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On the use of intergumentary characters in bird phylogeny: the case of *Tinamus osgoodi* (Palaeognathae: Tinamidae) and plumage character coding

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➤ **Resumen** — Los caracteres tegumentarios raramente han sido incluidos en Ornitología Sistemática, a pesar de que la mayoría de los caracteres utilizados para diferenciar especies son de plumaje, ranfoteca (cubierta córnea del pico y narinas) y podoteca (escamas de las patas), y de que muchos de estos caracteres contribuyen a las diagnosis tradicionales de los grandes grupos de Órdenes. Varios estudios recientes han utilizado caracteres tegumentarios en un contexto cladístico, en particular, una filogenia comprensiva de perdices que incluyó a los 9 géneros, todas las 47 especies actualmente reconocidas, y algunas de las subpecies claramente definidas. En este trabajo re-evaluamos la posición en dicha filogenia de la especie oscura *Tinamus osgoodi*. En análisis previos, esta perdiz selvática había sido recuperada junto a las especies de *Crypturellus,* que también tienen plumaje de colores oscuros. Todas estas especies son posiblemente melánicas, o presentan un patrón de coloración de plumaje que afecta a muchos pterylae a la vez. Discutimos la dependencia de algunos caracteres del plumaje de perdices, y re-analizamos la matriz de datos tegumentaria recodificando dichos caracteres en las especies oscuras. Utilizando pesos implicados para la reconstrucción filogenética, recuperamos la mayoría de los agrupamientos esperados, incluyendo a *Tinamus osgoodi* como un miembro de su género. Es interesante destacar que la posición de dicha especie no influyó en las especies oscuras de *Crypturellus*, las cuales podrían haber sido afectadas por el mismo esquema de codificación, y sin embargo, se agruparon junto a sus congéneres, indicando que la interacción con otros caracteres jugó un papel crucial en la recuperación de estos taxa en sus respectivos géneros. Finalmente, comentamos sobre el uso de caracteres tegumentarios y la incidencia de su codificación en Ornitología Sistemática.

Palabras clave: Tinamidae, caracteres tegumentarios, melanismo, sistemática.

➤ **Abstract** — Integumentary characters have rarely been included in Systematic Ornithology in spite of the fact that most characters used to differentiate species are of plumage, ramphoteca (corneous sheath of the bill and nares) and podoteca (horny scales of the legs), and many such characters contribute to higher-order groupings of traditional diagnosis. Several recent studies have used integumentary characters in a cladistic context, particularly a comprehensive phylogeny of tinamous that included the 9 genera, all 47 currently recognized species, and some distinct subspecies. Here we re-evaluate the position in that phylogeny of the uniformly dark species *Tinamus osgoodi*. This forest tinamou was recovered in the previous analysis as closely related to species of *Crypturellus* that also exhibited dark plumage coloration. All these species are possibly melanic, or alternatively, exhibit a plumage coloration pattern affecting many pterylae at once. We discuss the non-independence of some plumage characters of tinamous, and re-analize the integumentary data set by re-coding these characters for the dark species. Using implied-weights for

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phylogeny reconstruction, we recover most of the expected groupings, including *Tinamus osgoodi* as one member of its genus. Interestingly this position did not influence the dark *Crypturellus* species, which could have been affected by the same coding scheme but instead grouped together with their congeners, indicating that interaction with other characters played a crucial role in the recovery of these taxa in their respective genera. Finally, we comment on the usefulness of integumentary characters and the incidence of their coding in Systematic Ornithology.

Keywords: Tinamidae; integumentary characters; melanism; systematics.

INTRODUCTION

The Order Tinamiformes includes only one family, Tinamidae, a group of Neotropical endemic birds with limited flight capabilities. The tinamous belong in the Palaeognathae, which are area sister to all extant birds (Neoaves), also including the ratites ostrich, rheas, kiwis, cassowaries, emu, and a number of large, extinct flightless birds such as the moas from New Zealand and the elephant birds from Madagascar (Cracraft, 1974; Cooper *et al.*, 1992; Lee *et al.*, 1997; van Tuinen *et al.*, 1998; Paton *et al.*, 2002; Livezey and Zusi, 2007; Hackett *et al.*, 2008; Harshman *et al.*, 2008; Bourdon *et al.*, 2009). The specific position of the clade within Palaeognathae is currently debated. The morphological evidence places the tinamous as sister to a monophyletic Ratites (e.g., Cracraft, 1974; Lee *et al.*, 1997; Livezey and Zusi, 2007; Bourdon *et al.*, 2009). By contrast, the molecular evidence places the tinamous nested within ratites as sister to a clade of the Australian and New Zealand taxa (kiwis, cassowaries and emu; e.g., Hackett *et al.*, 2008; Harshman *et al.*, 2008). In spite of this higher-level controversy, the monophyly of tinamous has never been questioned.

The Tinamidae includes 9 genera and 47 currently recognized species (Cabot, 1992). A recent phylogeny of the family includes all species, together with distinctive subspecies of *Eudromia* and *Rhynchotus* and three outgroup taxa in the ratites (i.e., 53 terminals (Bertelli *et al.*, 2002). This analysis was based primarily on integumentary characters, specifically characters of the adult and natal plumage (pterylae and neossoptilus, respectively), ramphoteca (corneous sheath of the bill and nares) and podoteca (horny scales of legs). This paper introduces a novel coding of plumage characters based on elements of the pigmented pattern of individual feathers. Bertelli *et al.* (2002) proposed a transformation scheme in which a sample feather of a given pterilium (a defined tract of feathers in the body) could be either barred, immaculate, or streaked. This basic scheme was further expanded to account for additional variation observed in the complex plumage of tinamous (Fig. 1), so new states were added as necessary, and the states were ordered such that a Sankoff matrix of character transformation was defined. Other features that fit in this scheme were coded separately, particularly the presence of ocelli (see Fig. 1G and Bertelli *et al.*, 2002). In addition, other integumentary characters were coded to cover most of the external features seen in the group, including iris color, and absence or presence of digit I (Bertelli *et al.*, 2002).

The analysis of Bertelli *et al.* (2002) was generally well resolved and successfully recovered tinamou genera as monophyletic with two exceptions, *Nothura* and *Tinamus*. The former case involved a small group of *Nothura* being paraphyletic with respect to another group. Similarly, *Tinamus guttatus* was paraphyletic with respect to a clade formed by *T. major*, *T. solitarius*, and *T. tao*. More remarkable, *T. osgoodi* appeared deeply nested within an otherwise monophyletic *Crypturellus*. This unexpected placement led Remsen *et al.* (2012) to consider the suggestion that *T. osgoodi* may in fact belong in *Crypturellus* on the basis of phenotypic characters. Bertelli and Porzecanski (2004) presented a preliminary analysis including integumentary as well as osteological evidence in combination with cytochrome *b* sequences and found support for a monophyletic *Tinamus*. Thus, the placement of *Tinamus* may be the result of the particularities of using integumentary data.

