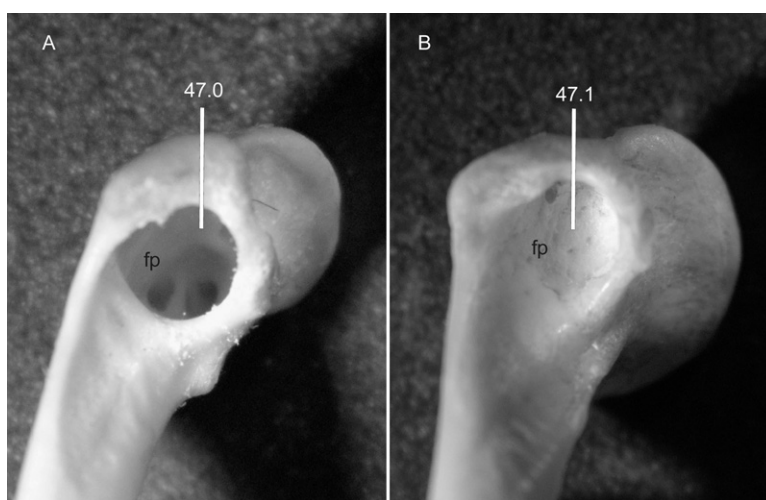


Figure 25. Character 47 and its postulated states. Humerus, fossa pneumotricipitalis, internal osseous wall: A, absent – 47.0; B, present – 47.1. Note in A the presence of trabecula ossea well inside the hollow head of humerus, beyond fossa pneumotricipitalis (fp). Ventral surface of humerus of (A) *Liosceles thoracicus* (MZUSP, uncatalogued) and (B) *Pteroptochos tarnii* (MCP 2397). Not to scale.

but not included in the phylogenetic analysis (*Sclerurus*, *Oreophylax*, *Cichlocolaptes*, *Synalaxis*, *Anumbius*, *Automolus*, *Lochmias*, *Limnornis*, *Phleocryptes*, *Xyphorhynchus*, *Formicivora*, *Hypocnemoides*, *Myrmeciza*, *Thamnophilus*, *Grallaricula*, *Myrmothera*, and *Chamaeza*; specimens at COP, MCP, and MHNT) as well as in all representatives of other families of the suborder Tyranni inspected for this feature (including Tyrannidae, Pipridae, Cotingidae, and Pittidae; MHNT and MCP specimens), strongly suggesting that it is widespread (and presumably plesiomorphic) among this suborder.

Remarks: The internal osseous wall that covers the bottom of the fossa pneumotricipitalis of most rhinocryptids is a solid but at some points relatively thin bony structure which, in some cases, may be minutely perforated by the dermestid beetles (particularly by the large larvae of certain species). This may create one or more pinholes that might be interpreted as minute foramina, as was seen in some specimens that were exposed for excessively long periods to the dermestid beetles. In specimens of *Psilorhamphus guttatus* (MCP 2699) and *Acropternis orthonyx* (QCAZ 3723) the bony wall of the fossa of one of the humeri was seen intact in an early inspection but some hours

later a pinhole had been opened by a larva that remained for some time gnawing the same point of the wall. Thus, pinholes (one or two in number) observed in the osseous wall of the fossa pneumotricipitalis of other specimens, particularly the older loaned museum specimens (e.g. *Pteroptochos tarnii* KUNHM 83525; *Scelorchilus rubecula* KUNHM 83511), were regarded as possible effects of the preparation of the material, an interpretation further supported by the fact that in other specimens of the same species these pinholes were not observed.

Additionally, to ensure that the absence of the osseous wall in the fossa pneumotricipitalis of the outgroup taxa and the rhinocryptid genus *Liosceles* was not an effect of the activity of the dermestid beetles – a possibility suggested by some colleagues – alcohol-stored specimens representing several families were examined before exposing them to the insects, namely *Liosceles thoracicus* (MZUSP, two uncatalogued specimens, field numbers 225 and 790; MPEG, uncatalogued, field number 598; INPA 879), *Melanopareia torquata* (MCP 2329, 2330), *Hylopezus macularius* (MPEG A-6921), *Hylopezus ochroleucus* (MCP 2567), *Formicarius analis* (MPEG A-4632), and *Pitangus sulphuratus* (MCP 2636). In all of these specimens careful dissection of the musculature inserting in the fossa pneumotricipitalis revealed a completely open fossa, with no trace of any type of wall, exactly as seen in the skeletal specimens prepared with dermestid beetles. In contrast to rhinocryptids (except *Liosceles*), in which the musculature inserts superficially in the osseous wall and adjoining surfaces, in these dissected specimens the musculature was inserted well inside the hollow head of the humerus. Thus, the conditions postulated for this character were regarded as perfectly valid.

48. Ulna, length relative to the humerus: much longer (0); as long or slightly shorter (1). In the Rhinocryptidae and some outgroup taxa (some Furnariidae and Melanopareiidae) the ulna is very short, being slightly shorter than (in some cases as long as) the humerus. See Mayr & Clarke (2003, character 82), who scored the long condition of the ulna (longer than humerus) for the order Passeriformes as a whole.
49. Ilium, dorsal iliac crests, configuration: well separated, with no fusion (0); largely or completely fused medially (1); Figure 26. In most rhinocryptids and a few outgroup taxa (one genus in Furnariidae and Dendrocolaptidae) the dorsal iliac crests converge medially and fuse with one another and the dorsal crest of the synsacrum, forming a median ridge called the *Crista ilio-synsacralis* (see Baumel & Witmer, 1993; Livezey & Zusi, 2006) and thus a closed *Canalis ilio-*

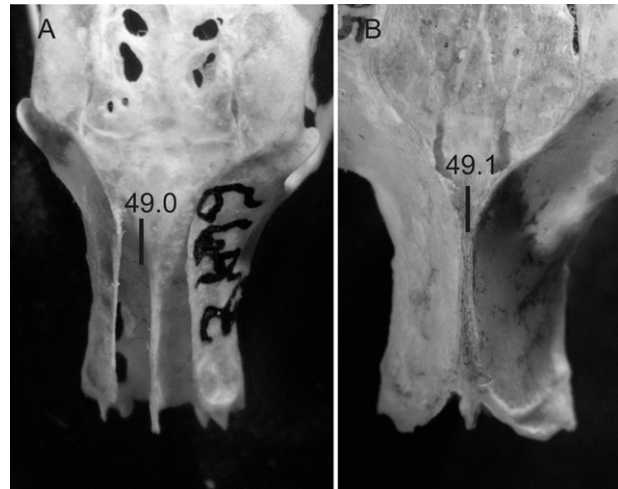


Figure 26. Character 49 and its postulated states. Ilium, dorsal iliac crests, configuration: A, well separated, with no fusion – 49.0; B, largely or completely fused medially – 49.1. Pelvis of (A) *Psilorhamphus guttatus* (MCP 2699) and (B) *Rhinocrypta lanceolata* (MCP 2395) in dorsal view. Not to scale.

synsacralis (Mayr & Clarke, 2003). See Mayr & Clarke (2003, character 92), who scored unfused, separated dorsal iliac crests as the widespread condition in the order Passeriformes.

50. Ilium, posterior projections, distance between the projections relative to the width of the caudal sacral vertebrae: more than twice as wide (0); between 1.2 and 1.8 times as wide (1); nearly as wide (2); Figure 27. In the Rhinocryptidae (except *Scelorchilus*) and an outgroup taxon (Dendrocolaptidae) the distance between the posterior (caudal) projections of the ilium is small, being approximately equivalent to the width of the caudalmost vertebrae of the synsacrum.
51. Synsacral vertebrae, paired fenestrae: present throughout the synsacrum (0); present only in the caudal portion (1); Figure 28. In *Pteroptochos* and *Scelorchilus* (Rhinocryptidae) and some outgroup taxa (Conopophagidae, Scleruridae, and Tyrannidae) the synsacrum has paired fenestrae (the *Fenestrae intertransversariae*) throughout its entire length.
52. Femur, caudal surface, proximal end, foramen: absent (0); present (1). In the outgroup family Dendrocolaptidae the caudal surface of the femur has a large foramen in its proximal end. See Feduccia (1973), Claramunt & Rinderknecht (2005; character 44) and Claramunt *et al.* (2010; character 28).
53. Tibiotarsus, cnemial crest, size relative to the rotular crest: nearly equal (0); longer (1); shorter (2). In the outgroup families Dendrocolaptidae

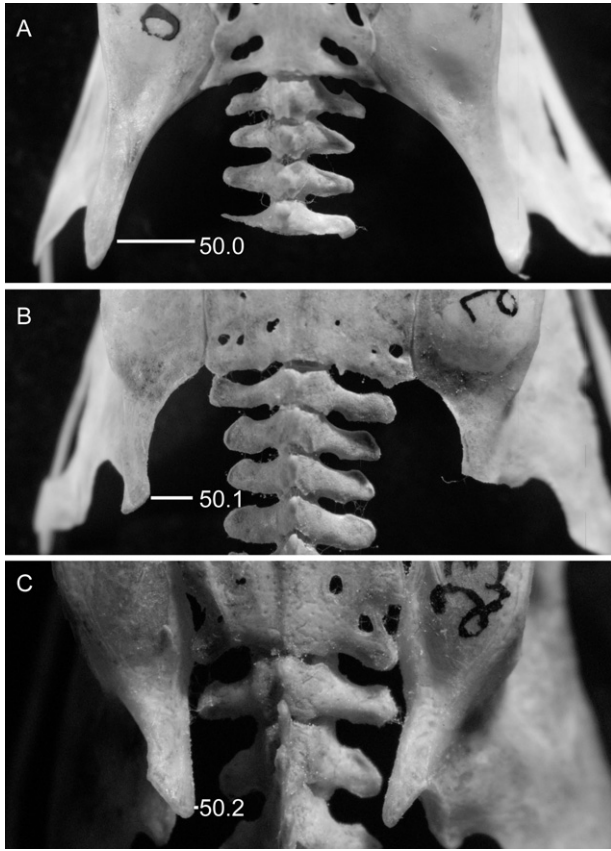


Figure 27. Character 50 and its postulated states. Ilium, posterior projections, distance between the projections relative to the width of the caudal sacral vertebrae: A, more than twice as wide – 50.0; B, between 1.2 and 1.8 times as wide – 50.1; C, nearly as wide – 50.2. Caudal end of the pelvis of (A) *Grallaria varia* (MCP 2210), (B) *Formicarius colma* (MCP 2467), and (C) *Rhinocrypta lanceolata* (MCP 2395) in dorsal view. Not to scale.

and Furnariidae most taxa have a short cnemial crest. See Feduccia (1973) and Claramunt & Rinderknecht (2005; character 45).

54. Tibiotarsus, intercnemial groove, width: narrow, restricted to the central part of the proximal portion of the tibiotarsus (0); wide, covering most of the proximal end of the tibiotarsus (1). In the outgroup family Dendrocolaptidae the intercnemial groove tends to be very wide. See Feduccia (1973), Claramunt & Rinderknecht (2005; character 46), and Claramunt *et al.* (2010; character 29).
55. Hypotarsus, posterolateral tendinal canal, configuration: closed (0); open (1); Figure 29. In some rhinocryptids and outgroup taxa of the families Conopophagidae, Formicariidae, and Dendrocolaptidae the posterolateral canal of the hypotarsus is widely open. See Feduccia & Olson (1982),

Claramunt & Rinderknecht (2005; character 48), Claramunt *et al.* (2010; 31), and Manegold, Mayr & Mourer-Chauviré (2004: 1158, fig. 3M).

56. Hypotarsus, posteromedial tendinal canal, configuration: closed (0); open (1); Figure 29. In some rhinocryptids and in a taxon of the outgroup family Dendrocolaptidae the posteromedial tendinal canal of the hypotarsus is open. See Claramunt & Rinderknecht (2005; character 48).
57. Tarsometatarsus, lateral plantar ridge, development: ends below the hypotarsus (0); continuous with the hypotarsus (1). In the outgroup families Dendrocolaptidae and Furnariidae some taxa have the plantar ridge of the tarsometatarsus in a continuous ridge with the posterior surface of the hypotarsus. See Claramunt & Rinderknecht (2005; character 49) and Claramunt *et al.* (2010; character 32).
58. Trochlea IV, length relative to the trochlea III: shorter (0); as long (1). Members of the outgroup family Dendrocolaptidae have trochleae IV and III of equal length. See Feduccia (1973), Claramunt & Rinderknecht (2005; character 52), and Claramunt *et al.* (2010; character 38).
59. Trochlea II, configuration: distinctly grooved (0); not grooved (1). In some outgroup taxa (Thamnophilidae and some Furnariidae) the trochlea II has no definable groove. See Feduccia (1973), Feduccia & Olson (1982) and Claramunt & Rinderknecht (2005; character 52).
60. Trochlea III, groove, depth: shallow (0); deep (1). In the outgroup family Dendrocolaptidae the groove of trochlea III is deeply excavated. See Feduccia (1973), Claramunt & Rinderknecht (2005; character 52) and Claramunt *et al.* (2010; character 37).
61. Trochlea IV, configuration: distinctly grooved (0); not grooved (1). In some outgroup families (Dendrocolaptidae, Furnariidae, and Thamnophilidae) the trochlea IV has no definable groove. See Feduccia (1973), Feduccia & Olson (1982), Claramunt & Rinderknecht (2005; character 52), and Claramunt *et al.* (2010; character 39).
62. Digit IV, basal phalanx, proximal end, medial notch: absent (0); present (1). In the Rhinocryptidae and some outgroup families (Grallariidae, Formicariidae, and Melanopareidae), the medial surface of the basal phalanx of digit IV is distinctly notched. This notch accommodates a knob protruding from the proximo-lateral corner of the basal phalanx of digit III (Feduccia & Olson, 1982).

Syrinx/trachea – supporting elements

63. Processus vocalis: absent (0); present (1). All members of the infraorder Furnariides have a

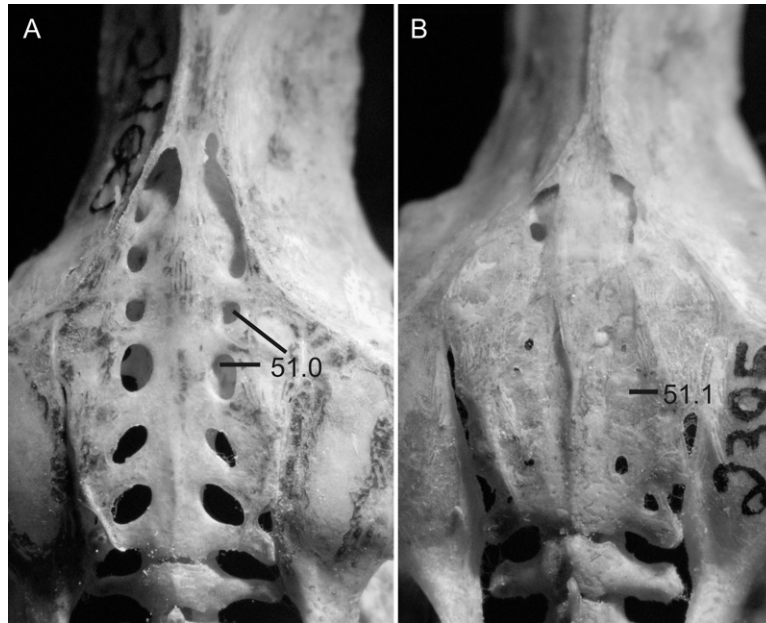


Figure 28. Character 51 and its postulated states. Synsacral vertebrae, paired fenestrae: A, present throughout the synsacrum – 51.0; B, present only in the caudal portion – 51.1. Pelvis of (A) *Scelorchilus rubecula* (MCP 2400) and (B) *Rhinocrypta lanceolata* (MCP 2395) in dorsal view. Not to scale.

