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A Phylogeny of the Tinamous (Aves: Palaeognathiformes) Based on Integumentary Characters

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Abstract.—A cladistic analysis of the tinamous, including the 47 currently recognized species and some distinct subspecies, was conducted based on 80 integumentary characters from adult and natal plumage, ramphoteca (corneum sheath of bill), and podoteca (horny scales of legs). For the adult plumage (50 characters), we studied feather pigmentation patterns from different pterylae (feather tracts). A criterion of overlap of basic pigmentation elements was used to assign costs to the transformation between the states in most of these characters in such a way that transformations between more similar conditions were less costly. The consensus tree was almost fully resolved, and about 50% of its groups were relatively well supported. Because the only outgroup that could be used provided a poor root, two possible rootings of the ingroup subtree were considered; in both cases, only one of the two traditional subfamilies (the steppe tinamous) was recovered, and the other (the forest tinamous) appeared as paraphyletic. The results of the present analysis are compared with those from an osteological data set, using a strict supertree technique. The combined tree has a large number of nodes, indicating a high degree of congruence between the two data sets. [Integumentary characters; Sankoff parsimony; supertrees; Tinamidae.]

Tinamous are terrestrial birds with limited flight capabilities and are endemic to the Neotropical region. The monophyly of Tinamidae has been historically recognized, and their relationships with other birds have been the subject of much research (Parker, 1864; Pycraft, 1900; Clay, 1950; Verheyen, 1960; Hudson et al., 1972; Elzanowski, 1987; Brom, 1991). Tinamous are basal among extant birds, although there has been controversy as to their exact position and affinities. They are the oldest of Neognathae (all modern birds except the Ratitae), or they belong to the Palaeognathae and then are the sister group of Ratitae (ostrich, rheas, and related australasian flightless birds). Among authors defending the first position are Huxley (1867), Fürbringer (1888), Beddard (1898), Chandler (1916), Glenny (1946), Zavattari and Cellini (1956), Verheyen (1960), Sibley and Frelin (1972), and Houde (1988). Among authors defending the second position are Parker (1864), Salvadori (1895), Pycraft (1900), Carlisle (1925), Lowe (1928), Wetmore (1930), Bock (1963), Meise (1963), Parkes and Clark (1966), Gysels (1970), Cracraft (1974), and Prager et al. (1976). More recent studies, whatever the analytical methods utilized, support the monophyly of Palaeognathae, i.e., Ratitae + Tinamidae (Cracraft, 1981, 1986, 1988; Saiff, 1988; Cracraft and Mindell, 1989; Bock and Bühler, 1990; Sibley and Ahlquist, 1990; Kurochkin, 1995; Lee et al., 1997; Groth and Barrowclough, 1999).

In spite of this body of work, very little is known about the phylogenetic relationships within Tinamidae. Salvadori (1895) first attempted a subdivision by defining two subfamilies, Tinaminae and Tinamotidinae, the latter including the genera that lack a hallux (*Eudromia* and *Tinamotis*). Much later, von Boettischer (1934), not citing Salvadori, proposed another classification; his Eudrominae is equivalent to Salvadori's Tinamotidinae, Tinaminae is more restricted (only *Crypturellus*, *Tinamus*, and *Nothocercus*), and Rhynchotinae contains the remaining genera (*Rhynchotus*, *Nothura*, *Nothoprocta*, and *Taoniscus*). In a review, Miranda-Ribeiro (1938) divided Brazilian tinamous into two subfamilies: Tinaminae, equivalent to von Boetticher's Tinaminae, and Nothurinae, grouping the former Rhynchotinae and Eudrominae. Regarding habitat preferences, Miranda-Ribeiro's scheme led to the general categorization of species as either forest-dwelling (Tinaminae) or steppe (Nothurinae) tinamous.

Since those remarkable early anatomical works, there have been few systematic studies of tinamous. Only Ward (1957, in a study of ectoparasites) and Jehl (1971, in a study of natal plumage) discussed the relationships among genera, largely supporting the views of von Boetticher (1934) and Miranda-Ribeiro (1938).