In this work, we revise our coding of the latter species. *Tinamus osgoodi* is uniformly dark and thus it may well be the case that a melanistic process is affecting many pterylae at once, blurring the independence of char-

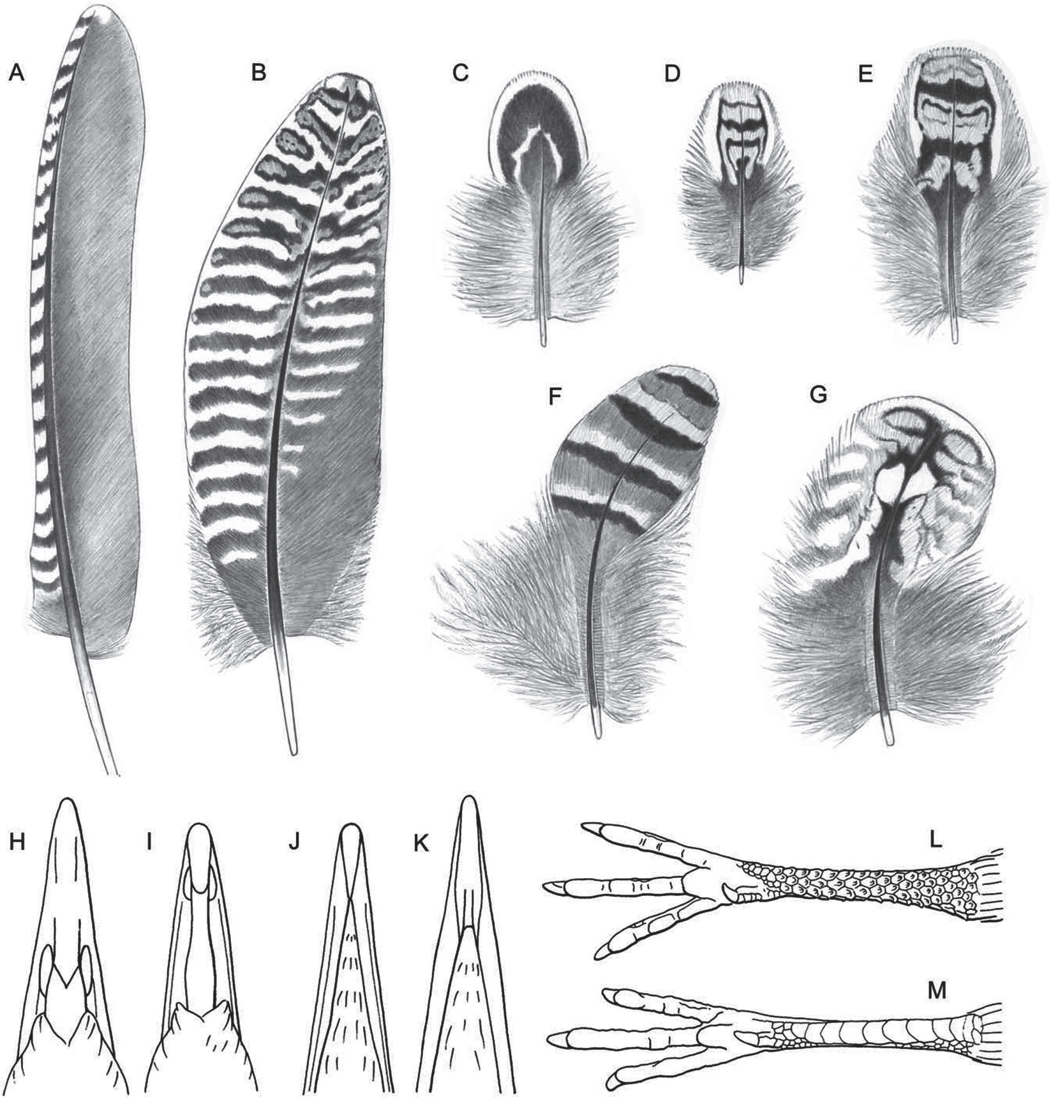

Fig. 1. Selected features of the wing (A-B) and contour (C-G) feathers, bill (H-K), and legs (L, M), modified from Bertelli *et al*. (2002). *Nothoprocta ornata* showing a bicolored barred and immaculate primary remige (A), and a secondary remige with both webs bicolored barred (B); scalloped feather in *Crypturellus tataupa* (C); *Nothura*-like patterns in *Nothura maculosa* (D) and *Nothoprocta cinerascens* (E); tricolored bars in *Rhynchotus rufescens* (F); and v-shaped ocelli of *Eudromia formosa* (G). Dorsal and ventral views of the bill of *Nothoprocta cinerascens* (H, J) and *Tinamus solitarius* (I, K) showing position of nares and ventral plates. Ventral view of the legs of *Nothoprocta ornata* (L) and *Tinamotis pentlandii* (M) showing transverse and reticulate scutes respectively.

acters that was observed in other species of tinamous and which justified the coding of separate plumage characters (Betelli *et al.*, 2002). Melanism in birds could be linked to a single aminoacid substitution since difference in plumage color used in species recognition between incipient species is linked to a single amino acid substitution in the melanocortin-1 receptor (Uy et. al., 2009), and thus, a very simple mutation could affect many of the studied characters.This may also be the case of two dark species of *Crypturellus*, the closely related *C. berlepschi* and *C. cinereus*, which were recovered as sister taxa and may have driven the placement of *T. osgoodi* within *Crypturellus*. Here we report on the rescoring of the plumage characters of the possibly melanic *T. osgoodi*, *C. berlepschi* and *C. cinereus*, thereby testing whether the unexpected position of the former was due to the way of coding of integumentary characters in our previous study. In addition, we comment on the usefulness of integumentary characters for phylogeny reconstruction in bird clades.

MATERIALS AND METHODS

Taxa and Characters

Our source of data was the matrix reported by Bertelli *et al.* (2002). Outgroup taxa were selected among ratites, specifically the kiwi *Apteryx australis* and the rheas *Pterocnemia pennata* and *Rhea americana*. Ingroup taxa included 47 tinamou species as well as two distinctive subspecies of *Eudromia* (*E. elegans elegans* and *E. e. albida*) and *Rhynchotus* (*R. rufescens maculicollis, R.r. rufescens* and *R. r. pallescens*). In addition, two specimens once thought to belong to an undescribed species were originally included in Bertelli *et al.* (2002) but not in this study given the uncertainty about the taxonomic validity of this form. Specimens examined are listed in Appendix 1.

This matrix contained 80 external characters including 8 characters of the ramphoteca, 1 of iris, 1 of digitus pedis I, 1 of feather structure (pennae), 50 of adult plumage (pterylae), 11 of natal plumage (neossoptilus), and 8 of podoteca. Due to the substantially different feathers of ratites, which lack the pennaceous structure typical of birds including tinamous, Bertelli *et al.* (2002) scored the outgroup taxa as non-comparable for the adult-plumage characters. Description of characters is provided in Appendix 2.