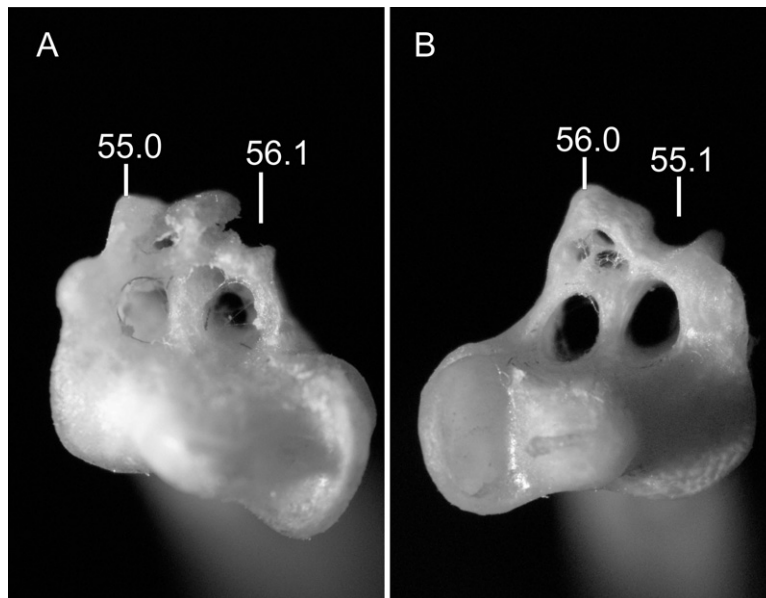


Figure 29. Characters 55 and 56 and their postulated states. Char. 55. Hypotarsus, posterolateral tendinal canal, configuration: A, closed – 55.0; B, open – 55.1. Char. 56. Hypotarsus, posteromedial tendinal canal, configuration: B, closed – 56.0; A, open – 56.1. Proximal end of right tarsometatarsus of (A) *Eugralla paradoxa* (MCP 2398) and left tarsometatarsus of (B) *Pteroptochos tarnii* (MCP 2397). Not to scale.

pair of Processi vocales, a feature which has been used to support the monophyly of the group (Ames, 1971).

64. Processus vocalis, composition: cartilage (0); cartilaginous caudal half, ossified cranial half (1);

mostly ossified, with a cartilaginous base (2); entirely ossified (3); Figure 30. In the Rhinocryptidae the Processus vocalis is extremely variable in composition, with all four conditions described above occurring in the family.

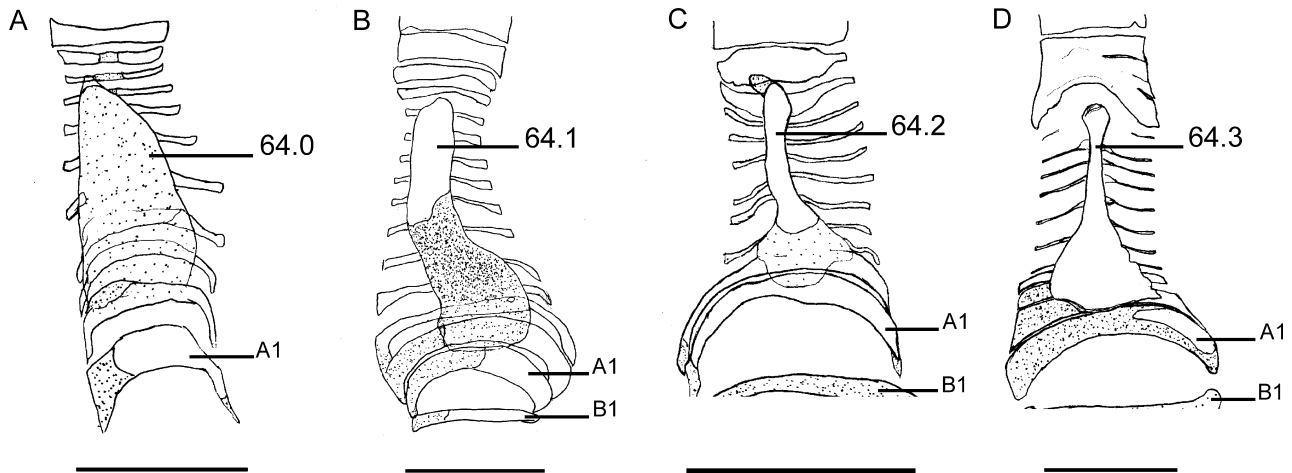


Figure 30. Character 64 and its postulated states. Processus vocalis, composition: A, cartilage – 64.0; B, cartilaginous caudal half, ossified cranial half – 64.1; C, mostly ossified, with a cartilaginous base – 64.2; D, entirely ossified – 64.3. Stippled areas are cartilaginous tissue, non-stippled areas are calcified structures. A1/B1 elements are indicated. Syringes of (A) *Melanopareia torquata* (MCP 2588), (B) *Liosceles thoracicus* (MZUSP, uncatalogued), (C) *Myornis senilis* (QCAZ 3724), and (D) *Furnarius rufus* (MCP 1058) in lateral view (shown are the right side in A, B and D and the left side in C). Scale bars = 2 mm.

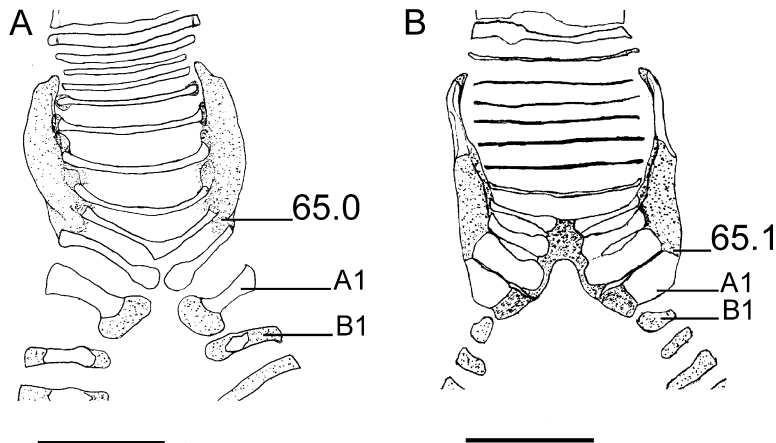


Figure 31. Character 65 and its postulated states. Processus vocalis, caudal end, attachment: A, from A2 craniad – 65.0; B, from A1 craniad – 65.1. Stippled areas are cartilaginous tissue, non-stippled areas are calcified structures. A1/B1 elements are indicated. Syringes of (A) *Melanopareia torquata* (MCP 2588) and (B) *Formicarius colma* (MCP 2478) in ventral view. Scale bars = 2 mm.

65. Processus vocalis, caudal end, attachment: from A2 craniad (0); from A1 craniad (1); Figure 31. In the Rhinocryptidae and several outgroup families (Formicariidae, Scleruridae, Furnariidae, and Dendrocolaptidae), the caudalmost point of attachment of the Processus vocalis is in the A1 element. Garrod (1877b) describes and illustrates state 0 for *Grallaria* and state 1 for *Pteroptochos*. See Gonzaga (2001; character 29).

66. Processus vocalis, lateral view, variation in width: relatively uniform (0); wide caudally, narrow cranially (1); wide caudally and cranially,

narrow in between (2); Figure 32. Most rhinocryptids and members of some outgroup families (Scleruridae, Dendrocolaptidae, and Furnariidae) have a Processus vocalis with a wide base and a comparatively narrow cranial half.

67. Processus vocalis, cranial portion, orientation: same as the main axis, i.e. cranially oriented (0); ventrad, i.e. there is a ventrally oriented deviation from the main axis (1); ventrad and then cranially (2); Figure 33. In several rhinocryptids and some outgroup taxa of the families Thamnophilidae and Grallariidae the Processus vocalis

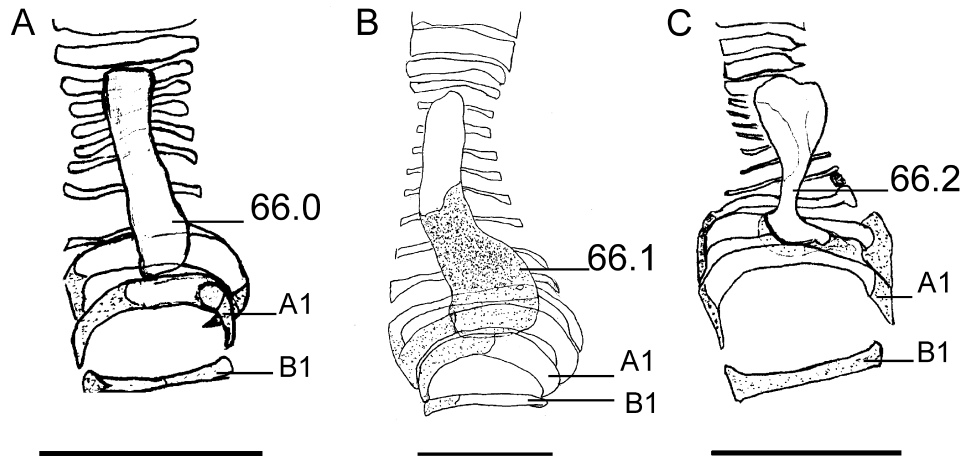


Figure 32. Character 66 and its postulated states. Processus vocalis, lateral view, variation in width: A, relatively uniform – 66.0; B, wide caudally, narrow cranially – 66.1; C, wide caudally and cranially, narrow in between – 66.2. Stippled areas are cartilaginous tissue, non-stippled areas are calcified structures. A1/B1 elements are indicated. Syringes of (A) *Psilorhamphus guttatus* (MCP 2045), (B) *Liosceles thoracicus* (MZUSP, uncatalogued), and (C) *Eugralla paradoxa* (MCP 2398) in lateral view. Scale bars = 2 mm.

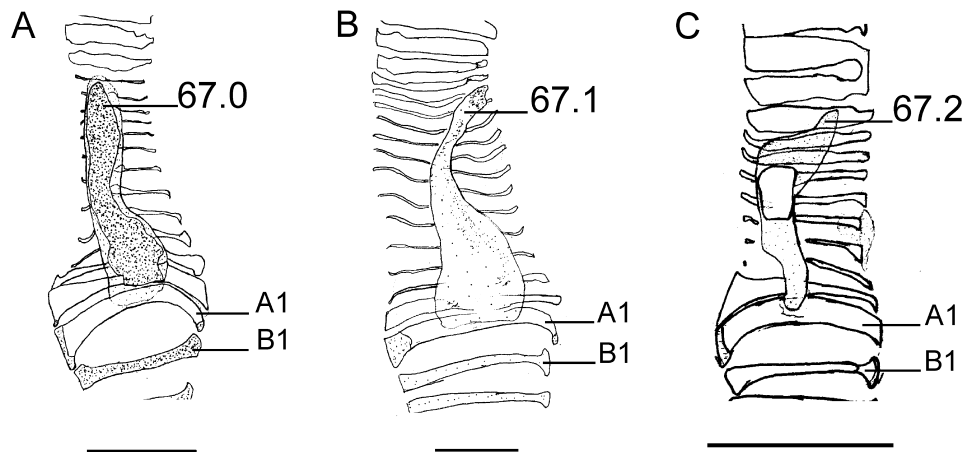


Figure 33. Character 67 and its postulated states. Processus vocalis, cranial portion, orientation: A, same as the main axis – 67.0; B, ventrally oriented – 67.1; C, ventrad and then craniad – 67.2. Stippled areas are cartilaginous tissue, non-stippled areas are calcified structures. A1/B1 elements are indicated. Syringes of (A) *Acropternis orthonyx* (QCAZ 3723), (B) *Pteroptochos castaneus* (AMNH 11694), and (C) *Eleoscytalopus indigoticus* (MCP 2332) in lateral view. Scale bars = 2 mm.

shows an oblique deviation from its main axis in the cranial portion, which is ventrally oriented (state 1). In *Eleoscytalopus* and *Merulaxis* (Rhinocryptidae), for which state 2 was erected, the condition is perhaps more properly described as a ventral expansion than a deviation of the cranial portion, to which follows another (narrow) expansion, pointing cranially, over the lateroventral surface of the trachea.

68. Processus vocalis, cranial portion, consistency: firm (0); soft (1). In *Eleoscytalopus* and *Merulaxis* (Rhinocryptidae), the Processus vocalis ends cra-

nially as a very soft, thin, hyaline surface to which the *Musculus tracheolateralis* is caudally inserted. See Bornschein *et al.* (1998) and Maurício *et al.* (2008, fig. 5).

69. Processus vocalis, caudal portion, dorsal projection: absent (0); present (1). In *Merulaxis* and *Eleoscytalopus* (Rhinocryptidae) there is an extremely thin, almost imperceptible dorsal projection in the caudal portion of the Processus vocalis. It is not certain if this feature is a projection of the Processus vocalis, as described by Bornschein *et al.* (1998), or a thickening of the

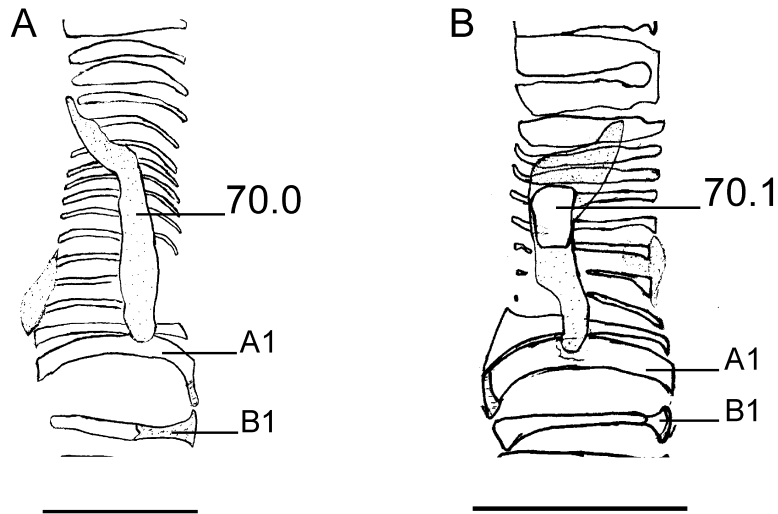


Figure 34. Character 70 and its postulated states. Processus vocalis, lateral surface, rectangular ossified plate: A, absent – 70.0; B, present – 70.1. Stippled areas are cartilaginous tissue, non-stippled areas are calcified structures. A1/B1 elements are indicated. Syringes of (A) *Merulaxis ater* (MCP 2001) and (B) *Eleoscytalopus indigoticus* (MCP 2332) in lateral view (A, left side; B, right side). Scale bars = 2 mm.

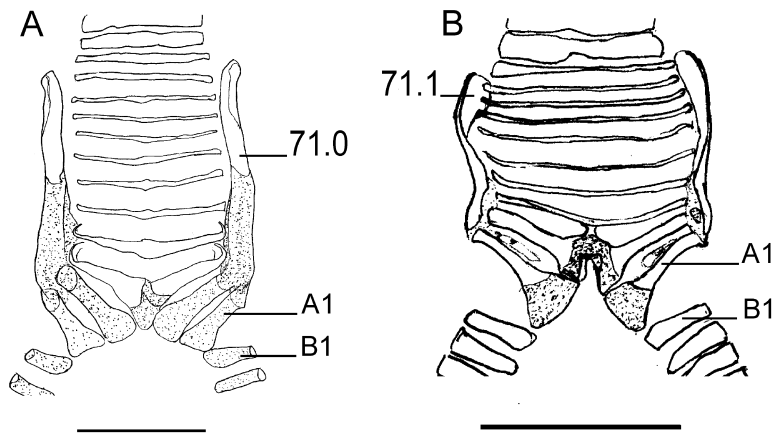


Figure 35. Character 71 and its postulated states. Processus vocalis, left one, size relative to the right processus: A, equal or subequal – 71.0; B, shorter – 71.1. Stippled areas are cartilaginous tissue, non-stippled areas are calcified structures. A1/B1 elements are indicated. Syringes of (A) *Liosceles thoracicus* (MZUSP, uncatalogued) and (B) *Scytalopus pachecoi* (MCP 1040) in dorsal view. Scale bars = 2 mm.

contiguous, caudodorsal portion of the Membrana trachealis.

70. Processus vocalis, lateral surface, rectangular ossified plate: absent (0); present (1); Figure 34. The rhinocryptid genus *Eleoscytalopus* has a nearly rectangular, ossified plate in the cranial half of the Processus vocalis. See Maurício *et al.* (2008).

71. Processus vocalis, left one, size relative to the right processus: equal or subequal (0); shorter (1); Figure 35. In some rhinocryptids the left Processus vocalis is distinctly shorter than the

right one, the latter generally reaching one A element cranially than the former.

72. Processus vocalis, horns: absent (0); present (1). In the outgroup families Scleruridae and Dendrocolaptidae the ventral and dorsal margins of the Processus vocalis have a distinct projection, or horn, directed medially. See Ames (1971), Raposo *et al.* (2006), and Zimmer, Robbins & Kopuchian (2008).