Here, we propose the first phylogenetic reconstruction of relationships within Tinamiformes (including all 47 currently recognized species; see Blake, 1977; Cabot, 1992), based upon the integument, including bill, leg, and plumage characters. As in most bird orders, the traditional classification of this group at all levels has been almost completely based on integumentary characters. Livezey (1991, 1995, 1998) and Chu (1998) were among the few to attempt phylogenetic analyses of bird groups using plumage characters. They found integumentary characters to be as reliable and useful a source of phylogenetic information as other types of morphological evidence. In addition to bill and leg characters, we extend here the topological criteria advanced by Livezey (1998) and Chu (1998) by treating each feather tract (pterilia) as a potentially useful source of characters. This approach yielded a set of 80 characters, and because skins were available in museums for all species, we were able to include all 47 forms of tinamous for which species rank is currently recognized. This availability of skins was especially important given that other types of morphological (e.g., osteological, myological) and molecular data are lacking for many of the species. We focused on feather design on each pterilia and developed a way to treat a structure as complex as a patterned tinamou feather.

Our hypothesis of relationships certainly cannot be considered as final. A definitive hypothesis should include a combination of the present data with additional sources of information currently being studied. We concentrate here on only the (types of) characters that have been used traditionally in tinamou systematics to determine whether they actually support current generic delimitations and whether they are phylogenetically informative and congruent with other sources of information. Integumentary characters are a useful source of phylogenetic information, and based on a recently developed supertree technique (Goloboff and Pol, in press), there is a high degree of congruence in the results derived from integumentary and other sources of information more commonly used in cladistic analyses of birds.

METHODS

Taxa

In our analysis, we included all 47 currently recognized species (Cabot, 1992; see Appendix 1) and a new species in process of description. Species status may be controversial in several forms. For instance, *Nothura chacoensis* may have been confused with *Nothura maculosa paludivaga* (Conover, 1950a; Mazar Barnett and Pearman, 2001), although both are treated as species in the modern literature (Cabot, 1992). However, the aim of our analysis was determination of higher relationships, for which the choice of subspecies is of little relevance as long as the main forms are represented. Three forms of *Rhynchotus*, formerly treated as either a species (Gray, 1869; Maijer, 1996) or a subspecies (Peters, 1931; Blake, 1977), and two of the seven known forms of *Eudromia elegans* (Conover, 1950b; Olrog, 1959; Navas and Bo, 1981) were included.

We used the ratites *Apteryx australis* (the brown kiwi, Apterigidae) and *Pterocnemia pennata* and *Rhea americana* (the lesser and greater rheas, Rheidae) as outgroups, following previous studies that supported ratites as the sister group to Tinamidae (e.g., Cracraft, 1981, 1988; Groth and Barrowclough, 1999). We examined skin specimens of all species included (see Appendix 1 for details). The number of specimens actually observed per species depended on the availability in museums and on expected intraspecific variability.

Characters

We identified 80 characters in the integument (Appendix 2). For character definition, we divided the body into standard topological areas following Clark (1993). Unobserved states were coded as missing (?), and cases of noncomparability were coded as negative (−); the latter was particularly important for the outgroup. In ratites, our natural outgroup, the plumage is not segregated into pterylae. Ratites also lack pennaceous structure and have no interlocking barbules of the vexilla, so that feathers are hirsute or hairlike (Chandler, 1916; Lowe, 1928; McGowan, 1989) and the primary homology of pigmentation is uncertain. In addition, Jehl (1971) failed to find designs in natal plumage that could be comparable between tinamous and ratites. Therefore, for the outgroup, we coded as missing all characters based on feather pigmentation, and outgroup–ingroup relations rely on only bill and leg characters.

We avoided repeated scoring of characters that show obvious dependence by making some conservative coding decisions. For the dorsum, all principal feather tracts (pterilia scapulohumeralis and pars spinalis and pars pelvica of pterilia dorsalis) show the same character states within each species. Thus, those three feather tracts were coded jointly in the single character 20. Analogously, we treated presence of ocelli covering many different parts of the upper wings as a single separate character instead of defining several different characters for each wing part. These two cases (pterilia dorsalis and ocelli in upper wings) represent logical exceptions to our strictly topological criterium by which each part of the bird is treated separately.