For this study, we rescored *Tinamus osgoodi*, *Crypturellus berlepschi*, and *C. cinereus* for 47 adult-plumage characters that scored the pattern of feather design in different pterylae. These species are suspected of melanism affecting many regions of the body at once, violating the presumed independence of characters; furthermore, the melanism could also affect the characters itself, as they could be «covered» by melanic pigment, and thus we coded these tinamous as missing (?) for characters 12-18, 20, 22, 25, 28, 38-48, 51-58, and 59. Data matrix is provided in Appendix 3.

Cladistic analysis

Bertelli *et al.* (2002) used a complex coding based on Sankoff transformation costs among different states of feather design. Bertelli *et al.* (2002) showed that the patterns of relationships recovered did not strongly depend on the cost matrix but rather on the data structure per se. Thus, for simplicity here we run the modified data matrix with all characters as unordered, so that any substantial change in the tree topology with respect to the previous phylogeny by Bertelli *et al.* (2002) would be immediately evident regardless of the complexity of the transformation scheme.

We run heuristic searches under equal and implied weights (default constant of concavity = 3; see Goloboff, 1993). Implied weight is a proven technique for effectively dealing with homoplasy in morphological characters. Goloboff *et al.* (2008) reported a net increase in nodal support when applying implied weights, and others have shown greater congruence across datasets when the morphological partition is analyzed under implied weights (e.g., Giannini and Simmons, 2005). All the analyses included 200 RAS + TBR (random addition sequence of terminals followed by tree bisection reconnection branch swapping) keeping up to 10 trees per replication. We calculated branch stability with a jackknife technique, symmetric resampling (Goloboff *et al.*, 2003) with 1000 replications in each analysis. All analyses were run in TNT (Goloboff *et al.*, 2008).

RESULTS

The analysis under equal weights resulted in 79 optimal trees at 386 steps; a TBR round on those trees found a final set of 84 optimal trees. The consensus tree contained only 21

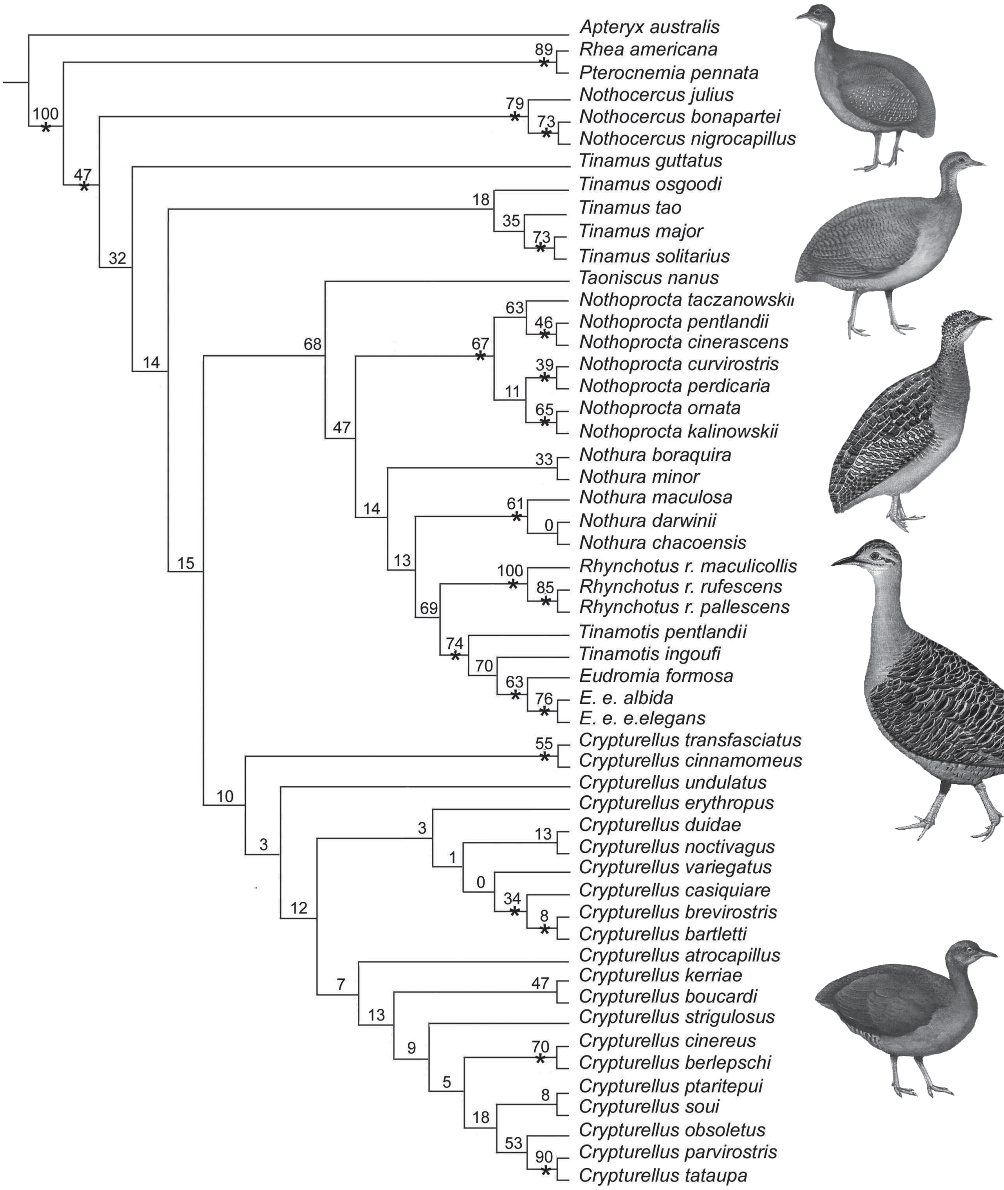

Fig. 2. Single optimal tree of 27.721 weighted steps obtained under implied weights with default concavity (= 3). Numbers above branches are stability values obtained by symmetric resampling (see text). Stars on branches indicate the groups recovered in a cladistic analysis under equal weights.

out of the 52 possible nodes of a fully resolved tree (marked in Fig. 2). By contrast, the analysis under implied weights recovered a single tree (27.721 weighted steps; Fig. 2). In this tree, Tinamidae is monophyletic and *Nothocercus* is sister to all other tinamous, with *N. julius* sister to the other two species. Next, *Tinamus* is paraphyletic, *Tinamus guttatus* is a sister taxa to all other tinamous and the remainder *Tinamus* species form a clade of successive sister species *T. osgoodi*, *T. tao*, *T. major* and *T. solitarius*. The next clade is a monophyletic *Crypturellus* sister to the Nothurinae. Within *Crypturellus*, *C. transfasciatus* + *C. cinnamomeus* and *C. undulatus* are successive sisters of two clades composed of 7 and 11 species, respectively, of which the latter includes *C. berlepschi* and *C. cinereus* forming a well supported clade sister of the grayish colored, relatively un-patterned *Crypturellus* (e.g., *C. tataupa*, *C. soui*).