73. Membrana trachealis: absent (0); present (1). All members of the infraorder Furnariides have ventral and dorsal Membrana trachealis, one of

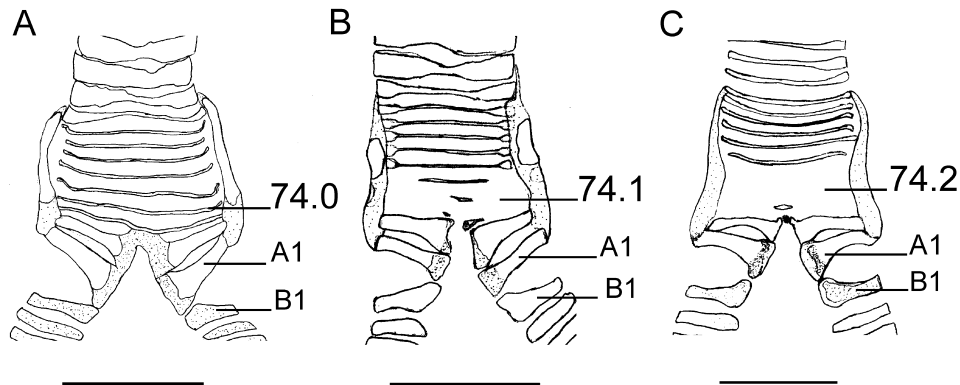


Figure 36. Character 74 and its postulated states. A3–A5 elements, dorsal surface, configuration: A, complete, not reduced – 74.0; B, A3 vestigial, A4 and A5 reduced – 74.1; C, A3 vestigial, A4 and A5 absent – 74.2. Stippled areas are cartilaginous tissue, non-stippled areas are calcified structures. A1/B1 elements are indicated. Syringes of (A) *Myornis senilis* (QCAZ 3724), (B) *Eleoscytalopus indigoticus* (MCP 2044), and (C) *Merulaxis ater* (MCP 2001) in dorsal view. Scale bars = 2 mm.

the two characters upon which the monophyly of the group has been advocated (Ames, 1971).

74. A3–A5 elements, dorsal surface, configuration: complete, not reduced (0); A3 vestigial, A4 and A5 reduced (1); A3 vestigial, A4 and A5 absent (2); Figure 36. Ordered based on ontogenetic evidence. In *Merulaxis* and *Eleoscytalopus* (Rhinocryptidae) the A3 element is very reduced dorsolaterally, with only a small segment being present medially, whereas A4 and A5 are dorsally absent in the former (state 2) and only reduced in the latter (state 1). In a fledgling of *E. indigoticus* (MCP 2574) all A elements, including A3–A5 (both ventrally and dorsally), were complete and composed of thick cartilage, each ring being very close to each other; in an immature of *Merulaxis ater* (MCP 1740) the A3 element was much more extensive than in adult birds (almost reaching the Processus vocalis) and A5 was present dorsally. Given that states 1 and 2 have an identical component (i.e. extreme reduction of A3) and considering the ontogenetic evidence for a progressive reduction of the relevant A elements (at least for A3 and A5), the present character is arranged in an ordered transformation series (0–1–2). See Bornschein *et al.* (1998) and Maurício *et al.* (2008).
75. A2–A6 elements, ventral surface, cartilaginous protuberance: absent (0); present (1); Figure 37. In *Merulaxis* and *Eleoscytalopus* (Rhinocryptidae), on the ventral surface of the syringe between A2 and A6 elements, there is a mass of roughly convex, relatively soft cartilaginous tissue, which is more rounded and prominent in the former. See Maurício *et al.* (2008), who recognized this feature only in *Merulaxis*.
76. Membrana trachealis, cranial half, A elements, configuration: complete, not reduced (0); A7–A12 or A8–A11 ventrally absent or nearly so (1); A4–A11 laterodorsally and lateroventrally reduced (2); A6/A7–A10 ventrally and dorsally absent (3). Reduction or absence of A elements in the cranial half of the Membrana trachealis, forming partial or complete ‘windows’, was observed in some outgroup families (Grallariidae, Dendrocolaptidae, and Furnariidae). In being restricted to the caudal portion (dorsal surface) of the syringe, the reduction/absence of A3–A5 elements is here regarded an independent character (74). See Ames (1971) and Maurício *et al.* (2008).
77. Syringe, ventrolateral surface, cranial half, sulcus: absent (0); present (1); Figure 38. In most rhinocryptid genera there is a sulcus in the ventrolateral surface of the cranial half of the syringe, which is formed by a dorsal inflection of some A elements and their membranes.
78. Syringe, caudal portion, A elements, fusion: no fusion (0); dorsal ends of A2 fused (1); dorsal ends of A2 fused and then fused to A3 (2); A3 and A4 fused dorsally (3); Figure 39. In *Myornis* and most species of *Scytalopus* (Rhinocryptidae) and in some outgroup taxa in the families Formicariidae, Scleruridae, and Furnariidae the dorsal ends of A2 are fused and this fused portion, in turn, is fused to A3 (state 2). See Zimmer *et al.* (2008; character 4).
79. Trachea, caudal portion, A elements, width: broad ventrally and dorsally (0); dorsally extremely narrow, ventrally broad (1). In the outgroup family Grallariidae several A elements just cranial to the Membrana trachealis are very narrow dorsally,

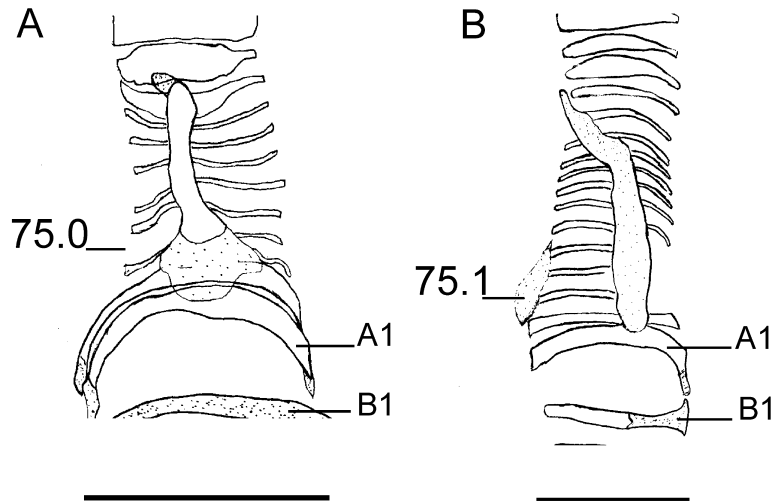


Figure 37. Character 75 and its postulated states. A2–A6 elements, ventral surface, cartilaginous protuberance: A, absent – 75.0; B, present – 75.1. Stippled areas are cartilaginous tissue, non-stippled areas are calcified structures. A1/B1 elements are indicated. Syringes of (A) *Myornis senilis* (QCAZ 3724) and (B) *Merulaxis ater* (MCP 2001) in lateral view. Scale bars = 2 mm.

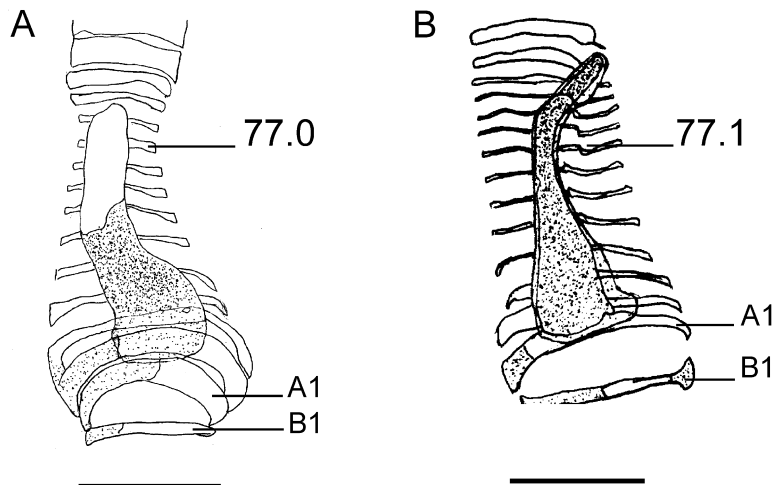


Figure 38. Character 77 and its postulated states. Syrinx, ventrolateral surface, cranial half, sulcus: A, absent – 77.0; B, present – 77.1. Stippled areas are cartilaginous tissue, non-stippled areas are calcified structures. A1/B1 elements are indicated. Syringes of (A) *Liosceles thoracicus* (MZUSP, uncatalogued) and (B) *Scelorchilus rubecula* (MCP 2400) in lateral view. Scale bars = 2 mm.

contrasting with their broad ventral halves. See Ames (1971).

80. Syrinx, A elements, lateral portion, composition: ossified tissue, as the rest of the element (0); cartilaginous tissue (1). In the outgroup families Thamnophilidae and Melanopareiidae the lateral portion of the A elements, within the limits of the Membranae tracheales, is cartilaginous whereas the rest of the element is ossified. See Gonzaga (2001).

81. Trachea, caudal portion, ventral surface, processes: absent (0); present (1). In the outgroup family Thamnophilidae a pair of long processes is present in the ventral surface of the trachea just cranial to the Membrana trachealis, in the region of origin of the intrinsic, ventral oblique muscle. These processes are composed of ossified tissue or firm cartilage. See Gonzaga (2001).

82. Trachea, caudal portion, A elements, fusion: no fusion (0); two to several elements fused (1). In the

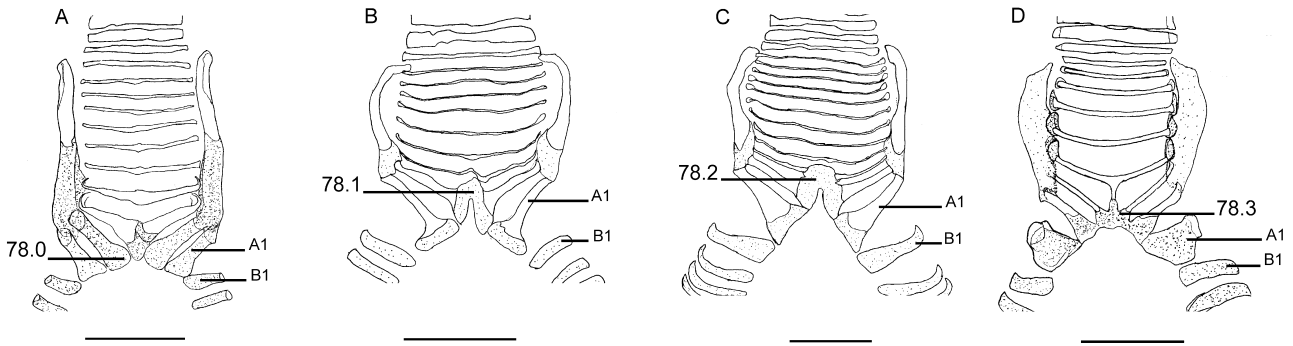


Figure 39. Character 78 and its postulated states. Syrinx, caudal portion, A elements, fusion: A, no fusion – 78.0; B, dorsal ends of A2 fused – 78.1; C, dorsal ends of A2 fused and then fused to A3 – 78.2; D, A3 and A4 fused dorsally – 78.3. Stippled areas are cartilaginous tissue, non-stippled areas are calcified structures. A1/B1 elements are indicated. Syringes of (A) *Liosceles thoracicus* (MZUSP, uncatalogued), (B) *Scytalopus femoralis* (LSUMZ 107640), (C) *Scytalopus macropus* (LSUMZ 120723), and (D) *Melanopareia torquata* (MCP 2588) in dorsal view. Scale bars = 2 mm.

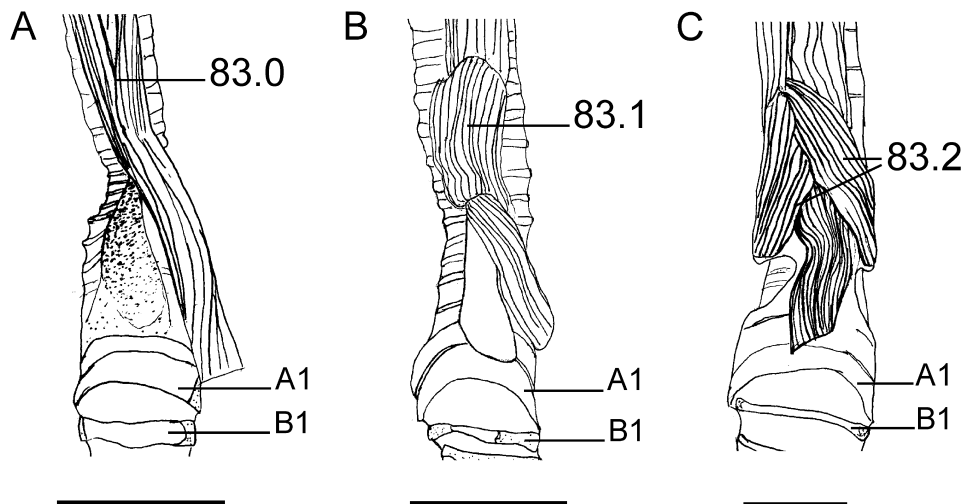


Figure 40. Character 83 and its postulated states. Syrinx and lower trachea, lateral surface, musculature, configuration: A, not forming an intrinsic muscle – 83.0; B, forming a single pair of intrinsic muscles – 83.1; C, forming two pairs of intrinsic muscles – 83.2. Stippled areas are cartilaginous tissue, non-stippled areas are calcified structures. A1/B1 elements are indicated. Syringes of (A) *Conopophaga lineata* (MCP 2490), (B) *Psilorhamphus guttatus* (MCP 2699) and (C) *Dendrocolaptes platyrostris* (MCP 2602) in lateral view (A, B, left side; C, right side). Scale bars = 2 mm.

outgroup families Furnariidae and Dendrocolaptidae two or more A elements just cranial to the Membranae tracheales are partially or completely fused, forming a ‘drum’. See Ames (1971), Raposo *et al.* (2006), and Zimmer *et al.* (2008).

Syrinx/trachea – musculature

83. Syrinx and lower trachea, lateral surface, musculature, configuration: not forming an intrinsic muscle (0); forming a single pair of intrinsic muscles (1); forming two pairs of intrinsic muscles (2); Figure 40. This character takes into consideration the main musculature covering the lateral surface of the syrinx and lower

trachea, be it the M. tracheolateralis or a voluminous intrinsic musculature contiguous with (and presumably derived from) it. In most Rhinocryptidae and some outgroup families (Grallariidae, Formicariidae, and Tyrannidae) the musculature in this area is a single mass of fibres (state 1). In the outgroup families Scleruridae, Furnariidae, and Dendrocolaptidae the musculature in this area is divisible into two components (sheets), a ventral one, the M. vocalis ventralis, and a dorsal one, the M. vocalis dorsalis (state 2). The latter condition has been regarded a synapomorphy for the enlarged Furnariidae (i.e. a group comprising the families Scleruridae, Furnariidae,

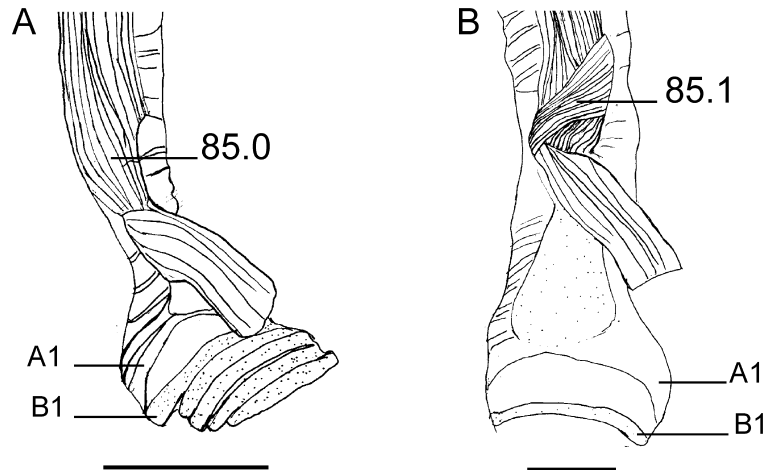


Figure 41. Character 85 and its postulated states. Syrinx and lower trachea, dorsoventral intrinsic muscle: A, absent – 85.0; B, present – 85.1. Stippled areas are cartilaginous tissue, non-stippled areas are calcified structures. A1/B1 elements are indicated. Syringes of (A) *Myornis senilis* (QCAZ 3724) and (B) *Pteroptochos castaneus* (AMNH 11694) in lateral view. Scale bars 2 mm.

and Dendrocolaptidae). Due to the similarities in position and fibre direction the conditions described above are considered homologous with the *M. obliquus lateralis* of the Tyrannoidea. A dorsolaterally originating and oblique sheet of fibres is here regarded a distinct character (85). See Ames (1971). Contrary to what has been found by Maurício *et al.* (2008), the rhinocryptid genera *Liosceles*, *Scytalopus*, and *Psilorhamphus* possess an intrinsic muscle that matches state 1 of the present character.