Bill and leg characters.—Bill characters (rostrum and regio nasalis) were based upon segmentation of the ramphoteca, shape, color of parts, and position of nares. Color of iris was the single character for regio orbitalis (strictly speaking, an organa sensuum character instead of integumentary; see Evans and Martin, 1993). We followed Blake's (1977) descriptions; whenever possible, we checked Blake's data against the color information on specimen labels. Blake's subtle distinctions were pooled into four main colors.

The single character scored for general leg structure relates to the hallux (digitus pedis I; character 9, cf. Figs. 1l, 1n). Characters of the hind legs include relative size, shape, arrangement of scales of different leg parts, and color (after Blake, 1977).

Adult plumage, feather design.—We based our description of adult plumage mainly on the predominant design of individual feathers from each pteryla. Variation in design is more important than variation in color; the former includes several different clearly recognizable patterns, whereas the latter encompasses only a limited range of subtly graduated brownish tonalities.

We identified three main feather designs (Fig. 3a). The first one includes transverse patterns, which we call bicolored barred. There was a wide range of variation (Figs. 2a, h, i), but it was impossible to define clear-cut states because of continuous gradation of bar width, intensity, and shape. The second main pattern, streaked, has a longitudinal stripe of varying width along the sides of the rachis (not including the rachis itself, which is always darker). The third main pattern is immaculate. In some cases, we differentiated brown, rufous, gray, and white ground color, depending on body area and usefulness of the distinction.

We analyzed the complexity of feather patterns using an overlap criterion of pigmentation. A feather pattern can be seen as several distinct elements superimposed. Consider first the three main patterns (barred, immaculate, and streaked), ordered as in Figure 3a. For transforming a barred into a streaked feather, under our criterion, the bars must be lost, becoming immaculate, and a longitudinal stripe must be gained. Because this progression is symmetrical, the converse also holds true. Thus, gaining or losing two feather elements (e.g., bars and stripes) must have a cost of two steps, whereas gaining or losing a single element (from immaculate to streaked or from immaculate to barred) must cost a single step. The costs of transformations reflect the relative degrees of similarity between the observed conditions.

The situation becomes more complex when other patterns are considered. The feather design in *Eudromia* consists of both transverse bars and a longitudinal stripe (Fig. 2g). Thus, distinct feather elements may overlap, forming a more complex feather design and creating alternative "pathways" of transformation from barred to streaked.

The plumage pattern of the back of *Tinamotis ingoufi* is unique (characters 18, 20, and 48; Appendix 2) but seems closer to longitudinal patterns (Fig. 2l). Blake (1977:76) described this bird as having feathers with "dark brown centers, bordered with gray and often with bright yellowish olive, the general appearance above mottled, spotted, and finely streaked." Upon closer examination, the dark brown centers are a variation of a wide longitudinal dark stripe. Therefore, we consider this state as more related to the streaked, with additional ornamentation. We observed three additional transverse patterns: tricolored barred (Fig. 2f), scalloped (scaly) (Fig. 2i), and *Nothura*-like barred (Figs. 2c–e). The tricolored barred adds a third color band to the basic bicolored barred; it is present almost exclusively in *Rhynchotus*, although it also appears in some *Nothoprocta*. We consider the scalloped pattern of some species of *Crypturellus* a derived barred (with dark bars crescentic or curved following the feather