The open areas tinamous, the Nothurinae, are recovered as monophyletic with good support. *Taoniscus nanus* is sister to all other nothurines. Next, a monophyletic *Nothoprocta*, and a paraphyletic *Nothura* (due to the placement of *N. boraquira* and *N. minor* in a separate clade) are successive sisters to *Rhynchotus* and a clade formed by a paraphyletic *Tinamotis* and a monophyletic *Eudromia*.

Level of branch stability varied greatly along the tree, with several clades below 50 % replicates present, and several clades with stability e» 70 %, even 100 % (e.g., *Rhynchotus*). Most of the groups with low stability in the implied-weights tree (e.g., < 50 %) are those not recovered in the consensus tree of the equal-weights analysis (Fig. 2), although all these groups appeared in trees from the optimal set. Some differences between the analyses are worth noting, specifically that the equal-weights analysis recovered *Tinamotis* as monophyletic (a group contradicted in the implied-weights analysis by the clade formed by Patagonian *Tinamotis ingoufi* and *Eudromia*).

DISCUSSION

This study aimed at evaluating the role of integumentary character coding in regard to the unexpected position of one species of tinamou, *Tinamus osgoodi*, recovered in a previous analysis as closely related to species of *Crypturellus* that also exhibited dark plumage coloration. In our fully-resolved phylogenetic result, the rescoring of adult-plumage characters placed *Tinamus osgoodi* in a clade together with other *Tinamus* species (*T. major*, *T. tao* and *T. solitarius*). The position of *T. guttatus* did not differ from that recovered by Bertelli *et al.* (2002). By contrast, *T. osgoodi* was recovered in a clade with other species of *Tinamus* in spite of the loss of information due to the number of non-comparable character states in the recoded matrix. Moreover, the other two dark species of tinamous, *Crypturellus berlepschi* and *C. cinereus*, that were also re-coded as non-comparable for most adult-plumage characters, were recovered within *Crypturellus* in a position not different from that reported in Bertelli *et al.* (2002). That is, certain plumage scorings affected the perceived phylogenetic relationships of *Tinamus osgoodi*, but not those of the two dark *Crypturellus* species. Evidently, other synapomorphies defined the placement of these taxa with somewhat controversial scoring, and this was revealed when the conflicting scorings were removed. This supports the hypothesis advanced here that the dark coloration of *Tinamus osgoodi* may represent a form of melanistic pattern in which many pterylae are affected at once. This also suggests that the data structure is different for the dark *Crypturellus* whose position was not affected in spite of receiving the same character treatment as *T. osgoodi*. The reason for this may lie in the phylogenetic pattern of the other characters, so the dark *Crypturellus* share the more derived states typical of the genus and hence their position with respect to the comparably dark but more basal *Tinamus osgoodi*. This result is more congruent with the preliminary results of Bertelli and Porzekanski (2004), in which the authors used integumentary data, osteology and DNA sequences recovering a monophyletic *Tinamus*. Note that this analysis used the matrix published by Bertelli *et al.* (2002). Therefore the non-integumentary evidence overcomes the placement of *Tinamus* within *Crypturellus* based on integumentary evidence alone. Here we show that recoding of integumentary characters results in a phylogeny altogether more congruent with the combined evidence so far presented (cf. Bertelli and Porzecanski, 2004). This highlights the fact that this may not be a problem of the characters themselves, but just an instance in which the scoring scheme did not fit one particular species.

Integumentary characters are not extensively used in Systematic Ornithology, but a number of recent examples show that, just as in the case of tinamous, integumentary characters prove to be as reliable as other types of phenotypic evidence. This becomes evident in cases like tinamous given that, with the proper coding, most of the expected groups (i.e., those erected by the traditional systematics, including genera and tribes) are recovered. Examples include Anatidae (Livezey, 1991; 1995), Rallidae (Livezey, 1998), Laridae (Chu, 1998), Spheniscidae (Giannini and Bertelli, 2004; Bertelli and Giannini, 2005; Bertelli *et al.*, 2006; Ksepka *et al.*, 2006; Clarke *et al.*, 2007), and higher-order relationships in Neornithes (Livezey and Zusi, 2007).

To conclude, the interplay of characters in this and other phylogenies in which integumentary characters were used, points to the need of recognizing these as historically informative, as well as the need to include as many characters, from as many organ systems, as available. Recoding integumentary characters to avoid possible problems of character non-independence by factors such as possible melanism, allowed the recovery of *Tinamus osgoodi* as a typical member of its genus in a position expected also from a traditional systematics standpoint.

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APPENDIX 1

Comparative material examined in the construction of the data set of 47 recognized species and subspecies (modified from Bertelli *et al*., 2002). Abbreviations of Institutions: AMNH, American Museum of Natural History, New York; FML, Fundación Miguel Lillo, Tucumán; LACMNH, Natural Museum of Los Angeles County, Los Angeles; MACN, Museo Argentino de Ciencias Naturales «Bernardino Rivadavia», Buenos Aires.

Apteryx australis australis (AMNH2029 63, 408894); *Rhea americana albescens* (FML648, 5943, 7479, 7480, 7481, 11280, 11354); *Pterocnemia pennata garleppi* (FML700); *Pterocnemia pennata pennata* (FML12019, 576); *Tinamus guttatus* (AMNH270403, 272134, LACMNH37843); *Tinamus major major* (LACMNH42107, 42108); *Tinamus major robustus* (AMNH10 1060, 233290, 468924, 468925, 468926); *Tinamus osgoodi osgoodi* (AMNH763823); *Tinamus solitarius solitarius* (AMNH139901, 272026, 468920, 468921, 468923, FML 514a, 514b, LACMNH28514, 46501, 46502, 46503, 46504, 46505, 46506, MACN3530, 34089, 34090, 34093, 34094, 36566); *Tinamus tao tao* (AMNH277444, 277446, 2881 22, 408891, 429001, LACMNH42103); *No-*