84. Syrinx and lower trachea, ventral surface, intrinsic muscle: absent (0); present (1). In the outgroup families Thamnophilidae and Tyrannidae there is a pair of intrinsic muscles originating medially in the ventral surface of the syrinx and lower trachea. In the Thamnophilidae this muscle originates just cranial to the Membrana trachealis and inserts laterally in the syrinx, on the Processus vocalis. The fact that Ames (1971) had referred to this muscle in the Thamnophilidae as *M. vocalis ventralis* implicitly established a hypothesis of homology with the muscle of the same name occurring in the Furnariidae and Dendrocolaptidae (Gonzaga, 2001). However, the position and general configuration of the intrinsic muscles in Thamnophilidae and Furnariidae/Dendrocolaptidae is very distinct, to a point at which no homology can be assumed between both types. On the other hand, the ventral origin and general configuration of the intrinsic musculature of the Thamnophilidae is similar to the *M. obliquus ventralis* present in several families of the infraorder Tyrannides. Given that the ventral

muscle of the Thamnophilidae falls perfectly within the broad characterization of the *M. obliquus ventralis* of the Tyrannides, i.e. a muscle with a ventral position in the lower trachea/syrinx and with oblique fibres oriented caudolaterally (Ames, 1971; Prum, 1990), we here postulate their homology.

85. Syrinx and lower trachea, dorsoventral intrinsic muscle: absent (0); present (1); Figure 41. Some rhinocryptids and an outgroup family (Melanopareiidae) have a thin, intrinsic sheet of muscle originating dorsally to the lateral muscle (i.e. the *M. tracheolateralis* or the lateral intrinsic muscle) that spirals caudoventrally across the surface of the latter muscle to insert on the ventral margin of the Processus vocalis. This muscle has been tentatively called *M. vocalis dorsalis* by Ames (1971), thus establishing an homologous correspondence between the present dorsoventral muscle with the muscles described above (characters 81 and 82), an hypothesis not supported by our data.
86. Musculus sternotrachealis, composition: a single fasciculus (0); divided into two fasciculi (1). In the outgroup family Thamnophilidae the *M. sternotrachealis* is divided into two voluminous fasciculi near its insertion in the syrinx, a cranial and a caudal one, a condition regarded as synapomorphic for the family. See Ames (1971) and Gonzaga (2001).
87. Musculus sternotrachealis, insertion in the trachea/syrinx: on the cranial end of the Processus vocalis only (0); on several A elements cranial to the Membranae tracheales, with some fibres

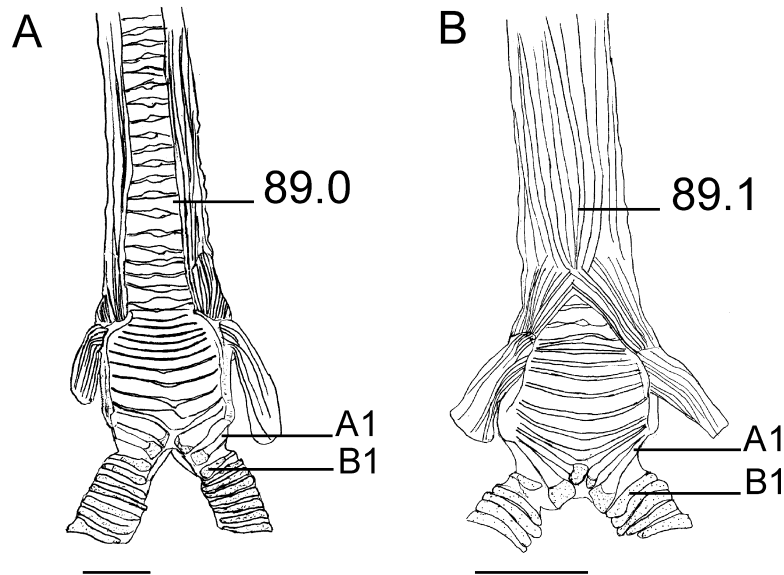


Figure 42. Character 89 and its postulated states. Musculus tracheolateralis, ventral surface, configuration: A, restricted to the lateral surfaces of the trachea – 89.0; B, both sides expand ventrally and meet along the ventral surface of the trachea – 89.1. Stippled areas are cartilaginous tissue, non-stippled areas are calcified structures. A1/B1 elements are indicated. Syringes/trachea of (A) *Teledromas fuscus* (MCP 2396) and (B) *Myornis senilis* (QCAZ 3724) in ventral view. Scale bars = 2 mm.

inserting on the cranial end of the Processus vocalis and with others being contiguous with fibres of the M. tracheolateralis (1); on the caudal end of the Processus vocalis and on the lateral surface of several A elements cranial to the Membranae tracheales, with some fibres being contiguous with fibres of the M. tracheolateralis (2). See Ames (1971).

88. Musculus sternotrachealis, origin in the skeleton: in the cranial margin of the craniolateral process of the sternum (0); in the medial surface of the vertebral segment of the second rib (1). In the Rhinocryptidae and several outgroup families (Formicariidae, Melanopareiidae, Scleruridae, Furnariidae, and Dendrocolaptidae) the M. sternotrachealis originates in the medial surface of the vertebral segment of the second rib (the first 'true' rib), near the articulation with the sternal segment of the latter. Plótnick (1958) was the first author to call attention for the distinct (i.e. non-sternal), costal origin of the M. sternotrachealis in the above mentioned families (except Melanopareiidae). See also Gonzaga (2001).
89. Musculus tracheolateralis, ventral surface, configuration: restricted to the lateral surfaces of the trachea (0); both sides expand ventrally and meet along the ventral surface of the trachea (1); Figure 42. In several rhinocryptids and some outgroup taxa in the families Melanopareiidae, Grallariidae, Formicariidae, Scleruridae, and

Dendrocolaptidae, the M. tracheolateralis expands ventrally, with crossing of fibres from one side to another, to cover the ventral surface of the trachea over several A elements cranially to the Membrana trachealis. Prum (1993) regarded the ventral union of the M. tracheolateralis to be a derived character for some Old World suboscines, stating that in the Furnariides and primitively in the Tyrannides this muscle is restricted to the lateral surfaces of the trachea, with no ventral meeting of fibres. However, as stated above, in several families of the infraorder Furnariides the M. tracheolateralis expands and meets ventrally. See Ames (1971) and Bornschein *et al.* (1998).

90. Lateral intrinsic muscle, insertion: on the cranial end of the Processus vocalis (0); on the centre of the Processus vocalis (1); on the caudal end (base) of the Processus vocalis and adjacent A elements (2). In the outgroup families Scleruridae, Furnariidae, and Dendrocolaptidae the insertion of the intrinsic musculature (i.e. the M. vocalis ventralis and M. vocalis dorsalis) is on the middle (state 1) or on the caudal end (base) of the Processus vocalis and adjacent A elements (state 2), caudally to the insertion of the M. sternotrachealis.

PHYLOGENETIC ANALYSES

Parsimony analysis of the character-state distribution among terminals (see matrix in Appendix 2)

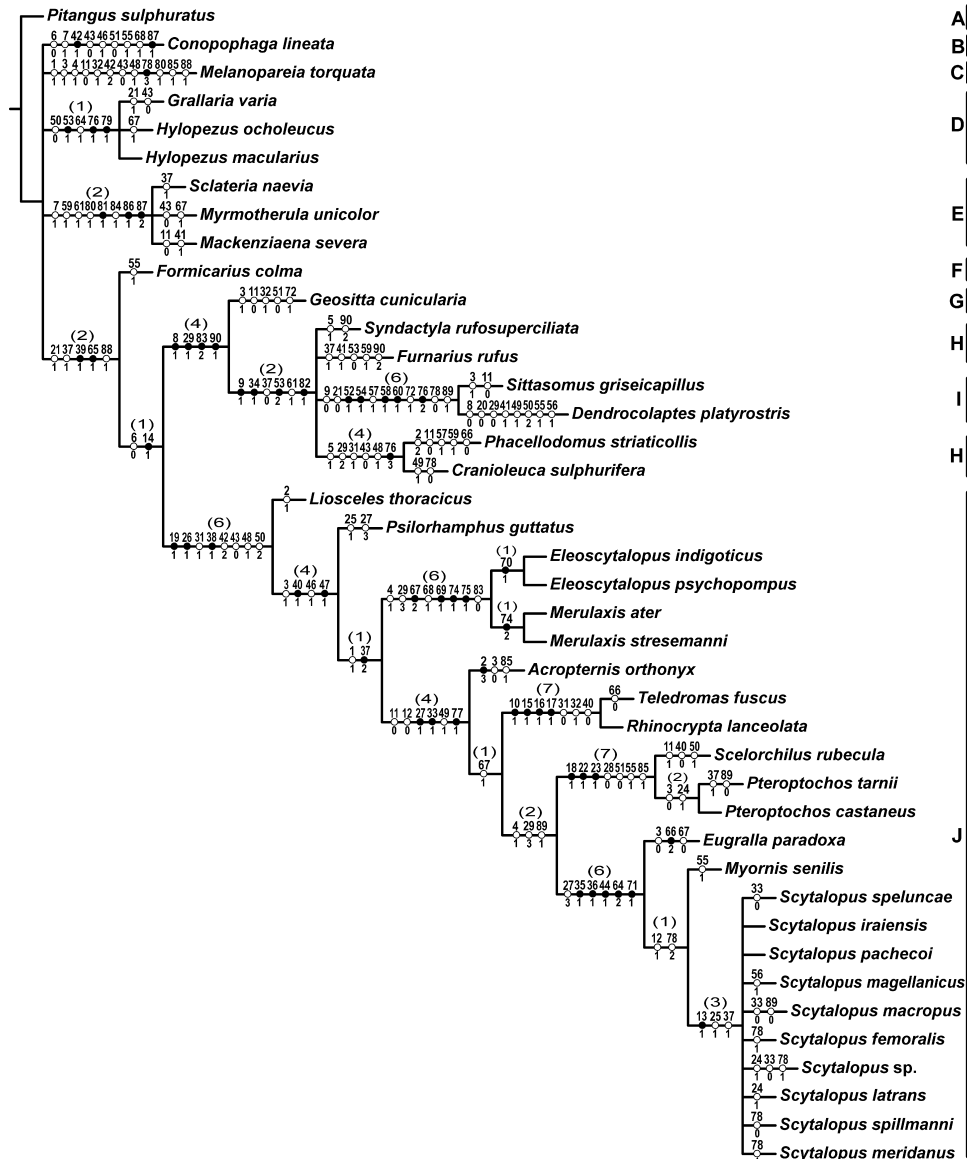


Figure 43. Strict consensus of 7428 equally most parsimonious trees derived from the cladistic analysis of the character state matrix in Appendix 2. On each branch, solid circles indicate exclusive synapomorphies and open circles homoplastic traits; numbers above circles represent characters as numbered in the character analysis section, with corresponding character-states appearing below circles. All characters are non-additive (except char. 74, whose states are ordered based on ontogenetic evidence) and unweighted. Bremer support indices are shown in parentheses above character numbers. Vertical bars on the right indicate family boundaries: A, Tyrannidae; B, Conopophagidae; C, Melanopareiidae; D, Grallariidae; E, Thamnophilidae; F, Formicariidae; G, Scleruridae; H, Furnariidae; I, Dendrocolaptidae; J, Rhinocryptidae.

resulted in 7428 equally most parsimonious trees ($L = 232$ steps, $CI = 0.48$, $RI = 0.83$), the strict consensus of which is shown in Figure 43. Character states with unambiguous optimizations are presented in that consensus diagram, while those having alternative equally parsimonious optimizations are not, as

neither ACCTRAN nor DELTRAN modes of character evolution were favoured during analysis. The analysis performed without the four incomplete terminals recovered 456 equally most parsimonious trees with the same tree statistics as mentioned above (except in being one step shorter), with the strict consensus

showing the same topology and character-state distribution as in the main analysis. Monophyly of the Rhinocryptidae as presently understood, i.e. an assemblage comprising the genera *Liosceles*, *Psilorhamphus*, *Merulaxis*, *Eleoscytalopus*, *Acropternis*, *Rhinocrypta*, *Teledromas*, *Scelorchilus*, *Pteroptochos*, *Eugralla*, *Myornis*, and *Scytalopus* and excluding *Melanopareia*, was supported by eight synapomorphies and high Bremer support (6). Within the family, the phylogeny showed a complete resolution at the genus level with all polytypic genera being recovered as monophyletic. On the other hand, there was no resolution of relationships within *Scytalopus*, whose clade is a large polytomy of ten taxa. To further explore relationships within the genus, all the 456 trees resulting from the analysis performed without the incomplete taxa were examined for the most frequent clades. The most frequent feature common to those trees was the basal position of *S. magellanicus* relative to the rest of the genus, recovered in 92% of the trees, followed by a sister-taxon relationship between *S. macropus* and *Scytalopus* sp., which was recovered in 60% of the trees.

It is beyond the scope of the present analysis to explore relationships between the families within Furnariidae, and therefore only nodes leading to the Rhinocryptidae will be described here. The most inclusive, higher level relationship recovered in the strict consensus of all trees is that comprising Formicariidae, Furnariidae, Scleruridae, Dendrocolaptidae, and Rhinocryptidae, which is supported by a Bremer value of 2 and five synapomorphies: ectethmoid largely separated from the jugal bar (char. 21.1, convergent in *Grallaria*); caudal end of the mandible with a small protuberance in the lateral margin (char. 37.1), with further changes within Rhinocryptidae (37.2, with a subsequent reversal to 37.1; see above) and a reversal (37.0) in the Furnariidae/Dendrocolaptidae clade with an additional change (37.1) in *Furnarius*; mandibular ramus mostly non-pneumatized (char. 39.1); Processus vocalis attached from A1 element cranial (char. 65.1); and M. sternotrachealis originating in the vertebral segment of the second rib (char. 88.1, convergent in *Melanopareia*). Within this clade, Scleruridae, Furnariidae, and Dendrocolaptidae – i.e. the traditional, enlarged Furnariidae – constituted a well-supported clade that was the sister group to the Rhinocryptidae. That node has a Bremer support of 1 and two synapomorphies: nasal septum with a long recurrent lamina (char. 6.0, convergent in *Conopophaga*); and alinasal turbinals ossified and fused to the vomer (char. 14.1).

The following section describes in detail all clades recovered within Rhinocryptidae in the present analysis and also provides a new classificatory scheme for the family.

NEW CLASSIFICATION OF THE RHINOCRYPTIDAE AND PHYLOGENETIC DIAGNOSES FOR CLADES

A new classification scheme is herein proposed to taxonomically recognize suprageneric groupings recovered within Rhinocryptidae by the present morphological phylogeny. However, recognition of suprageneric taxa in this new classification relies on the degree of clade support, with names being assigned only to relatively robust clades – in this case those that received Bremer support values of 4 or higher. This conservative approach aims to provide nomenclatural stability, as convincingly justified by de Pinna *et al.* (2007). This classification is also in agreement with the sequencing convention (Wiley, 1981), which produces an exact reflection of the tree without the necessity of naming every branch point, keeping to a minimum the number of rank categories and associated taxon names.

In the diagnoses presented below character/character state numbers (e.g. Char. 38.1) are according to the character analysis section above.

FAMILY RHINOCRYPTIDAE

SUBFAMILY LIOSCELINAE, NEW TAXON

Genus *Liosceles*

SUBFAMILY RHINOCRYPTINAE

TRIBE PSILORHAMPHINI, NEW RANK

Genus *Psilorhamphus*

TRIBE MERULAXINI, NEW TAXON

Genus *Eleoscytalopus*

Genus *Merulaxis*

TRIBE RHINOCRYPTINI, NEW RANK

SUBTRIBE ACROPTERNINA, NEW TAXON

Genus *Acropternis*

SUBTRIBE RHINOCRYPTINA, NEW RANK

Genus *Rhinocrypta*

Genus *Teledromas*

SUBTRIBE PTEROPTOCHINA, NEW RANK

Genus *Pteroptochos*

Genus *Scelorchilus*

SUBTRIBE SCYTALOPODINA, NEW RANK

Genus *Eugralla*

Genus *Myornis*

Genus *Scytalopus*

FAMILY RHINOCRYPTIDAE WETMORE, 1926

Type genus: *Rhinocrypta* G. R. Gray, 1841

Included subfamilies: Lioscelinae, new taxon, and Rhinocryptinae

Diagnosis.

Exclusive changes:

Char. 19.1, Non-pneumatized ectethmoid.

Char. 26.1, Lacrimal partially fused to the ectethmoid, with a suture discernible between the bones.

Char. 38.1, Foramen in the medial process of the mandible absent.

Non-exclusive changes:

Char. 31.1, Region of the parietal and frontal bones largely non-pneumatized, with reversal (31.0) in the clade *Rhinocrypta* + *Teledromas*; convergent with the outgroup clade *Phacellodomus* + *Cranioleuca*.

Char. 42.2, Caudal margin of the sternum with two pairs of notches; convergent in the outgroup genus *Melanopareia*.

Char. 43.0, Foramen in the medial face of the brachial tuberosity of the coracoid absent; convergent in the outgroup genera *Conopophaga*, *Melanopareia*, *Grallaria*, *Myrmotherula* and in the clade *Phacellodomus* + *Cranioleuca*.

Char. 48.1, Ulna as long as or shorter than humerus; convergent in the outgroup genus *Melanopareia* and the clade *Phacellodomus* + *Cranioleuca*.