thocercus bonapartei bonapartei (AMNH115 6020, 1156030, 132201, 176517); *Nothocercus julius* (AMNH55329, 111255, 35595, 468947, 468948); *Nothocercus nigrocapillus* (AMNH136764); *Crypturellus atrocapillus atrocapillus* (AMNH819597, 819789); *Crypturellus bartletti* (AMNH230472, 239610, 525515, 824044); *Crypturellus berlepschi* (AMNH230459, 468976, 468977, 468978, 819167); *Crypturellus boucardi boucardi* (AMNH10342, 10346, 11020, 34502, 1061 96, LACMNH24389); *Crypturellus brevirostris* (AMNH203471, 233702, 239611, 469 113); *Crypturellus casiquiare* (AMNH4340 24); *Cryturellus cinnamomeus cinnamomeus* (AMNH55335, 813097, LACMNH77810); *Crypturellus cinereus* (AMNH221110, 2548 26, 281109, 468965, 468967, LACMNH36103, 42104, 42105, 42106); *Crypturellus duidae* (AMNH272157, 273139); *Crypturellus erythropus erythropus* (AMNH120285, 283052, 283053, 469628, 469129); *Crypturellus kerriae* (AMNH123204); *Crypturellus noctivagus noctivagus* (AMNH313713, 3137 14, 317184, 469092, LACMNH59478, 600 00, 60001); *Crypturellus obsoletus obsoletus* (AMNH53331, 313706, 313711, 317185, 313903, FML361a, 361b, 4872, 6224, 6225, 6226, 6227, LACMNH27765, 37848, 46511, 46512, 46513, 46514, 46515, 46516, 46517, 46518, 46519, 46520, 46521, 46522, 46523, 46524, 46525, 46526, 46527, MACN31740, 34080, 34081, 34084, 34451, 36565, 38172); *Crypturellus ptaritepui* (AMNH8 31256); *Crypturellus parvirostris* (FML6222, 7848, LACMNH26743, 27421, 27422, 28390, 31344, 32282, 32286, 42072, 42073, 42074, 42075, 42076, 42077, 42078, 42079, 42080, 44149, 101690, MACN8560, 33241, 38183, 38184, 39188); *Crypturellus soui albigularis* (LACMNH32274, 32275, 34330, 34331, 34332, 34333, 34334, 34335, 37844, 37845, 42081, 42082, 42083, 42084, 42085, 42086, 42087, 42088, 42089, 42090, 42091, 42092, 42093, 60003); *Crypturellus soui caquetae* (LACMNH36102); *Crypturellus soui caucae* (LACMNH36100, 36101); *Crypturellus soui harterti* (LACMNH31097); *Crypturellus soui inconspicuus* (LACMNH110165); *Crypturellus soui modestus* (LACMNH16466, 16467, 16468, 16469); *Crypturellus soui mustelinus* (LACMNH41864, 41865); *Crypturellus soui panamensis* (LACMNH30310); *Crypturellus soui soui* (AMNH129302, FML1739); *Crypturellus strigulosus* (AMNH 238770, 238772, 238773, 285466, 430138, LACMNH26744, 26745, 26746, 34337, 37847, 42102); *Crypturellus tataupa tataupa* (FML48, 360a, 360b, 511, 627, 631, 847, 929, 1139, 1428, 15214, 1707, 1176, 6219, 6229, 6221, 6976, 6978, 7598, 7842, 7843, 7844, 7846, 7847, 9500, 7845, 9598, 9594, 9981, 9982, 9983, 10057, 10632, 10633, 10634, 11027, 11028, 11029, 11030, 11031, 11032, 11381, 12368, 12369, 13729, LACMNH28191, 35337, 35338, 46507, 58482, MACN31217, 33453, 34088, 38174, 38178); *Crypturellus transfasciatus* (AMNH119535, 119538, 154696, 154697, 170771); *Crypturellus undulatus undulatus* (AMNH34880, 127223a, 127223b, 469089, 819154, FML1722, 1723, 1724, 1725, 1726, MACN 2055, 4109, 8979, 37393, 42394); *Crypturellus variegatus* (AMNH125255, 469101, 804359, 804360, 804361, LACMNH42094, 42095, 42096, 42097, 42098, 42099, 42100, 42101, 59479, 60002); *Rhynchotus rufescens catingae* (LACMNH26735, 26736); *Rhynchotus rufescens maculicollis* (FML362a, 362b, 967, 974, 1052, 1053, 6649, 7175, 7840, 9816, 9817, 9818, 10861, 10862, 12192, 15218, MACN2300, 8148, 32836, 42312); *Rhynchotus rufescens pallescens* (FML9986, 14017, LACMNH104785, MACN2177, 2526, 40339, 40340, 40981); *Rhynchotus rufescens rufescens* (FML363a, 363b, 7122, LACMNH 32287, 32288, MACN4579, 39192, 52681); *Nothoprocta cinerascens cinerascens* (FML 357, 1483, 1495, 1873, 5298, 5947, 6452, 7825, 7827, 7829, 8952, 9093, 9094, 9265, 9755, 9735, 9821, 10115, 10226, 10372, 10430, 10431, 10715, 10907, 10908, 10911, 10937, 10947, 10963, 10964, 11104, 11105, 11106, 11266, 12691, 15271, MACN8148, 8428, 409806); *Nothoprocta curvirostris curvirostris* (AMNH166330, 866315, 469156, 469157, 469155); *Nothoprocta kalinowskii* (AMNH169176); *Nothoprocta ornata rostrata*

(FML358a, 358b, 964, 969, 973, 5173, 5243, 5416, 5417, 5655, 6024, 6026, 10872, 12011, 12193, 12194, 12195, MACN8502, 35871, 42306, 42308, 42311); *Nothoprocta pentlandii pentlandii* (FML359a, 359b, 470, 1734, 7831, 7835, 7836, 8043, 8060, 8414, 8450, 9009, 9053, 9055, 9056, 9057, 9062, 9610, 9611, 9822, 10028, 10373, 10429, 10628, 10910, 102536, 12690, 12692, 12693, 13728, 13730, 13735, MACN8148, 9648, 32837, 42310); *Nothoprocta perdicaria perdicaria* (LACMNH25239, 25240); *Nothoprocta perdicaria sanborni* (FML364, 3986, 4024, 4026, 4027, 4028, 4029, 4030, 4037, 4043, 4094, 7826, 7828, 7830, 7832, 7833, 7834, 7837, LACMNH25241, 25242, 25243, 25244, 25245, 25246, MACN2398, 4312, 4453, 4604, 4605, 4608, 4809); *Nothoprocta taczanowskii* (AMNH169552); *Nothura boraquira* (AMNH24001, 240990, 240991, 240995, 241002, FML11497, 11500, 11498, 11499, LACMNH26737, 26738, 26739, 31345); *Nothura darwinii darwinii* (FML7478, 14550, 14551, MACN 8339, 31516, 35038, 412040); *Nothura darwinii salvadorii* (FML365, 1727, 1728, 1729, 1808, 2222, 9059, 9496, 9498, 10029, 10432, 10867, 11022, 11025, 11397, 11398, 11399); *Nothura chacoensis* (MACN42899); *Nothura maculosa annectes* (FML7838, 7839, 8778); *Nothura maculosa maculosa* (FML364, 1687, 2779, 4889, 4988, 4990, 4991, 5120, 7120, 7151, 15235, LACMNH 28466, 28914, MACN601a, 6169, 8314, 51469, 52173, 52366, 53027, 53028, 53270, 53480, 142988); *Nothura maculosa nigroguttata* (FML914); *Nothura maculosa major* (LACMNH32281, 32283, 32284); *Nothura maculosa pallida* (FML1497, 1543, 5295, 7965, 10149, 12211); *Nothura maculosa paludivaga* (FML5515, 5555, 5558, 9984, 9985); *Nothura minor* (AMNH348095, 3480 96, 28913); *Taoniscus nanus* (AMNH237448, 261898, MACN53007); *Eudromia elegans elegans* (FML942, 14459, 14460, 14462, 14469, MACN471, 9631, 35468, 5325, 52463, 52665, 52141, 53256, 53274); *Eudromia elegans intermedia* (FML465a, 465b, 465c, 465d, 465e, 965, 975, 5665, 7841, 8415, 8446, 8448, 11119, 11120, 11121, 11122); *Eudromia elegans magnistriata* (FML7475, 7477, 11780); *Eudromia elegans multiguttata* (FML966); *Eudromia elegans patagonica* (FML583a, 583b, 10995, 12036, 12037, 12041, 13117, 13710, 14458, 14461, 14464, 14465, 14466, 14467, 14468, 14470, 14471, LACMNH54426, 54427); *Eudromia elegans riojana* (FML10245, 10246, 10247, 10248, 10249, 10250, 11287, 11288, 11289, 11290, 11291, 11292, 11294, 11295, 11296, 11337, 11342, 11343, 11344, 11345, 11346); *Eudromia formosa formosa* (FML 970, 972, 11107, 11108, 12849, 13048, MACN2497a, 2497b, 32232, 4664, 4693, 8148, 9451, 40240, 40985, 41056, 52831); *Eudromia formosa mira* (MACN41056); *Tinamotis ingoufi* (FML8027, 12038, 13303, 13711, MACN142, 159, 2736, 2773, 29289, 52250, 52296, 52478, 52748); *Tinamotis pentlandii* (FML698, MACN33922).