Char. 50.2, Distance between the posterior projections of the ilium nearly equal to the width of the caudalmost sacral vertebrae, with reversal (50.1) in *Scelorchilus*; convergent in the outgroup genus *Dendrocolaptes*.

Bremer support for this clade: 6.

SUBFAMILY LIOSCELINAE, NEW TAXON

Type genus: *Liosceles* Sclater, 1865

Included genus: *Liosceles*

Diagnosis.

Non-exclusive change:

Char. 2.1, Premaxilla with a smoothly arched nasal process; condition also present in *Eleoscytalopus* and some *Scytalopus* taxa.

In addition, the new subfamily is phylogenetically diagnosed by a combination of features that include all apomorphic states supporting the family's node (mentioned above under the family's diagnosis) plus the plesiomorphic states of the transformation series that supports the subfamily Rhinocryptinae: a wide nasal process of the premaxilla (char. 3.0), a condition independently appearing in *Acropternis*, *Pteroptochos*, and *Eugralla* due to a reversal from state 1 to 0 in these genera; manubrium with long processes (char. 40.0), a condition acquired by reversal from state 1 to 0 in *Rhinocrypta*, *Teledromas*, and *Scelorchilus*; scapula with a relatively small acromion (char. 46.0); and fossa pneumotricipitalis of the humerus totally open, i.e. internal osseous wall absent (char. 47.0).

Genus: *Liosceles* Sclater, 1865 (type species: *Pteroptochus thoracicus* Sclater, 1865)

Included species: *Liosceles thoracicus* (Sclater, 1865)

Diagnosis.

As for Lioscelinae.

SUBFAMILY RHINOCRYPTINAE (WETMORE, 1926)

Type genus: *Rhinocrypta* G. R. Gray, 1841.

Included taxa: tribes Psilorhamphini, Merulaxini, new taxon, and Rhinocryptini.

Diagnosis.

Exclusive changes:

Char. 40.1, Manubrium with very short or vestigial processes, with reversal (40.0) in *Scelorchilus* and the *Rhinocrypta* + *Teledromas* clade.

Char. 47.1, Fossa pneumotricipitalis of the humerus completely closed by an osseous wall, with no opening to the interior of the bone.

Non-exclusive changes:

Char. 3.1, Narrow nasal process of the premaxilla, with reversal (3.0) in *Acropternis*, *Pteroptochos*, and *Eugralla*; convergent in the outgroup genera *Melanopareia*, *Geositta*, and *Sittasomus*.

Char. 46.1, Scapula with a very prominent acromion, exposed in medial view; convergent in the outgroup genus *Conopophaga*.

Bremer support for this clade: 4.

TRIBE PSILORHAMPHINI (WOLTERS, 1978),

NEW RANK

Type genus: *Psilorhamphus* Sclater, 1855

Included genus: *Psilorhamphus*

Diagnosis.

Non-exclusive changes:

Char. 25.1, Lateral portion of the ectethmoid rostrally oriented; convergent in *Scytalopus*.

Char. 27.3, Lacrimal vestigial; convergent in the clade *Eugralla* + *Myornis* + *Scytalopus*.

Genus *Psilorhamphus* Sclater, 1855 (type species: *Leptorhynchus guttatus* Ménétriés, 1835)

Included species: *Psilorhamphus guttatus* (Ménétriés, 1835).

Diagnosis.

As for tribe Psilorhamphini.

UNNAMED CLADE: MERULAXINI + RHINOCRYPTINI

Diagnosis.

Exclusive change:

Char. 37.2, Caudal end of the mandible with a well-developed protuberance in the lateral margin, with reversal (37.1) in *Pteroptochos tarnii* and *Scytalopus*.

Non-exclusive change:

Char. 1.1, Short premaxillary rostrum; convergent in the outgroup genus *Melanopareia*.

Bremer support for this clade: 1.

TRIBE MERULAXINI, NEW TAXON

Type genus: *Merulaxis* Lesson, 1831.

Included genera: *Eleoscytalopus* and *Merulaxis*.

Diagnosis.

Exclusive changes:

Char. 67.2, Cranial portion of the Processus vocalis ventrally and then cranially oriented.

Char. 69.1, Processus vocalis with a dorsal projection in the caudal portion.

Char. 74.1, A3–A5 elements dorsally reduced, with a further change (74.2) in *Merulaxis*.

Char. 75.1, Cartilaginous protuberance present in the ventral surface of the syrinx between A2 and A6 elements.

Non-exclusive changes:

Char. 4.1, Non-pneumatized maxilla; convergent in the clade formed by *Scelororchilus*, *Pteroptochos*, *Eugralla*, *Myornis*, and *Scytalopus* and in the outgroup genus *Melanopareia*.

Char. 29.3, Interorbital septum covering about one-quarter of the interorbital space, with only vestiges of an osseous beam in the caudal portion; convergent in the clade *Scelororchilus* + *Pteroptochos* + *Eugralla* + *Myornis* + *Scytalopus*.

Char. 68.1, Cranial portion of the Processus vocalis with a soft consistency; convergent in the outgroup genus *Conopophaga*.

Char. 83.0, Lateral surface of lower trachea/syrinx with no intrinsic musculature; also found in the outgroup genera *Conopophaga*, *Melanopareia*, *Sclateria*, *Myrmotherula*, and *Mackenziaena*.

Bremer support for this clade: 6.

Genus *Merulaxis* Lesson, 1831 (type species: *Merulaxis ater* Lesson, 1831)

Included species: *Merulaxis ater* Lesson, 1831 and *M. stresemanni* Sick, 1960.

Diagnosis.

Exclusive change:

Char. 74.2, A3 element dorsally vestigial and A4 and A5 elements dorsally absent.

Bremer support for this clade: 1.

Genus *Eleoscytalopus* Maurício, Mata, Bornschein, Cadena, Alvarenga and Bonatto, 2008 (type species: *Myiothera indigotica* Wied, 1831).

Included species: *Eleoscytalopus indigoticus* (Wied, 1831) and *E. psychopompus* (Teixeira and Carnevali, 1989).

Diagnosis.

Exclusive change:

Char. 70.1, Processus vocalis with a rectangular ossified plate.

Bremer support for this clade: 1.

TRIBE RHINOCRYPTINI (WETMORE, 1926), NEW RANK

Type genus: *Rhinocrypta* G. R. Gray, 1841

Included taxa: subtribes Acropternina, Rhinocryptina, Pteroptochina, and Scytalopodina.

Diagnosis.

Exclusive changes:

Char. 27.1, Lacrimal bone wide dorsally and narrower ventrally, with a further change (27.3) in the clade *Eugralla* + *Myornis* + *Scytalopus*.

Char. 33.1, Ventral surface of the zygomatic process with a conspicuous lamina, with reversal (33.0) in three *Scytalopus* taxa.

Char. 77.1, Cranial half of the syrinx with a sulcus in its ventrolateral surface.

Non-exclusive changes:

Char. 11.0, Short transpalatine process, with reversal (11.1) in *Scelororchilus*; convergent in the outgroup genera *Melanopareia*, *Mackenziaena*, *Geositta*, *Phacellodomus*, *Sittasomus*, and *Pitangus*.

Char. 12.0, Straight or slightly curved jugal bar, with reversal (12.1) in the clade *Myornis* + *Scytalopus*; also found in most outgroup taxa.

Char. 49.1, Dorsal iliac crests medially fused, forming the *Crista iliosynsacralis*; convergent in the outgroup genera *Cranioleuca* and *Dendrocolaptes*.

Bremer support for this clade: 4.

SUBTRIBE ACROPTERNINA, NEW TAXON

Type genus: *Acropternis* Cabanis and Heine, 1859.

Included genus: *Acropternis*.

Diagnosis.

Exclusive change:

Char. 2.3, Nasal process of the premaxilla developed into a high crest.

Non-exclusive changes:

Char. 3.0, Wide nasal process of the premaxilla (mesorrinum); convergent in *Pteroptochos* and *Eugralla* due to a reversal from state 1 to 0 in these genera and primitively present in *Liosceles* and most outgroup taxa.

Char. 85.1, Syringeal dorsoventral intrinsic muscle present; convergent in the clade *Pteroptochos* + *Scelororchilus* and the outgroup genus *Melanopareia*.

Genus *Acropternis* Cabanis and Heine, 1859 (type species: *Merulaxis orthonyx* Lafresnaye, 1843).

Included species: *Acropternis orthonyx* (Lafresnaye, 1843).

Diagnosis.

As for subtribe Acropternina.

UNNAMED CLADE:

RHINOCRYPTINA + PTEROPTOCHINA + SCYTALOPODINA

Diagnosis.

Non-exclusive change:

Char. 67.1, Cranial portion of the Processus vocalis ventrally oriented, with reversal (67.0) in *Eugralla*; convergent in the outgroup taxa *Myrmotherula* and *Hylopezus ochroleucus*.

Bremer support for this clade: 1.

SUBTRIBE RHINOCRYPTINA (WETMORE, 1926),
NEW RANK

Type genus: *Rhinocrypta* G. R. Gray, 1841

Included genera: *Rhinocrypta* and *Teledromas*.

Diagnosis.

Exclusive changes:

Char. 10.1, Maxillopalatine with a narrow shaft and a contrastingly wide plate.

Char. 15.1, Compound vomer with alinasal turbinals converging distally.

Char. 16.1, Alinasal turbinals of the compound vomer twisted dorsally.

Char. 17.1, Lateral condyle of the mandibular process of the quadrate wider than the caudal end of the jugal bar.

Non-exclusive changes:

Char. 31.0, Parietal and frontal bones completely pneumatized; a reversal to a condition primitively found in all but two outgroup taxa.

Char. 32.1, Fused postorbital and zygomatic processes; convergent in the outgroup genera *Melanopareia* and *Geositta*.

Char. 40.0, Manubrium with long processes; a reversal – convergent in *Scelorhynchus* – to a condition primitively found in *Liosceles* and all outgroup taxa.

Bremer support for this clade: 7.

Genus *Rhinocrypta* G. R. Gray, 1841 (type species: *Rhinomya lanceolata* Geoffroy-Saint Hilaire, 1832).

Included species: *Rhinocrypta lanceolata* (Geoffroy-Saint Hilaire, 1832).

Diagnosis.

No autapomorphy identified for the genus, but it can be distinguished from its sister taxon *Teledromas* by the possession of a Processus vocalis wide basally and narrow cranially (char. 66.1).

Genus *Teledromas* Wetmore and Peters, 1922 (type species: *Rhinocrypta fusca* Sclater & Salvin, 1873).

Included species: *Teledromas fuscus* (Sclater & Salvin, 1873).

Diagnosis.

Non-exclusive change:

Char. 66.0, Processus vocalis, in lateral view, relatively uniform in width.

UNNAMED CLADE: PTEROPTOCHINA + SCYTALOPODINA

Diagnosis.

Non-exclusive changes:

Char. 4.1, Non-pneumatized maxilla; convergent with Merulaxini and the outgroup genus *Melanopareia*.

Char. 29.3, Interorbital septum covering about one-quarter of the interorbital space, with only vestiges of an osseous beam in the caudal portion; convergent in Merulaxini.

Char. 89.1, Musculus tracheolateralis with both sides meeting in the ventral surface of the trachea, with reversal (89.0) in *Pteroptochos tarnii* and *Scytalopus macropus*; a condition also found in *Liosceles* and several outgroup genera.

Bremer support for this clade: 2.

SUBTRIBE PTEROPTOCHINA (SCLATER, 1858),
NEW RANK

Type genus: *Pteroptochos* Kittlitz, 1830.

Included genera: *Pteroptochos* and *Scelorhynchus*.

Diagnosis.

Exclusive changes:

Char. 18.1, Ectethmoid extending well above the level of the culmen.

Char. 22.1, Rostral surface of the ectethmoid with a projection over its lateral portion.

Char. 23.1, Rostral surface of the ectethmoid with a projection in the medial portion.

Non-exclusive changes:

Char. 28.0, Foramen present in the rostral surface of the lacrimal; also present in the outgroup genus *Pitangus*.

Char. 51.0, Synsacral vertebrae with paired fenestrae throughout the entire length of the synsacrum; convergent in the outgroup genera *Conopophaga*, *Geositta*, and *Pitangus*.

Char. 55.1, Posterolateral tendinal canal of the hypotarsus open; convergent in *Myornis* and the outgroup genera *Dendrocolaptes*, *Formicarius*, and *Conopophaga*.

Char. 85.1, Syringeal dorsoventral intrinsic muscle present; convergent in *Acropternis* and the outgroup genus *Melanopareia*.

Bremer support for this clade: 7.

Genus *Pteroptochos* Kittlitz, 1830 (type species: *Pteroptochos megapodius* Kittlitz, 1830).

Included species: *Pteroptochos megapodius* Kittlitz, 1830, *P. tarnii* (King, 1831), and *P. castaneus* Philippi and Landbeck, 1864.

Diagnosis.

Non-exclusive changes:

Char. 3.0, Wide nasal process of the premaxilla; convergent in *Acropternis* and *Eugralla* and primitively found in *Liosceles* and most outgroup taxa.

Char. 24.1, Ectethmoid with a medial opening; convergent in *Scytalopus* sp. and *S. latrans*.

Bremer support for this clade: 2.

Genus *Scelorhynchus* Oberholser, 1923 (type species: *Pteroptochos rubecula* Kittlitz, 1830).

Included species: *Scelorhynchus rubecula* (Kittlitz, 1830) and *S. albicollis* (Kittlitz, 1830).

Diagnosis.

Non-exclusive changes:

Char. 11.1, Long transpalatine process; this condition is also found in *Liosceles*, *Psilorhamphus*, *Merulaxini*, and half of the outgroup genera.

Char. 40.0, Manubrium with long processes; a reversal – convergent in *Rhinocryptina* – to a condition primitively found in *Liosceles* and all outgroup taxa.

Char. 50.1, Distance between the posterior projections of the ilium within 1.2–1.8 times the width of the caudalmost sacral vertebrae; a reversal to a condition found in most outgroup genera.

SUBTRIBE SCYTALOPODINA (J. MÜLLER, 1847)
NEW RANK

Type genus: *Scytalopus* Gould, 1837

Included genera: *Eugralla*, *Myornis* and *Scytalopus*.

Diagnosis.

Exclusive changes:

Char. 35.1, Short temporal fossa.

Char. 36.1, Paraoccipital process with a dorsal, pointed projection.

Char. 44.1, Unfused clavicles, with no hypocleideum.

Char. 64.2, Processus vocalis mostly ossified, with a cartilaginous base.

Char. 71.1, Left Processus vocalis shorter than the right one.

Non-exclusive change:

Char. 27.3, Lacrimal vestigial; convergent in *Psilorhamphus*.

Bremer support for this clade: 6.

Genus *Eugralla* Lesson, 1842 (type species: *Trogodytes paradoxus* Kittlitz, 1830).

Included species: *Eugralla paradoxa* (Kittlitz, 1830).

Diagnosis.

Exclusive change:

Char. 66.2, Processus vocalis, in lateral view, wide caudally and cranially and narrow in between.

Non-exclusive changes:

Char. 3.0, Wide nasal process of the premaxilla (mesorrhinum); convergent in *Pteroptochos* and *Acropternis* due to a reversal from state 1 to 0 in these genera; primitively present in *Liosceles* and most outgroup taxa.

Char. 67.0, Cranial portion of the Processus vocalis cranially oriented (i.e. oriented as the main axis of the Processus); a reversal to a condition found in *Liosceles*, *Psilorhamphus*, *Acropternis*, and most outgroup taxa.

UNNAMED CLADE: *MYORNIS* + *SCYTALOPUS*

Included genera: *Myornis* and *Scytalopus*.

Diagnosis.

Non-exclusive changes:

Char. 12.1, Jugal bar sinusoidal; a reversal to a condition found in the basal genera *Liosceles*, *Psilorhamphus*, *Merulaxis*, and *Eleoscytalopus* and in the outgroup taxa *Sclateria*, *Formicarius*, *Conopophaga*, and *Melanopareia*.

Char. 78.2, Dorsal ends of A2 fused and then fused to A3, with reversal (to 78.1 and 78.0) in some *Scytalopus* taxa; condition also found in the outgroup taxa *Geositta*, *Furnarius*, *Syndactyla*, *Phacellodomus*, and *Formicarius*.

Bremer support for this clade: 1.

Genus *Myornis* Chapman, 1915 (type species: *Merulaxis senilis* Lafresnaye, 1840).

Included species: *Myornis senilis* (Lafresnaye, 1840).

Diagnosis.

Non-exclusive change:

Char. 55.1, Posterolateral tendinal canal of the hypotarsus open; convergent in *Pteroptochina* and the outgroup genera *Dendrocolaptes*, *Formicarius*, and *Conopophaga*.

Genus *Scytalopus* Gould, 1837 (type species: *Motacilla magellanica* Gmelin, 1789).

Included species: *S. latrans* Hellmayr, 1924; *Scytalopus unicolor* Salvin, 1895; *S. parvirostris* Zimmer, 1939; *S. speluncae* (Ménétriés, 1835); *S. diamantinensis* Bornschein, Maurício, Belmonte-Lopes, Mata & Bonatto, 2007; *S. petrophilus* Whitney, Vasconcelos, Silveira and Pacheco, 2010; *S. pachecoi* Maurício, 2005; *S. iraiensis* Bornschein et al., 1998; *S. macropus* Berlepsch and Stolzmann, 1896; *S. sanctaemartae* Chapman, 1915; *S. micropterus* (Sclater, 1858); *S. femoralis* (Tschudi, 1844); *S. atratus* Hellmayr, 1922; *S. bolivianus* Allen, 1889; *S. panamensis* Chapman, 1915; *S. chocoensis* Krabbe & Schulenberg, 1997; *S. rodriguezi* Krabbe, Salaman, Cortés, Quevedo, Ortega & Cadena, 2005; *S. stilesi* Cuervo, Cadena, Krabbe, & Renjifo, 2005; *S. robbinsi* Krabbe & Schulenberg, 1997; *S. vicinior* Zimmer, 1939; *S. latebricola* Bangs, 1899; *S. meridanus* Hellmayr, 1922; *S. caracae* Hellmayr, 1922; *S. spillmanni* Stresemann, 1937; *S. parkeri* Krabbe & Schulenberg, 1997; *S. novacapitalis* Sick, 1958; *S. magellanicus* (Gmelin, 1789); *S. griseicollis* (Lafresnaye, 1840); *S. altirostris* Zimmer, 1939; *S. affinis* Zimmer, 1939; *S. acutirostris* (Tschudi, 1844); *S. urubambae* Zimmer, 1939; *S. simonsi* Chubb, 1917; *S. zimmeri* Bond and Meyer de Schauensee, 1940; *S. superciliaris* Cabanis, 1883; *S. fuscus* Gould, 1837; *S. canus* Chapman, 1915;

S. opacus Zimmer, 1941; *S. schulenbergi* Whitney, 1994; *S. argentifrons* Ridgway, 1891.

Diagnosis.

Exclusive change:

Char. 13.1, Emarginated lateral margin of the rostral portion of the jugal bar.

Non-exclusive changes:

Char. 25.1, Lateral portion of the ectethmoid rostrally oriented; convergent in *Psilorhamphus*.

Char. 37.1, Caudal end of the mandible with a small protuberance in the lateral margin; convergent in *Pteroptochos tarnii* and primitively found in *Liosceles*, *Psilorhamphus*, and the outgroup taxa *Formicarius* and *Geositta*.

Bremer support for this clade: 3.

DISCUSSION

MONOPHYLY OF RHINOCRYPTIDAE

The present morphology-based analysis constitutes a robust test of monophyly of the family as it includes representatives of all families of the infraorder Furnariides and all genera of Rhinocryptidae – including a heterogeneous sampling of the highly speciose genus *Scytalopus*. The only other study aimed at testing the monophyly of the family was the recent sequence-based analysis presented by Ericson *et al.* (2010), which included representatives of most families of Furnariides (except Scleruridae) and all rhinocryptid genera, but a much less heterogeneous sampling of *Scytalopus*. The two studies are therefore complementary. The Rhinocryptidae as recovered in our morphological phylogeny is perfectly congruent with all molecular phylogenies with adequate taxonomic coverage (Moyle *et al.*, 2009; Ericson *et al.*, 2010) in excluding the genus *Melanopareia* from the family and supporting the allocation of the problematic genera *Psilorhamphus* and *Teledromas* within Rhinocryptidae. The resulting monophyletic Rhinocryptidae has strong Bremer support (i.e. 6), includes 12 genera (*Liosceles*, *Psilorhamphus*, *Eleoscytalopus*, *Merulaxis*, *Acropternis*, *Rhinocrypta*, *Teledromas*, *Pteroptochos*, *Scelorchilus*, *Eugralla*, *Myornis*, and *Scytalopus*), and is defined by the following eight synapomorphies, the first four of which are features not previously mentioned for the family: non-pneumatized ectethmoid (char. 19.1), absence of foramen in the medial face of the brachial tuberosity of the coracoid (char. 43.0), ulna as long as or shorter than humerus (char. 48.1), distance between the posterior projections of the ilium nearly equal to the width of the caudalmost sacral vertebrae (char. 50.2), absence of a foramen in the medial process of the mandible (char. 38.1), caudal margin of the sternum with two pairs of notches (char. 42.2), lacrimal par-

tially fused to the ectethmoid (char. 26.1), and parietal and frontal bones largely non-pneumatized (char. 31.1). Additionally, the last four characters have never been formally suggested as synapomorphic for the family, although the last two have been regarded as ‘characteristics that unite members of the tapaculo family’ (termed ‘lacrimal bones fused into the ectethmoid’ and ‘incomplete skull ossification’, respectively) by Krabbe & Schulenberg (2003: 752). The four-notched sternum was optimized as a synapomorphy of the Rhinocryptidae in the only previous morphology-based cladistic study that included members of the family (*Pteroptochos* and *Rhinocrypta*) (Claramunt & Rinderknecht, 2005), judging from the consensus tree and the data matrix presented.

Below, a detailed account regarding the systematic placement of each of the ‘problematic’ genera is provided.

Melanopareia: Comprehensive taxon and character sampling is particularly important to elucidate the position of *Melanopareia* because morphology-based studies (Ames, 1971; Feduccia & Olson, 1982) found it natural to place *Melanopareia* within Rhinocryptidae, as first suggested by W. W. Miller on the basis of this genus’ possession of a four-notched sternum (Wetmore, 1926). However, these morphological studies did not include cladistic analyses of characters and based their decisions solely upon particular features whose systematic value is subjective if not analysed within a strict cladistic context. Feduccia & Olson (1982) noted that *Melanopareia* lacked some features typical of rhinocryptids such as the absence of a foramen in the medial process of the mandible but concluded that ‘... our examination showed its osteology to be in accordance with its placement in the Rhinocryptidae’ (p. 6). However, apart from some general similarities, one can find only two objective characters in the literature that would support *Melanopareia* as part of the Rhinocryptidae, namely the possession of a lacrimal partially fused to the ectethmoid and the four-notched sternum (Feduccia & Olson, 1982; Krabbe & Schulenberg, 2003; Ericson *et al.*, 2010). On the basis of material available for the present study, however, the lacrimal was not partially fused to the ectethmoid in *Melanopareia*, and instead its lacrimal was found to be completely fused to the ectethmoid with no signs of suture, as in the great majority of the members of Furnariides. On the other hand, a number of character-states – including the four-notched sternum – were found here to occur in the Rhinocryptidae and in the Melanopareiidae (Fig. 43), but these shared conditions were solidly optimized in the parsimony analysis as convergences between distantly related groups: *Melanopareia* was

part of a polytomy with the families Conopophagidae, Grallariidae, Thamnophilidae, and a large, structured clade that included Formicariidae, Scleruridae, Furnariidae, Dendrocolaptidae, and Rhinocryptidae. Another morphological feature that supports the exclusion of *Melanopareia* from the Rhinocryptidae is its retention of the primitive morphology of the stapes (flat footplate) instead of the typical suboscine condition present in all rhinocryptids (inflated footplate), including *Psilorhamphus* and *Teledromas* (Feduccia, 1974; Ericson *et al.*, 2010). In any event, the present morphology-based phylogeny corroborates the erection of the family-level taxon Melanopareiidae for the genus *Melanopareia* as first proposed by Irestedt *et al.* (2002) and later formalized by Ericson *et al.* (2010).

Psilorhamphus: Although it has been suggested that *Psilorhamphus* might lie outside Rhinocryptidae (Ridgely & Tudor, 1994) and that it bears little external resemblance to typical members of the family (Krabbe & Schulenberg, 2003; Ericson *et al.*, 2010), *Psilorhamphus* proved to be a typical member of the group in terms of osteology, with 12 synapomorphies supporting it as a rhinocryptid (eight in the family node and four in the subsequent node) and no character state linking it to other family of Furnariides (see Fig. 43). Therefore, the allocation of the genus to the Rhinocryptidae as first implemented by Plótnick (1958) was a correct systematic decision, with two of the characters that supported this author's decision – *M. sternotrachealis* originating in the vertebral segment of the second rib and presence of two pairs of notches in the sternum – having been cladistically optimized here as support for such a placement (the first character for the Formicariidae + Furnariidae + Scleruridae + Dendrocolaptidae + Rhinocryptidae clade and the latter for the rhinocryptid clade). Recent molecular phylogenies also corroborated this placement (Maurício *et al.*, 2008; Ericson *et al.*, 2010).

Teledromas: Based on similarity of vocalizations (Ridgely & Tudor, 1994; N. Krabbe, unpubl. data), general shape, details of the nasal operculum, tarsal scutellation, flank pterylography, and straight shape of humerus between *Teledromas* and *Melanopareia*, Irestedt *et al.* (2002) suggested that they were members of the same clade. Given that *Melanopareia* proved to be a distinct lineage of uncertain affinities, they placed both genera in the new family Melanopareiidae even though no sequence data of *Teledromas* were available. Subsequent molecular phylogenies that included *Teledromas* samples showed this genus to be well embedded within Rhinocryptidae (Moyle *et al.*, 2009; Ericson *et al.*, 2010), a placement corroborated in the present analysis. In

fact, anatomically *Teledromas* is very similar to *Rhinocrypta*, both having several shared derived character states (see above). The alleged similarity of *Teledromas* to *Melanopareia* (Irestedt *et al.*, 2002), at least in terms of general aspect and shape of the humerus, found no support here. Moreover, although vocalizations were considered as the main evidence for a close link between *Teledromas* and *Melanopareia* (Irestedt *et al.*, 2002; Ericson *et al.*, 2010) detailed structural analyses of the vocal repertoire of *Teledromas* support its inclusion within the Rhinocryptidae (J. I. Areta, unpubl. data).

RELATIONSHIPS BETWEEN RHINOCRYPTIDAE AND OTHER FAMILIES OF FURNARIIDES

Once a monophyletic Rhinocryptidae is defined, the next natural question to be answered is about its family-level relationships. Although the present study was not specifically designed to address this question, the phylogeny recovered here was resolved at this level and this finding will be briefly discussed below.

The sister relationship of Rhinocryptidae to the Scleruridae + Furnariidae + Dendrocolaptidae clade as recovered in this study is not a completely novel systematic arrangement. On the basis of a general similarity in the shape of the maxillopalatine bone, Garrod (1877a) argued for a sister relationship between Rhinocryptidae and Furnariidae (then including Scleruridae), but with Dendrocolaptidae being regarded as a more distant group. More recent anatomical studies, on the other hand, have suggested a closer relationship of rhinocryptids to the Grallariidae, Formicariidae, and Conopophagidae (Ames, 1971), an association corroborated by the DNA–DNA hybridization studies of Sibley & Ahlquist (1985, 1990). The latter studies further indicated that within that assemblage the family Conopophagidae was the sister-group to the Rhinocryptidae.

No cladistic analysis recovered a sister relationship of the Rhinocryptidae as depicted in the present study, but most taxonomically comprehensive analyses have found topologies that are consistent with it in a slightly broader context. Irestedt *et al.* (2002, 2009), Chesser (2004), Claramunt & Rinderknecht (2005), Claramunt (2010), Ericson *et al.* (2010), and Derryberry *et al.* (2011) recovered a large clade exclusively containing the families Rhinocryptidae, Scleruridae, Furnariidae, Dendrocolaptidae, and Formicariidae (as in the present study), within which Rhinocryptidae was either sister to a clade formed by the remaining four families, sister to the Formicariidae or was part of a polytomy with the latter plus a Scleruridae + Furnariidae + Dendrocolaptidae clade. Only the topology found by Moyle *et al.* (2009) challenged this general arrangement in that it included

the Grallariidae as sister to the Rhinocryptidae. Although support for such a hypothesis was moderate to low, Moyle *et al.* (2009) recognized formally the Rhinocryptidae + Grallariidae clade under the superfamily-level taxon Grallarioidea. However, despite the large number of base pairs of the analysed dataset (about 4000 bp of the nuclear genes RAG 1 and RAG 2) and the dense taxonomic sampling of the Moyle *et al.* (2009) study, there is much stronger evidence for a clade containing only Rhinocryptidae, Formicariidae, Furnariidae, Scleruridae, and Dendrocolaptidae than for a sister-taxon relationship of rhinocryptids to the Grallariidae. The evidence supporting the former hypothesis includes both morphological (Claramunt & Rinderknecht, 2005; this study) and molecular phylogenies (Irestedt *et al.*, 2002, 2009; Chesser, 2004; Claramunt, 2010; Ericson *et al.*, 2010; Derryberry *et al.*, 2011), with the latter studies including from 1500 to 3600 characters from several distinct genes (including RAG 1). Moreover, the recent genome-wide study of Hackett *et al.* (2008) included an unprecedented number of characters (32 000 bp) sampled for representatives of most higher-level groups of living birds, including four genera/families of Furnariides, and recovered with strong support the topology (*Thamnophilus* (*Grallaria* (*Scytalopus* + *Dendrocolaptes*))), a result consistent with the above phylogenies except that of Moyle *et al.* (2009). Therefore, diverse and independent lines of evidence reject the hypothesis of a sister relationship of Rhinocryptidae to the Grallariidae but support a clade containing only the former and the families Formicariidae, Scleruridae, Furnariidae, and Dendrocolaptidae. See also Rice (2005), who suggested merging of the Rhinocryptidae into the Formicariidae based on a molecular phylogeny that included only representatives of these two families plus Grallariidae, Conopophagidae, and Thamnophilidae.

RELATIONSHIPS WITHIN RHINOCRYPTIDAE

Several previous hypotheses of relationships within Rhinocryptidae were corroborated in the present study, but others were not. The polytypic genera *Merulaxis*, *Eleoscytalopus*, *Pteroptochos*, and *Scytalopus* were recovered as monophyletic in the analysis, but because only one of the two species of *Scelorichilus* was included here, its monophyly remains to be properly tested with the inclusion of *S. albicollis*.

The paraphyletic nature of *Scytalopus* with respect to the inclusion of the white-bellied taxa '*S*' *indigoticus* and '*S*' *psychopompus* in the genus, as shown by Maurício *et al.* (2008), was corroborated here, thus supporting the erection of the genus *Eleoscytalopus* to place these two species. This proposition was based primarily upon a molecular phylogenetic analysis

that recovered an *Eleoscytalopus* + *Merulaxis* clade, but also included some syringeal and osteological data from an early phase of the project that resulted in the present study (see Maurício *et al.*, 2008). The syringeal character-states suggested by these authors as support for a sister-taxon relationship between *Eleoscytalopus* and *Merulaxis* – cranial portion of the Processus vocalis with a soft consistency and A3–A5 elements dorsally reduced/absent – were optimized here together with six others (four syringeal and two osteological; see above) as synapomorphies for a clade containing exclusively these two genera, although the placement of this clade within the Rhinocryptidae was considerably distinct between the two studies (Fig. 43).

A close relationship between *Scelorichilus* and *Pteroptochos* has been suggested by early taxonomists (e.g. Sclater, 1874) and was recently corroborated by molecular data (Chesser, 1999; Maurício *et al.*, 2008; Moyle *et al.*, 2009; Ericson *et al.*, 2010). In the present study this relationship was strongly supported, with seven synapomorphies, none of which has been previously mentioned as evidence of a relationship between these genera. One of these synapomorphies, presence of a dorsoventral intrinsic muscle in the syrinx, was described as having a generalized occurrence in the Rhinocryptidae (Ames, 1971), and was suggested as a synapomorphy for the family as a whole (Rice, 2005). This hypothesis is herein refuted as this dorsally originating intrinsic muscle actually has a very restricted occurrence in the family (i.e. only in *Acropternis*, *Scelorichilus*, and *Pteroptochos*).

A *Rhinocrypta* + *Teledromas* clade was recovered by Moyle *et al.* (2009) and the present study, but Ericson *et al.* (2010) found *Teledromas* as sister to a *Rhinocrypta* + *Acropternis* clade. Morphological evidence in favour of the *Rhinocrypta* + *Teledromas* arrangement was solid. Besides being defined by seven synapomorphies, a general similarity in size and proportions of the sternum, cranium, and pelvis characterizes the members of the *Rhinocrypta* + *Teledromas* clade. Two of the seven synapomorphic conditions supporting this branch were previously described for *Rhinocrypta* only, namely parietal and frontal bones fully pneumatized (Feduccia & Olson, 1982; Krabbe & Schulenberg, 2003) and postorbital and zygomatic processes fused (Claramunt & Rinderknecht, 2005).