APPENDIX 2

For details and comments of the 80 integumentary characters (Anatomia Topographica Externa) used in the present study, see Bertelli *et al.* (2002).

Rostrum (Figs. 1H-K)

0) Bill shape: straight (0); slightly decurved (1); decurved toward tip (2); strongly decurved (3).

1) Rostrum maxillare (upper mandible), dorsal plate, lateral grooves: absent (0); present (1).

2) Rostrum maxillare (upper mandible), length of proximal dorsal plate relative to distal dorsal plate: longer (0); similar (1); shorter (2).

3) Rostrum mandibulare (lower mandible), ventral plate, lateral grooves: posteriorly convergent and contacting each other (0); parallel (1); posteriorly divergent (2).

4) Rostrum mandibulare (lower mandible), ventral plate, lateral grooves: absent (0); present (1).

5) Color of maxilla: blackish (0); horn (1); brownish (2); reddish (3); olive (4); grayish (5).

6) Color of mandible: blackish (0); pale with dark tip (1); pink to reddish (2); brownish (3); olive (4); grayish (5); horn (6); yellowish (7).

Regio Nasalis (Figs. 1H-I)

7) *Naris (nostrils),* position in upper mandible: posterior, contacting pterilio capitalis (0); contacting and medial (1); not contacting, medial (2); not contacting, anterior (3); not contacting, extreme anterior (4).

Regio Orbitalis: Oculus (Organa Sensuum)

8) Color of iris: brownish (0); yellowish (1); reddish (2); whitish (3).

Membrum Pelvicum

Digiti

9) *Digitus pedis* I (hallux or first digit of hind limb): present (0); absent (1).

Pennae

10) Vexillum, Pars pennacea, feather structure: absent (0); present (1).

Pterylae (Figs. 1A-G)

Pteryla capitalis

11) Corona + occiput (crown + nape), occipital feathers: indistinct (0); forming a crest like in Nothoprocta (1); long, recurved, and filamentous like in Eudromia (2).

12) Corona + occiput (crown + nape), feather pattern: streaked (0); immaculate (1); bicolored barred (2); Nothura-like pattern (3).

13) Corona, supercilium (eyebrow + postocular eyeline): absent (0); slightly marked (1); strongly marked and white (2).

14) Regio malaris, moustachial stripe: absent (0); present (1).

15) Regio auricularis (ear patch), auricular stripe: absent (0); present (1).

16) Jugulum (chin), feather pattern: whitish immaculate (0); brownish-rufous immaculate (1); grayish immaculate (2); streaked (3); bicolored barred (4).

Pteryla dorsalis

17) Pars cervicalis (dorsal neck), feather pattern: immaculate (0); bicolored barred (1); Nothura-like pattern (2); streaked (3).

18) Pars interscapularis (dorsal collar), feather pattern: immaculate (0); bicolored barred (1); Nothura-like pattern (2); tricolored barred (3); mixed pattern (4); ingoufi-like pattern (5).

19) Pars interscapularis (dorsal collar), V-shaped ocelli: absent (0); present (1).

20) Pars spinalis + pars pelvica + pteryla scapulohumeralis (dorsum + mantle + rump), feather pattern: immaculate (0); bicolored barred (1); Nothura-like pattern (2); tricolored barred (3); mixed pattern (4); ingoufi-like pattern (5); dimorphic: male immaculate, female bicolored barred (6).

21) Pars spinalis + pars pelvica + pteryla scapulohumeralis (dorsum, mantle, and rump), V-shaped ocelli: absent (0); present (1).

Pteryla ventralis

22) Pars cervicalis (lateral neck), feather pattern: bicolores barred (0); immaculate (1); streaked (2); dimorphic: male immaculate, female bicolored barred (3).

23) Pars cervicalis (lateral neck), dorsal light stripe: absent (0); slightly marked (1); strongly marked (2).

24) Pars cervicalis (lateral neck), ventral light stripe: absent (0); present (1).

25) Pars cervicalis (ventral neck), feather pattern: bicolored barred (0); immaculate (1); streaked (2); dimorphic: male immaculate, female bicolored barred (3).

26) Pars cervicalis (ventral neck, throat), rounded ocelli: absent (0); present (1).

27) Pars cervicalis (lateral and ventral neck, throat), feathers with white rachis: absent (0); present (1).

28) Pars pectoralis (breast), feather pattern: immaculate (0); bicolored barred (1); streaked (2); mixed pattern (3); Nothura-like pattern (4); dimorphic: male immaculate, female bicolored barred (5).

29) Pars pectoralis (ventral collar), ocelli: absent (0); rounded light spots (1); V-shaped light spots (2).

30) Pars sternalis, superior (breast), feather pattern: brownish or rufous immaculate (0); whitish inmaculate (1); bicolored barred (2).

31) Pars sternalis, inferior (abdomen): brownish or rufous immaculate (0); whitish inmaculate (1); bicolored barred (2).