On the basis of external similarities it has been suggested that the genera *Merulaxis*, *Eugralla*, *Myornis*, and *Scytalopus* form a clade, and that within this clade *Merulaxis* and *Myornis* would be sister-taxa (Krabbe & Schulenberg, 1997, 2003; Irestedt *et al.*, 2002). Recent molecular studies recovered such a clade, but *Merulaxis* was sister to the recently

described genus *Eleoscytalopus* instead of to *Myornis* (Maurício *et al.*, 2008; Mata *et al.*, 2009; Ericson *et al.*, 2010). The present study partially corroborated the molecular findings, as it recovered *Eleoscytalopus* as sister to *Merulaxis* and also a well-supported *Eugralla* + *Myornis* + *Scytalopus* clade, but these two clades were placed in very distinct points of the rhinocryptid morphology-based tree: whereas the former is a basal branch the latter is an apical clade embedded within a clade containing the large-bodied genera. Of the six synapomorphies that define the *Eugralla* + *Myornis* + *Scytalopus* clade only the unfused clavicles were previously mentioned as a supporting character for this grouping (Maurício *et al.*, 2008; see also Feduccia & Olson, 1982). Within this clade all molecular phylogenies recovered *Eugralla* as sister to *Scytalopus* and *Myornis* as basal to both (Maurício *et al.*, 2008; Mata *et al.*, 2009; Moyle *et al.*, 2009; Ericson *et al.*, 2010), thus differing from the morphological data which showed *Eugralla* as sister to a *Myornis* + *Scytalopus* clade. The morphological data did not allow us to test previous hypotheses of relationships in the genus *Scytalopus* (e.g. Arctander & Fjeldså, 1994; Krabbe & Schulenberg, 1997; Bornschein *et al.*, 1998; Maurício, 2005; Mata *et al.*, 2009). The strict consensus of most parsimonious trees could not even recover the phylogenetic subdivision of the genus into an Andean and a Brazilian component as proposed by Mata *et al.* (2009).

The present study did not corroborate the division of the family into the subfamilies Rhinocryptinae and Scytalopodinae as proposed by Moyle *et al.* (2009). The comprehensive molecular phylogeny of Ericson *et al.* (2010) also diverged from the results of the former authors in that the Scytalopodinae, to be a monophyletic group, should include *Scelorhynchus* and *Pteroptochos*, both being part of Rhinocryptinae *sensu* Moyle *et al.* (2009), as well as *Eleoscytalopus* and *Merulaxis*, not sampled in the latter study. The genera *Liosceles* and *Psilorhynchus* formed a clade in Ericson *et al.* (2010) that was sister to a *Teledromas* + *Rhinocrypta* + *Acropternis* clade, thus approaching the composition of the Rhinocryptinae as recovered by Moyle *et al.* (2009) who, however, did not sample *Psilorhynchus*. In contrast to these molecular phylogenies, the basal relationships recovered by the present morphological analysis consisted of *Liosceles* and *Psilorhynchus* as being successively basal to a clade containing the remaining ten genera, within which *Eleoscytalopus* + *Merulaxis* were sister to a group composed of the remaining eight genera. Of this branching scheme, the basal position of *Liosceles* relative to the rest of the family and the grouping of eight genera were supported by four or six synapomorphies and relatively strong Bremer values (i.e. 4), and thus at least these nodes may be regarded as

good topological alternatives of the deeper rhinocryptid cladogenesis relative to the molecular findings.

In summary, clades supported by six or more synapomorphies and Bremer values of 6 or 7, such as *Eleoscytalopus* + *Merulaxis*, *Scelorhynchus* + *Pteroptochos*, *Rhinocrypta* + *Teledromas*, and *Eugralla* + *Myornis* + *Scytalopus* (Fig. 43), were the main points of congruence between the present morphological phylogeny and the previous phylogenetic work with the family, all sequence-based. On the other hand, more inclusive nodes (i.e. those including more than three genera) were dissimilar between this study and the molecular phylogenies, although two of those nodes received Bremer support values of 4 in the morphological analysis. None of the synapomorphies supporting these basal nodes was previously mentioned in the literature.

THE IMPORTANCE OF MORPHOLOGY IN PHYLOGENETIC INFERENCE

The differences between the results of Moyle *et al.* (2009) and Ericson *et al.* (2010) regarding the placement of some genera, in addition to the substantial topological differences found by the latter authors when the three nuclear genetic markers are analysed separately (Ericson *et al.*, 2010: 343, fig. 3), revives the debate concerning species trees versus gene trees: 'If the evolution of a gene differs from that of a species, trees reconstructed from molecular data may give well-supported wrong answers to questions about species phylogeny' (Hillis & Wiens, 2000) and 'There are many factors that may cause molecular analyses to reconstruct clades that are both incorrect and statistically well supported...' (Wiens, 2004). In this context, it is important to bear in mind that 'a typical set of morphological characters should draw on information from many different unlinked genes [...], whereas the characters in a given molecular data set are often linked and inherited as a single unit' (Wiens, 2004). Therefore, as Wiens (2004: 654) states, given that we are not at a stage where all molecular phylogenies can be reconstructed without error, it is important to have rigorous morphology-based phylogenies as a 'reality check' for molecular results. It is also important to consider the more complex (i.e. less parsimonious) evolutionary pathway of morphological characters implied by the molecular phylogenies. For example, the phylogenetic placement of *Liosceles* both in Moyle *et al.* (2009) and in Ericson *et al.* (2010) implies reversals or parallel transformations in several characters, among which are complex ones such as the presence/absence of an osseous wall in the fossa pneumotricipitalis (character 47) and fusion of the dorsal iliac crests to form the *Crista*

iliosynsacralis (character 49). Likewise, although the clade *Teledromas* + *Rhinocrypta* was supported by seven morphological synapomorphies, had a Bremer support of 7 and was recovered by Moyle *et al.* (2009), it was never recovered by Ericson *et al.* (2010). The clade (*Teledromas* (*Acropternis* + *Rhinocrypta*)) recovered by the combined analysis of Ericson *et al.* (2010) would imply reversals in *Acropternis* or independent evolution in *Teledromas* and *Rhinocrypta* of seven character states, including four that are exclusive to the clade formed by these two genera in the morphological tree. Here and again, we echo the claims of Wiens (2004: 654) about the importance of having rigorous morphology-based phylogenies as a 'reality check' for molecular results.

GENERIC BOUNDARIES

Although the implementation of phylogenetic methods has tremendously improved our capacity to establish the limits of genera more objectively in comparison to traditional phenetic approaches, a considerable degree of subjectivity remains at the moment of choosing at which node it is more adequate to place a generic name to maintain a phylogenetic classification (see Chu, 1998). A general criterion frequently applied to address this question is to avoid recognition of phenotypically too heterogeneous genera, using previous classifications as landmarks for comparisons. For example, if a phylogeny supports that a taxon traditionally classified in a given genus is actually sister to a morphologically very distinct genus, it may be preferable to erect a new generic name for that taxon instead of creating a heterogeneous entity, provided that such heterogeneity is inconsistent with the current genus-level classification within the higher taxon involved [see Maurício *et al.* (2008), Derryberry *et al.* (2010), and Claramunt *et al.* (2010) for examples of this approach in Furnariidae]. Implementation of quantitative analysis of phenotypic heterogeneity to help guide taxon-ranking decisions, as done by Claramunt *et al.* (2010) for dendrocolaptid genera, tends to make that approach even more objective. It is beyond the scope of the present paper to apply that type of analysis, but at least a brief, non-quantitative analysis of the morphological diversity of the *Eugralla* + *Myornis* + *Scytalopus* clade seems necessary as generic limits within this group have been somewhat disputed. In accordance with recent molecular findings (Maurício *et al.*, 2008; Mata *et al.*, 2009; Moyle *et al.*, 2009; Ericson *et al.*, 2010), the topology of the morphological phylogeny did not reject recognition of the monotypic genera *Eugralla* and *Myornis*, both falling outside a *Scytalopus*-only clade. However, one may argue that the merging of these two monotypic

genera with *Scytalopus* would be more informative of their relationships and consistent with the opinion (Vuilleumier, 1985: 295) that generic limits between these three similarly coloured genera 'may be hard to draw'. It is important to mention that *Myornis senilis* was long placed in *Scytalopus* until Chapman's (1915) proposal of a monotypic genus for it, arguing that in having a conspicuously elevated base of the bill, rounded wings and a long tail (longer than wing) it diverged at the generic level from *Scytalopus*. After Chapman's (1915) description of *Myornis* only Hilty & Brown (1986) merged *senilis* within *Scytalopus*, an arrangement rejected by all subsequent authors since Fjeldså & Krabbe (1990) (see also Ridgely & Tudor, 1994; Krabbe & Schulenberg, 1997). *Eugralla paradoxa*, on the other hand, has always been regarded as generically distinct from *Scytalopus* and, primarily on the basis of its possession of a strongly elevated and flattened culmen similar to that of the large and peculiar *Acropternis orthonyx*, it was treated alongside the latter under the genus name *Triptorhinus* (Cabanis, 1847; Sclater, 1855). However, the osteological basis for the elevated culmen of *Eugralla* – its main generic character – is a strong arching of the nasal process of the premaxilla that is also present in *Myornis* skulls (called 'crest' in Feduccia & Olson, 1982, character 2, state 2 of the present study), a character state that separates both from any of the *Scytalopus* taxa examined here. Additionally, other anatomical features point to the distinctiveness of the former two genera compared with *Scytalopus*. *Eugralla* is further characterized by three autapomorphies (Fig. 43) whereas *Myornis* shows a level of atrophy of its clavicles not paralleled by any *Scytalopus* taxa examined. Natural history aspects such as nest placement, vocalizations, and microhabitat have also been highlighted as distinctive between *Eugralla/Myornis* and *Scytalopus* (Parker *et al.*, 1985; Fjeldså & Krabbe, 1990). In summary, uniting these three genera under the same genus would result in a relatively heterogeneous entity that would be inconsistent with the current genus-level classification of the Rhinocryptidae. Maintaining these three genera as currently accepted warrants coherence of the generic classification within the family as well as nomenclatural stability and, therefore, is the alternative recommended here.

It has been suggested that *Scytalopus macropus* might be generically distinct from *Scytalopus* (Whitney, 1994), but the only feature that suggests its distinctiveness is the fact that it is by far the largest and heaviest of all congeners; its general shape, proportions, and anatomy are quite typical of the genus. Furthermore, none of the 456 trees resulting from the analysis performed without the incomplete taxa recovered *S. macropus* as basal relative to the

remaining taxa, a position most frequently (92%) occupied by *S. magellanicus*, the type species of the genus.

BIOGEOGRAPHY

Biogeographically, the topology of the rhinocryptid tree as recovered in the present morphological analysis comprises (1) a basal Amazonian component that includes only the genus *Liosceles*, two Atlantic forest components, namely (2) *Psilorhamphus* and (3) *Eleoscytalopus* + *Merulaxis*, which are successively basal to (4) a diverse component essentially restricted to the western half of South America (west of the north–south oriented Paraguay/Paraná river axis) that is formed by the remaining eight genera. In this large group, biogeographically meaningful units include an arid lowland Chaco and Monte clade comprising *Teledromas* and *Rhinocrypta*, a Chilean matorral and *Nothofagus* forest clade including *Scelorchilus* and *Pteroptochos* and an essentially montane clade including *Eugralla*, *Myornis*, and *Scytalopus*. Of this latter group, only the genus *Scytalopus* reaches the Atlantic forest region and nearby areas of eastern South America.

At this moment it is premature to suggest any clear association between the cladogenesis uncovered by the morphological phylogeny and specific geological/palaeoclimatic events. However, some tentative correlations are suggested here.

The placement of the main axis of the Paraná/Paraguay river basin coincides with the area that separates two sister-clades, the Atlantic forest clade *Eleoscytalopus* + *Merulaxis* and the western clade. It is well documented that this region was inundated by the sea at some points during the Tertiary, from the Atlantic coast to the Bolivian territory (Lundberg *et al.*, 1998), and this type of event certainly would have isolated at opposite sides of the submerged area most flightless birds such as rhinocryptids.

The intense and complex Andean orogenesis during the Tertiary (Lundberg *et al.*, 1998; Gregory-Wodzicki, 2000) probably promoted cladogenesis within the family such as the separation between the cis-Andean clade *Teledromas* + *Rhinocrypta* and the Andean/trans-Andean clade *Scelorchilus* + *Pteroptochos* + *Eugralla* + *Myornis* + *Scytalopus*. The genus *Scytalopus* originated in the Andes and subsequently dispersed eastward to reach south-eastern Brazil and adjacent Argentina. This hypothesis has been defended by several authors, notably Sick (1985) and Vielliard (1990), and was corroborated by recent molecular phylogenetic analyses (Maurício *et al.*, 2008; Mata *et al.*, 2009). However, the idea of a generalized Andean origin for the Atlantic forest rhinoc-

ryptids (Sick, 1985; Willis, 1992) found no support in the present study, as three of the four genera occurring in this region (*Psilorhamphus*, *Eleoscytalopus*, and *Merulaxis*) were recovered as basal clades within the family.

ACKNOWLEDGEMENTS

We are most grateful to Carla S. Fontana for giving us constant support at the Laboratório de Ornitologia of the MCT/PUCRS and to Mariana Gonçalves, Helena Mata, Cristiano E. Rovedder, Márcio Repenning, Ismael Franz, Úrsula Rasquim, and Cybele Marques of the same laboratory for their friendship and help in many aspects. We are deeply indebted to Márcio Repenning, Carlos Antonio Rodríguez, Carlos Gussoni, Ricardo Belmonte-Lopes, Bianca Luiza Reinert, Bruno Renó, Cassiano Gatto, Léo Malagoli, Carlos Eduardo Agne, Carlos Mariano Kovacs, Juan Manuel Guayasamin, Alberto Quintana, Vitor de Q. Piacentini, Gustavo Sebastián Cabanne, and Fábio R. do Amaral for their help during fieldwork. We thank Ingrid Holzmann, Darío Morán, Adriana Centeno, Luis Pagano, Lalo Etcheverry, Carlos Darrieu, Carlos Kovacs, and Ors Kovacs for their invaluable logistical support in Argentina. For logistical support in Brazil we thank Aline Montagna da Silveira, José Luiz Braga Maurício, Seli Nachtigall Maurício, Rita de Cássia Nachtigall Maurício, Vera Regina Braga Maurício, Marília Montagna da Silveira, Paulo Gilberto da Silveira, Marcelo Ferreira de Vasconcelos, Christian Andretti, Glayson A. Bencke, Vinicius A. Bastazini, Jan Karel Mähler Jr, Cibele Indrusiak, Carla S. Pavanelli, Norma Hahn, Luciano Wolf, and Cláudio Zawadski. We are grateful to Antônio Sérgio Varela Jr, Edelti Albertoni, and Juliana Souza (FURG) for allowing use of photographic equipment under their care. We thank Leandro Bugoni (FURG) for critically reading and commenting on the manuscript. For giving us collecting permits in Argentina we are most grateful to Maurício Failla of the Dirección de Fauna Silvestre of Rio Negro. Many thanks to Carlos A. Lucena, Margatere Lucena, Edson Pereira, Fernando Jerep, Viviane Santana, Mariangeles Arce, Bárbara Calegari, Hector Alcaraz, and Christian Cramer for logistical and other support at Laboratório de Ictiologia of MCT/PUCRS. We thank Elisa A. Bonaccorso (QCAZ), J. V. Remsen Jr, Santiago Claramunt, Steven W. Cardiff (LSUMZ), Mark B. Robbins (KUNHM), Paul Sweet (AMNH), Alexandre Aleixo (MPEG), Luís Fábio Silveira (MZUSP), Mario Cohn-Haft (INPA), and Rômulo Ribon (MZUFV) for the loan of specimens, and Herculano Alvarenga (MHNT), Miguel Lentino, Margarita Martínez, Yemayá Padrón, and Josmar Márquez (COP) for allowing examination of specimens under their care. We thank Bret Whitney

and Vítor de Q. Piacentini for transporting specimens from USA to Brazil loaned by LSUMZ, KUNHM, and AMNH. We thank Andrés M. Cuervo for providing specimens of some Andean taxa and Thomas S. Schulenberg and Niels Krabbe for information regarding specimen identification. We are grateful to Luiz Antônio Pedreira Gonzaga for commenting on and discussing several morphological characters used in the present study. G.N.M. is grateful to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the doctoral fellowship (process number 141149/2006-0) which supported most of this work.

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APPENDIX 1

MATERIAL EXAMINED

For each specimen examined for this study we provide institution acronym/catalogue number, sex (when known, within brackets: [m], male; [f], female), state or province (in some cases department) and country of origin, and the type of material (skeleton, syrinx) available for each specimen. An asterisk (*) identifies nearly complete skeletons for which most leg and wing bones from one side of the bird were left in the skin for 'shmoo'-type preparation. Unless stated otherwise, a partial skeleton is a specimen without skull, wing and leg bones from both sides (all left with the corresponding traditional study skin). Alcohol-preserved specimens are those which were deeply

dissected for inspection of osteological characters without preparation of the skeleton; these were received on loan as entire wet specimens. Syrinx material may be cleared and double stained (C & S) or only double stained (S).

Institutions of provenance of the material examined and acronyms of the respective collection are as follows: Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul (MCP), Porto Alegre, Brazil; Universidade Federal do Rio Grande, Coleção de Aves da FURG (CAFURG), Rio Grande, Brazil; Museu Paraense Emílio Goeldi (MPEG), Belém, Brazil; Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil; Museu de História Natural de Taubaté (MHNT), Taubaté, Brazil; Museu de Zoologia João Moojen, Universidade Federal de Viçosa (MZUFV), Viçosa, Brazil; Museo de Zoología 'QCAZ', Pontifícia Universidad Católica del Ecuador (QCAZ), Quito, Ecuador; Colección Ornitológica Phelps (COP), Caracas, Venezuela; Louisiana State University, Museum of Natural Science (LSUMZ), Baton Rouge, USA; University of Kansas, Museum of Natural History (KUNHM), Kansas City, USA; and American Museum of Natural History (AMNH), New York, USA. All specimens were examined under ideal conditions at the Museu de Ciências e Tecnologia of the Pontifícia Universidade Católica do Rio Grande do Sul, except those deposited at MHNT and COP, which were examined during visits to these institutions.

INGROUP (RHINOCRYPTIDAE)

Pteroptochos tarnii: MCP 2397 [f], Rio Negro, Argentina (complete skeleton*; syrinx C & S); AMNH 11693 [m], Bio Bio, Chile (syrinx S); KUNHM 83525 [m], Llanquihue, Chile (complete skeleton).

Pteroptochos castaneus: AMNH 11694 [m], Bio Bio, Chile (syrinx C & S).

Scelorchilus rubecula: MCP 2400 [m], Rio Negro, Argentina (complete skeleton*; syrinx C & S); KUNHM 83511 [m], Llanquihue, Chile (complete skeleton); AMNH 11692, Rio Negro, Argentina (syrinx S).

Rhinocrypta lanceolata: MCP 2395 [m], Rio Negro, Argentina (complete skeleton*; syrinx C & S); KUNHM 78016 [m], Buenos Aires, Argentina (complete skeleton); KUNHM 92996 [m], Presidente Hayes, Paraguay (syrinx S).

Teledromas fuscus: MCP 2396 [m], Rio Negro, Argentina (complete skeleton*; syrinx C & S).

Liosceles thoracicus: LSUMZ 111370 [m], Loreto, Peru (complete skeleton); MPEG O-3953, Amazonas, Brazil (complete skeleton; syrinx S); MPEG uncatalogued (field number JAP 598), Acre?, Brazil (partial skeleton; syrinx C & S); MPEG uncatalogued (field

number JAP 456), Acre?, Brazil (partial skeleton; syrinx C & S); MZUSP uncatalogued (field number 215), Rondônia, Brazil (complete skeleton; syrinx C & S); MZUSP uncatalogued (field number 790), Rondônia, Brazil (partial skeleton, skull without rostrum; syrinx C & S); MZUSP uncatalogued (field number 225), Rondônia, Brazil (partial skeleton, skull without rostrum; syrinx S); INPA 879, Amazonas, Brazil (partial skeleton; syrinx S); MHNT 4493, Rondônia, Brazil (partial skeleton).

Psilorhamphus guttatus: MCP 2699, Paraná, Brazil (complete skeleton; syrinx S); MCP 2045 [m], Paraná, Brazil (partial skeleton; syrinx C & S); MCP uncatalogued, Paraná, Brazil (partial skeleton; syrinx S); MCP 1720 [m], São Paulo, Brazil (partial skeleton; syrinx S); MHNT 4812 [m], São Paulo, Brazil (complete skeleton).

Merulaxis ater: MCP 2001 [m], São Paulo, Brazil (partial skeleton with complete skull; syrinx C & S); MCP 2002 [m], São Paulo, Brazil (partial skeleton; syrinx C & S); MCP 1864, São Paulo, Brazil (partial skeleton; syrinx S); MCP 2209, São Paulo, Brazil (complete skeleton*; syrinx C & S); MCP uncatalogued, São Paulo, Brazil (complete skeleton*; syrinx S); MCP 1740 [m], Paraná, Brazil (partial skeleton; syrinx S); MHNT 160 [m], São Paulo, Brazil (complete skeleton); MHNT 652 [f], São Paulo, Brazil (complete skeleton); MHNT 1409 [f], São Paulo, Brazil (partial skeleton).

Merulaxis stresemanni: MZUFV 1408 [m], Minas Gerais/Bahia, Brazil (partial skeleton; syrinx S).

Eugralla paradoxa: MCP 2398 [m], Rio Negro, Argentina (complete skeleton*; syrinx C & S); MCP 2401 [f], Rio Negro, Argentina (partial skeleton; syrinx S).

Myornis senilis: LSUMZ 84015 [m], Amazonas, Peru (complete skeleton); QCAZ 3724, Pichincha, Ecuador (complete skeleton*; syrinx C & S).

Eleoscytalopus indigoticus: MCP 1728 [m], Bahia, Brazil (partial skeleton; syrinx S); MCP 1730 [m], Bahia, Brazil (partial skeleton; syrinx S); MCP 1859, Minas Gerais, Brazil (partial skeleton; syrinx S); MCP 1860, Minas Gerais, Brazil (partial skeleton; syrinx C & S); MCP 1861, Minas Gerais, Brazil (partial skeleton; syrinx S); MCP 1862, Minas Gerais, Brazil (partial skeleton; syrinx C & S); MCP 1863, Minas Gerais, Brazil (partial skeleton; syrinx S); MCP 2331, Minas Gerais, Brazil (partial skeleton; syrinx C & S); MCP 2332, Minas Gerais, Brazil (partial skeleton; syrinx C & S); MCP 1721, Rio de Janeiro, Brazil (partial skeleton; syrinx S); MCP 2044, São Paulo, Brazil (partial skeleton; syrinx C & S); MCP 1731, Paraná, Brazil (partial skeleton; syrinx C & S); MCP 2198, Paraná, Brazil (syrinx S); MCP 2199, Paraná, Brazil (syrinx C & S); MCP 2201, Paraná, Brazil (partial skeleton with complete

skull; syrinx S); MCP 2202, Paraná, Brazil (syrinx S); MCP 2468, Paraná, Brazil (complete skeleton; syrinx C & S); MCP 2200, Paraná, Brazil (complete skeleton; syrinx S); MCP 2469, Santa Catarina, Brazil (syrinx S); MCP 2575, Paraná, Brazil (syrinx S); MCP 2573, Paraná, Brazil (syrinx S); MCP 2572, Paraná, Brazil (syrinx S); MCP 2574, Paraná, Brazil (syrinx S).

Eleoscytalopus psychopompus: MCP 1722 [m], Bahia, Brazil (partial skeleton; syrinx S); MCP 1734 [m], Bahia, Brazil (partial skeleton; syrinx S).

Scytalopus magellanicus: MCP 2399 [m], Rio Negro, Argentina (complete skeleton*; syrinx C & S); KUNHM 83575 [m], Llanquihue, Chile (complete skeleton).

Scytalopus macropus: LSUMZ 120723, Huánuco, Peru (alcoholic specimen; syrinx C & S).

Scytalopus femoralis: LSUMZ 107640, Pasco, Peru (alcoholic specimen; syrinx C & S).

Scytalopus sp.: LSUMZ 89465, Amazonas, Peru (alcoholic specimen; syrinx C & S).

Scytalopus spillmanni: QCAZ 3536, Imbabura, Ecuador (complete skeleton*; syrinx C & S).

Scytalopus latrans: QCAZ 3535, Napo, Ecuador (complete skeleton*; syrinx C & S).

Scytalopus meridanus: COP uncatalogued (field number JEM 203), Venezuela (complete skeleton*); COP uncatalogued (field number JM 205), Venezuela (partial skeleton, skull without rostrum; syrinx S).

Scytalopus iraiensis: MCP 958 [m], Rio Grande do Sul, Brazil (partial skeleton; syrinx S); MCP 2224, Paraná, Brazil (partial skeleton with complete skull); MCP 2046 [m], Minas Gerais, Brazil (partial skeleton; syrinx S).

Scytalopus speluncae: MCP 2433, Santa Catarina, Brazil (partial skeleton; syrinx S); MCP 2430, Santa Catarina, Brazil (partial skeleton; syrinx S); MCP 2429, Santa Catarina, Brazil (partial skeleton; syrinx C & S); MCP 1169 [m], Rio Grande do Sul, Brazil (partial skeleton; syrinx S); MCP 987 [f], Rio Grande do Sul, Brazil (partial skeleton; syrinx S); MCP 1176, Rio Grande do Sul, Brazil (partial skeleton; syrinx S); MCP 1175 [m], Rio Grande do Sul, Brazil (partial skeleton; syrinx S); MCP 2225, Paraná, Brazil (partial skeleton with complete skull; syrinx S).

Scytalopus pachecoi: MCP 962 [m], Rio Grande do Sul, Brazil (partial skeleton; syrinx S); MCP 949, Rio Grande do Sul, Brazil (partial skeleton; syrinx S); MCP 959 [m], Rio Grande do Sul, Brazil (partial skeleton; syrinx S); MCP 977 [m], Rio Grande do Sul, Brazil (partial skeleton; syrinx S); MCP 976 [m], Rio Grande do Sul, Brazil (partial skeleton; syrinx C & S); MCP 1075 [m], Rio Grande do Sul, Brazil (partial skeleton; syrinx C & S); MCP 1040 [m], Rio Grande do Sul, Brazil (partial skeleton; syrinx C & S); MCP 1174, Rio Grande do Sul, Brazil (partial skeleton;

syrinx S); MCP 1188 [m], Santa Catarina, Brazil (complete skeleton*; syrinx C & S).

Acropternis orthonyx: QCAZ 3723 [m], Pichincha, Ecuador (complete skeleton*; syrinx C & S); COP uncatalogued [f] (field number AMC 1246), Táchira, Venezuela (complete skeleton*; syrinx S).

Additionally, several detailed, high-resolution photographs of the following skeletal specimens were examined: *Pteroptochos castaneus*: AMNH 24361 [m] (from the same individual as the syrinx AMNH 11694; see above), several detailed pictures of all parts of the skeleton, with complementary data (e.g. finer details of some bones) provided by Santiago Claramunt. *Pteroptochos tarnii*: AMNH 24348 [m] (from the same individual as the syrinx AMNH 11693; see above), several pictures of all parts of the skeleton, with complementary data (e.g. finer details of some bones) provided by Santiago Claramunt; KUNHM 78802, Chubut, Argentina, detailed pictures of the skull, legs, and the pelvis. *Scelorchilus rubecula*: AMNH 23962 (from the same individual as the syrinx AMNH 11692; see above), several pictures of all parts of the skeleton, with complementary data (e.g. finer details of some bones) provided by Santiago Claramunt; KUNHM 83498 [m], Llanquihue, Chile, detailed pictures of the skull, legs and the pelvis; KUNHM 83499 [m], Llanquihue, Chile, detailed pictures of the skull, legs and the pelvis. *Acropternis orthonyx*: LSUMZ 88163 [m], Amazonas, Peru, two pictures of the scapular and pelvic girdles. *Myornis senilis*: LSUMZ 88108 [f], Amazonas, Peru, two pictures of the scapular and pelvic girdles. *Eugralla paradoxa*: AMNH 24358, Región IX, Chile, several pictures of the scapular and pelvic girdles; KUNHM 83474 [m], Llanquihue, Chile, detailed pictures of the skull, legs and the pelvis.

OUTGROUP

Thamnophilidae

Mackenziaena severa: MCP 2553 [m], Paraná, Brazil (complete skeleton; syrinx S); MCP 2505 [m], Paraná, Brazil (complete skeleton; syrinx C & S).

Myrmotherula unicolor: MCP 2506 [f], Paraná, Brazil (complete skeleton; syrinx C & S); MCP uncatalogued [m], Paraná, Brazil (partial skeleton; syrinx S).

Sclateria naevia: MCP 2508, Rondônia, Brazil (complete skeleton; syrinx C & S).

Conopophagidae

Conopophaga lineata: MCP 2490, Paraná, Brazil (complete skeleton; syrinx C & S); MCP 2633, Rio Grande do Sul, Brazil (complete skeleton; syrinx S); MCP 1521, Rio Grande do Sul, Brazil (partial skeleton; syrinx S); MCP uncatalogued, Rio Grande do

Sul, Brazil (partial skeleton; syrinx S); MHNT 1077, São Paulo, Brazil (complete skeleton); MHNT 1117, São Paulo, Brazil (complete skeleton).

Grallariidae

Grallaria varia: MCP 2210 [m], São Paulo, Brazil (complete skeleton*; syrinx C & S); MHNT 772, São Paulo, Brazil (complete skeleton); MHNT 1079, São Paulo, Brazil (complete skeleton).

Hylopezus macularius: MPEG A-6921, Maranhão, Brazil (complete skeleton; syrinx C & S); MPEG A-7243, Pará, Brazil (complete skeleton; syrinx S).

Hylopezus ochroleucus: MCP 2036, Minas Gerais, Brazil (complete skeleton; syrinx S); MCP 2567, Bahia, Brazil (partial skeleton; syrinx C & S).

Melanopareiidae

Melanopareia torquata: MCP 2271, Minas Gerais, Brazil (complete skeleton; syrinx S); MCP 2329, Minas Gerais, Brazil (partial skeleton, skull without rostrum; syrinx C & S); MCP 2588, Bahia, Brazil (partial skeleton; syrinx C & S); MCP 2330, Minas Gerais, Brazil (partial skeleton, skull without rostrum; syrinx C & S); MPEG uncatalogued (field number MAR 337), Amazonas, Brazil (complete skeleton, skull mostly destroyed by shot; syrinx S).

Formicariidae

Formicarius colma: MCP 2478, Rondônia, Brazil (partial skeleton; syrinx C & S); MPEG A-7115, Rondônia, Brazil (complete skeleton; syrinx S); MCP 2467, Paraná, Brazil (complete skeleton; syrinx S).

Scleruridae

Geositta cunicularia: MCP 2632, Rio Grande do Sul, Brazil (complete skeleton*; syrinx C & S); MCP 1873, Rio Grande do Sul, Brazil (partial skeleton; syrinx S).

Dendrocolaptidae

Sittasomus griseicapillus: MCP 1949, Rio Grande do Sul, Brazil (complete skeleton; syrinx C & S); MCP 2646, Santa Catarina, Brazil (complete skeleton).

Dendrocolaptes platyrostris: MCP 2602, Santa Catarina, Brazil (complete skeleton*; syrinx S); MCP 2601, Santa Catarina, Brazil (partial skeleton; syrinx C & S).

Furnariidae

Furnarius rufus: MCP 1629, Rio Grande do Sul, Brazil (complete skeleton*); MCP 2634, Rio Grande do Sul, Brazil (syrinx S); MCP 1058, Rio Grande do Sul, Brazil (syrinx C & S); MCP 708, Rio Grande do Sul, Brazil (complete skeleton*); MCP 1803, Rio Grande do Sul, Brazil (complete skeleton*); MCP

1054, Rio Grande do Sul, Brazil (syrinx S); CAFURG 430, Rio Grande do Sul, Brazil (complete skeleton).

Phacellodomus striaticollis: MCP 2639, Rio Grande do Sul, Brazil (complete skeleton*; syrinx C & S); CAFURG 432, Rio Grande do Sul, Brazil (partial skeleton).

Cranioleuca sulphurifera: MCP 775, Rio Grande do Sul, Brazil (complete skeleton*; syrinx C & S); MCP 1874, Rio Grande do Sul, Brazil (complete skeleton).

Syndactyla rufosuperciliata: MCP 596 [f], Rio Grande do Sul, Brazil (complete skeleton*; syrinx C &

S); MCP 1385, Rio Grande do Sul, Brazil (complete skeleton*; syrinx S); CAFURG 431, Rio Grande do Sul, Brazil (complete skeleton*).

Tyrannidae

Pitangus sulphuratus: MCP 2288 [m], Rio Grande do Sul, Brazil (complete skeleton); MCP 1677, Rio Grande do Sul, Brazil (complete skeleton*); MCP 1073, Rio Grande do Sul, Brazil (syrinx C & S); MCP 2636, Rio Grande do Sul, Brazil (syrinx S); MCP 614, Rio Grande do Sul, Brazil (syrinx S); CAFURG 433, Rio Grande do Sul, Brazil (complete skeleton).