32) Pars abdominalis (belly), feather pattern: brownish immaculate (0); whitish inmaculate (1); rufous immaculate (2); bicolored barred (3); scalloped (4).

33) Pars venti (undertail coverts), feather pattern: immaculate (0); bicolored barred (1); scalloped (2); rufous immaculate (3).

34) Pars sternalis + pars abdominalis + pars venti (chest + belly + undertail coverts), furlike aspect of feathers: absent (0); present in the belly (1); present from the chest to the belly (2).

Pteryla lateralis

35) Pteryla lateralis (flank, upper side), feather pattern: immaculate (0); bicolored barred (1); scalloped (2); Nothura-like pattern (3); tricolored barred (4).

36) Pteryla lateralis (flank, upper side), rounded ocelli: absent (0); present (1).

Pteryla caudalis (tail)

37) Rectrices (tail): rudimentary, indistinct from upper tail coverts (0); poorly developed but distinct from upper tail coverts (1).

Pteryla alae (wing feathers, Figs. 1A-B)

38) Remiges alulae (bastard wing), vexillum pennae externum (outer vane), feather pattern: bicolored barred (0); brownish immaculate (1); rufous immaculate (2).

39) *Remiges alulae* (bastard wing), vexilum pennae internum (inner vane), feather pattern: bicolored barred (0); brownish immaculate (1); rufous immaculate (2).

40) Remiges primarii (primary remiges), vexillae pennae externum (outer vane), feather pattern: bicolored barred (0); brownish immaculate (1); rufous immaculate (2).

41) Remiges primarii (primary remiges), vexillae pennae internum (inner vane), feather pattern: bicolored barred (0); brownish immaculate (1); rufous immaculate (2).

42) Remiges secundarii externa (outer secundary remiges, i.e., the secondaries adjacent to primaries), vexillae pennae externum (outer vane), feather pattern: brownish immaculate (0); rufous immaculate (1); bicolored barred (2).

43) Remiges secundarii externa (outer secundary remiges, i.e., the secondaries adjacent to primaries), vexillae pennae internum (inner vane), feather pattern: brownish immaculate (0); rufous immaculate (1); bicolored barred (2).

44) Remiges secundarii interna (inner secundary remiges, i.e., the secondaries next to the body), vexillae pennae externum (outer vane), feather pattern: brownish immaculate (0); rufous immaculate (1); bicolored barred (2); tricolored barred (3).

45) Remiges secundarii interna (inner secundary remiges, i.e., the secondaries next to the body), vexillae pennae internum (inner vane), feather pattern: immaculate (0); bicolored barred (1); tricolored barred (2).

46) Tectrices primariae dorsales (greater primary coverts), vexillae pennae externum (outer vane), feather pattern: rufous immaculate (0); brownish immaculate (1); bicolored barred (2); *Nothura*-like pattern (3).

47) Tectrices primariae dorsales (greater primary coverts), vexillae pennae externum (inner vane), feather pattern: rufous immaculate (0); brownish immaculate (1); bicolored barred (2); *Nothura*-like pattern (3).

48) Tectrices secundariae dorsales (lesser and median coverts), inner and outer vane, feather pattern: brownish immaculate (0); bicolored barred (1); *Nothura*-like pattern (2); tricolored barred (3); mixed pattern (4); *ingoufi*-like pattern (5); dimorphic: male immaculate, female bicolored barred (6).

49) Tectrices secundariae dorsales (lesser and median coverts), V-shaped ocelli: absent (0); present (1).

50) Tectrices dorsales (greater, median and lesser coverts), rounded ocelli: absent (0); present (1).

51) Tectrices primariae ventrales minores (lesser underprimary coverts), feather pattern: rufous immaculate (0); brownish immaculate (1); whitish immaculate (2); bicolored barred (3).

52) Tectrices primariae ventrales mediae (median underprimary coverts), feather pat-

tern: rufous immaculate (0); brownish immaculate (1); whitish immaculate (2); bicolored barred (3).

53) Tectrices primariae ventrales majores (greater underprimary coverts), feather pattern: rufous immaculate (0); brownish immaculate (1); whitish immaculate (2); bicolored barred (3).

54) Tectrices secundariae ventrales minores (lesser underwing coverts), feather pattern: rufous immaculate (0); brownish immaculate (1); whitish immaculate (2); bicolored barred (3).

55) Tectrices secundariae ventrales mediae (median underwing coverts), feather pattern: rufous immaculate (0); brownish immaculate (1); whitish immaculate (2); bicolored barred (3).

56) Tectrices secundariae ventrales majores (greater underwing coverts), feather pattern: rufous immaculate (0); brownish immaculate (1); whitish immaculate (2); bicolored barred (3).

Pteryla membri pelvici

57) Pars femoralis (flank, lower side), feather pattern: immaculate (0); bicolored barred (1); scalloped (2); tricolored barred (3); *Nothura*-like pattern (4); dimorphic: male immaculate, female bicolored barred (5).

58) Pars femoralis (flank, lower side), rounded ocelli: absent (0); present (1).

59) Pars cruralis (thigh), feather pattern: brownish immaculate (0); bicolored barred (1); scalloped (2); tricolores barred (3); rufous immaculate (4).

60) Pars cruralis (thigh), rounded ocelli: absent (0); present (1).

Podoteca (Fig. 1L-M)

61) Podoteca lateralis, lateral-tarsi scutes, general aspect on medial view: one row (0); two or three rows (1); more than three rows (2); without longitudinal array (3).

62) Podoteca ventralis, plantar-tarsi scutes, number: numerous scutes (0); two or three rows of medium-sized scutes (1); one row of large scutes (2).

63) Podoteca ventralis, plantar-tarsi scutes, surface aspect: relatively smooth (0); relatively roughened (1); distinctly rasplike (2).

64) Podoteca ventralis (plantar-tarsi scutes), scale pattern: transverse scutes (0); reticulate scutes (1).

65) Acrotarsium, dorsal-tarsi scutes, adjacent scutes of proximal end: juxtaposed (0); imbricated (1).

66) Acrotarsium, dorsal-tarsi scutes, distal end: base of the third and fourth toes covered by separated scutes (0); base of the third and fourth toe covered by a single scute (1).

67) Acropodium, scute number on hind toe: one (0); two (1); three (2); four or five (3).

68) Tarsi, color pattern: brownish (0); grayish (1); pinkish to reddish (2); yellowish (3); greenish to olive (4).

Neossoptilus (Natal Plumage)

69) Trunk, dorsal surface, overall pattern: brown or straight (0); lightly barred (1); barred with black (2).

70) Rump, pale patch in lower back: present (0); absent (1).

71) Dorsal feathers, development of rachis and aftershaft: both rudimentary (0); both developed (1).

72) Forehead: pale (0); undifferentiated from the crown (1).

73) Preorbital line: absent (0); present (1).

74) Supraorbital line: absent (0); present (1).

75) Postorbital line: absent (0); present (1).

76) Malar line: absent (0); present (1).

77) Auricular line: absent (0); present (1).

78) Lateral crown: not bordered by lines (0); bordered by simple whitish line (1); bordered by double line, whitish and dark (2).

79) Dorsal crown: line absent (0); single line (1); double line (2).

APPENDIX 3

Data matrix used in the present analysis.

		1	2	3	4	5	6	7
	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789
A. australis	1100123400	0————	——————	——————	——————	——————	-301100[01]0-	——————
P. pennata	0111123101	0————	——————	——————	——————	——————	-301[01]00-0-	——————
R. americana	0111123101	0————	——————	——————	——————	——————	-221010-0-	——————
T. solitarius	1120100300	1021014100	1001000000	0231000111	1120202210	0131111101	010210021?	0001111100
T. major	1120157300	1021010100	1001000000	2231000111	1120202210	0131111101	0102100110	0001111100
T. tao	111010[56]200	1021014110	1001000000	0231010111	1100002210	0011111101	010210021?	??????????
T. *guttatus*	11201??300	1020010100	1000000000	0000000111	1122202210	1011111101	010210014?	??????????
T. osgoodi	1110105200	10???????0	?0?00?00?0	????0?01??	?????????0	0???????0?	010210021?	??????????
C. berlepschi	1110105220	10???????0	?0?00?01?0	????0?01??	?????????0	0???????0?	022000010?	??????????
C. cinereus	1110105220	10???????0	?0?00?01?0	????0?01??	?????????0	0???????0?	012000010?	??????????
N. bonapartei	1120107300	1010001110	1010010000	2231010101	0022212210	1133333111	1101100312	1001100000
N. julius	1120101300	1010000110	1000000010	0001011111	1120202210	1011111111	0101100312	1001100010
N. nigrocap.	112010[05]300	1010000010	1010010000	0231000111	1120202110	1011111111	110110031?	??????????
C. undulatus	1110107200	1020000110	1000000010	0001010111	1120002210	0021121101	01200001[14]1	1001111101
C. soui	111012[15]210	1010000000	0010010000	0000000111	1100001100	0011111000	01200000[34]2	1001100000
C. tataupa	1111132200	1010000000	0010010000	0042000111	1100001100	0011111202	0020000121	1001111101
C. parvirostris	1111132200	1010000000	0010010000	0042000111	1100001100	0011111202	002000002?	??????????
C. obsoletus	1110125210	1010002000	0010010000	0042000111	1100001100	0011111202	012000004?	??????????
C. erythropus	1110106200	1010000000	1010010000	0001010111	1120002210	0021121101	002000012?	??????????
C. noctivagus	1110106200	1011000000	1010010000	0111010111	1120002210	0021121101	002000013?	??????????
C. duidae	1110107200	1011000000	1010010000	0001010111	1120002210	0021121101	002000011?	??????????
C. variegatus	1110106200	1010000000	1010010000	0111010111	1120002210	0021121101	0020000130	1001111101
C. boucardii	111012[67]200	1010000000	[6]010010000	0001000111	11202022[6]0	0011111[5]00	0120000020	1001111101
C. kerriae	111012?200	1010002000	0010010000	0001000111	1120202210	0011111000	0120000020	1001111101
C. cinnamomeus	1110107200	1021000100	10[3]00[3]00[5]0	0011010111	1122202210	0011111101	0120000020	1001111101

C. atrocapillus	1110107200	1010001000	1010010000	0031000111	1100002210	0021121101	0?2000002?	??????????
C. barletti	1110155200	1010000000	1010010000	0110010111	1100002210	0021121101	012000001?	??????????
C. casiquiare	11101??2?0	1010000000	1010010000	111?010111	1100002210	00?11?1101	012000003?	??????????
C. strigulosus	1110107220	1010001000	0010010000	0001000111	1120002200	0021111000	012000000?	??????????
C. *transfasciat.*	11101072?0	1021000100	10000000[01]0	1111010111	1122202210	0021121101	012000002?	??????????
C. *ptaritepui*	1110121230	1010002000	0010010000	0000000111	1100000000	0011111000	012000114?	??????????
C. *brevirostris*	11101052?0	1010000000	1010010000	0111010111	1100002210	0021121101	012000001?	??????????
N. minor	1101127010	1030110320	2020020020	00011100[01]1	0[01]2[02]2[01]2220	0??????100	012000113?	??????????
N. maculosa	11011230[01]0	1030110320	2020020020	00011[13]000[01]	0022212220	011311110[01]	0120001330	1110011120
N. chacoensis	11011230[01]0	1030110320	2020020000	00011[13]0000	0022212220	0113111100	0120001330	1110011120
N. boraquira	1101127010	1030110320	2020020020	0001110001	0120202220	0131333100	0120001[12]3?	??????????
N. darwinii	1101123000	1030110320	2020020020	00011[13]0001	0[01]22212220	011311110[01]	012000133?	??????????
N. ornata	31021010[01]0	1130114230	2000000010	2001210001	0120212130	0133333000	0210001[12][13]0	1110011120
N. kalinowskii	31021??0?0	1120114230	2000000010	2001210001	0121212130	0133333101	0210001[12]??	??????????
N. cinerascens	2101155000	1130110220	2000001011	0001141001	01202021[123]0	0131333100	0210001[12]10	1110011120
N. pentlandii	3102103000	1130114220	20000[01]1001	0001231001	0120202120	0011111010	0110001210	1110011120
N. perdicaria	3102105000	1130114210	2000000000	0001230001	0110102220	010[03]303100	0210001230	1110011120
N. taczanowskii	3102103000	1130114220	2000011011	0000211001	0022212220	0133333101	021000133?	??????????
N. curvirostris	3102121000	1130114220	2000000010	0000230001	0120202220	0101301100	0210001230	1110011120
E.e. elegans	2101100001	1202110341	4122020030	2201010000	0022212241	0133333101	0300111-10	1110011122
E.e. albida	2101100001	1202110341	4122020030	2001010000	0022212241	0133333100	0300111-10	1110011122
E. formosa	2101100001	1202110341	4122020032	2001010001	012[02]212141	01[13][13]333101	0300111-1?	??????????
R.r. pallescens	100-005010	1000110030	3010010010	2031040002	2212322230	0103003303	02001113[13]0	1110011120
R.r. maculicol.	100-005010	1000110330	3020020010	2201040022	2211322230	0100300303	0200111310	1110011120
R.r. rufescens	100-005010	1000111030	3010010000	0031040022	2212322230	0103003303	02001113[13]0	1110011120
T. pentlandii	2101123001	1002110340	4022120030	2223110001	0120212140	0131333104	0200111-[14]?	???011120
T. ingoufi	2101144011	1002113351	5122120022	2223110022	2212112251	0133333104	0200111-1?	??????????
T. nanus	1101127010	1030110320	2000000010	0001110011	11000022[12]0	0022222100	0120001130	1?10011120