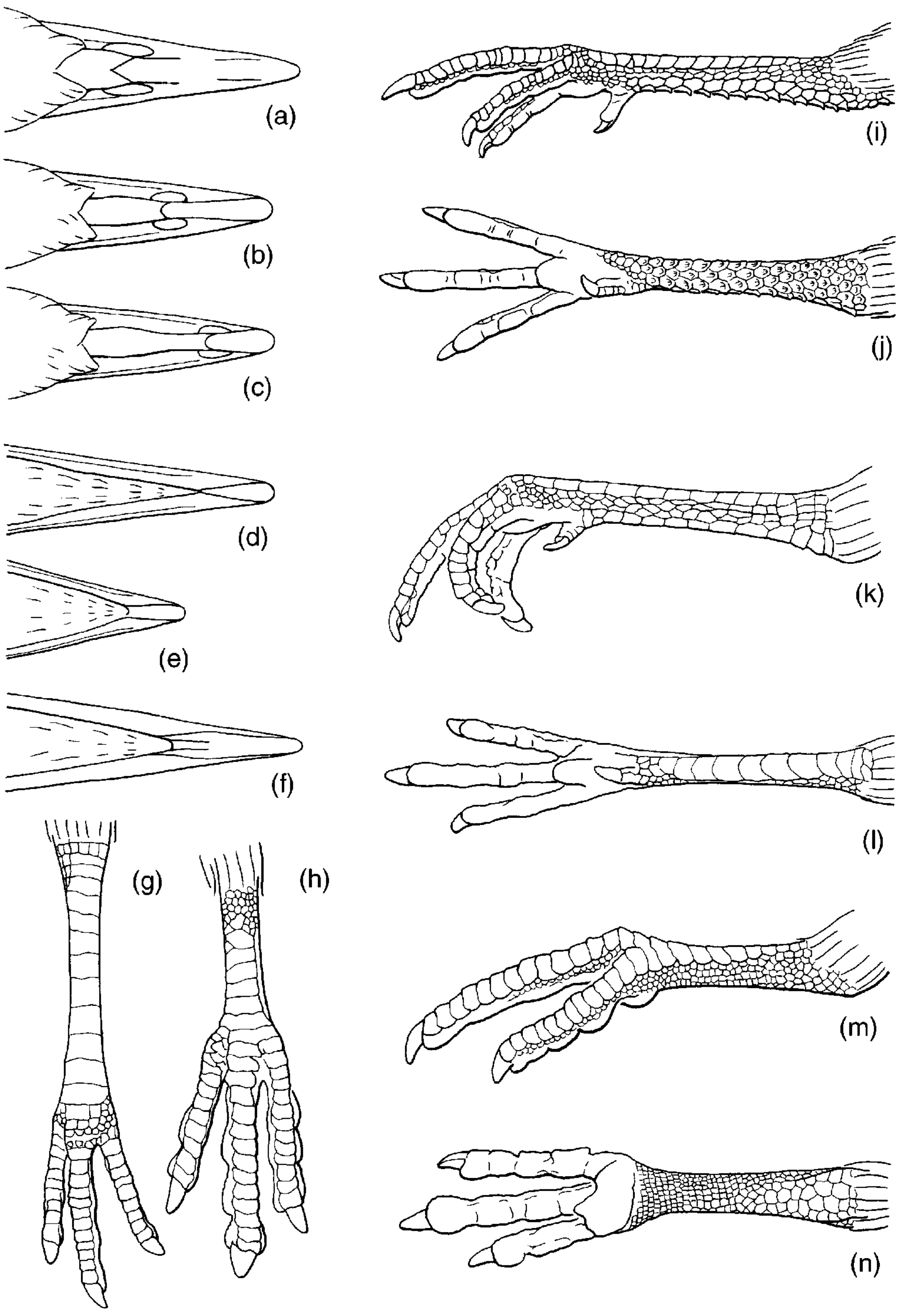

FIGURE 1. Selected characters of the bill and legs: (a–c) bill, dorsal view, showing position of nares; (d–f) bill, ventral plate; (g, h) leg, frontal; (i, k, m) leg, lateral; (j, l, n) leg, ventral. (a) *Nothoprocta cinerascens*. (b, g) *Crypturellus obsoletus*. (c, i, j) *Tinamus solitarius* (d) *C. obsoletus*. (e) *Nothura maculosa*. (f, k, l) *Nothoprocta ornata*. (g, h) *C. obsoletus*. (h, m, n) *Tinamotis pentlandi*.

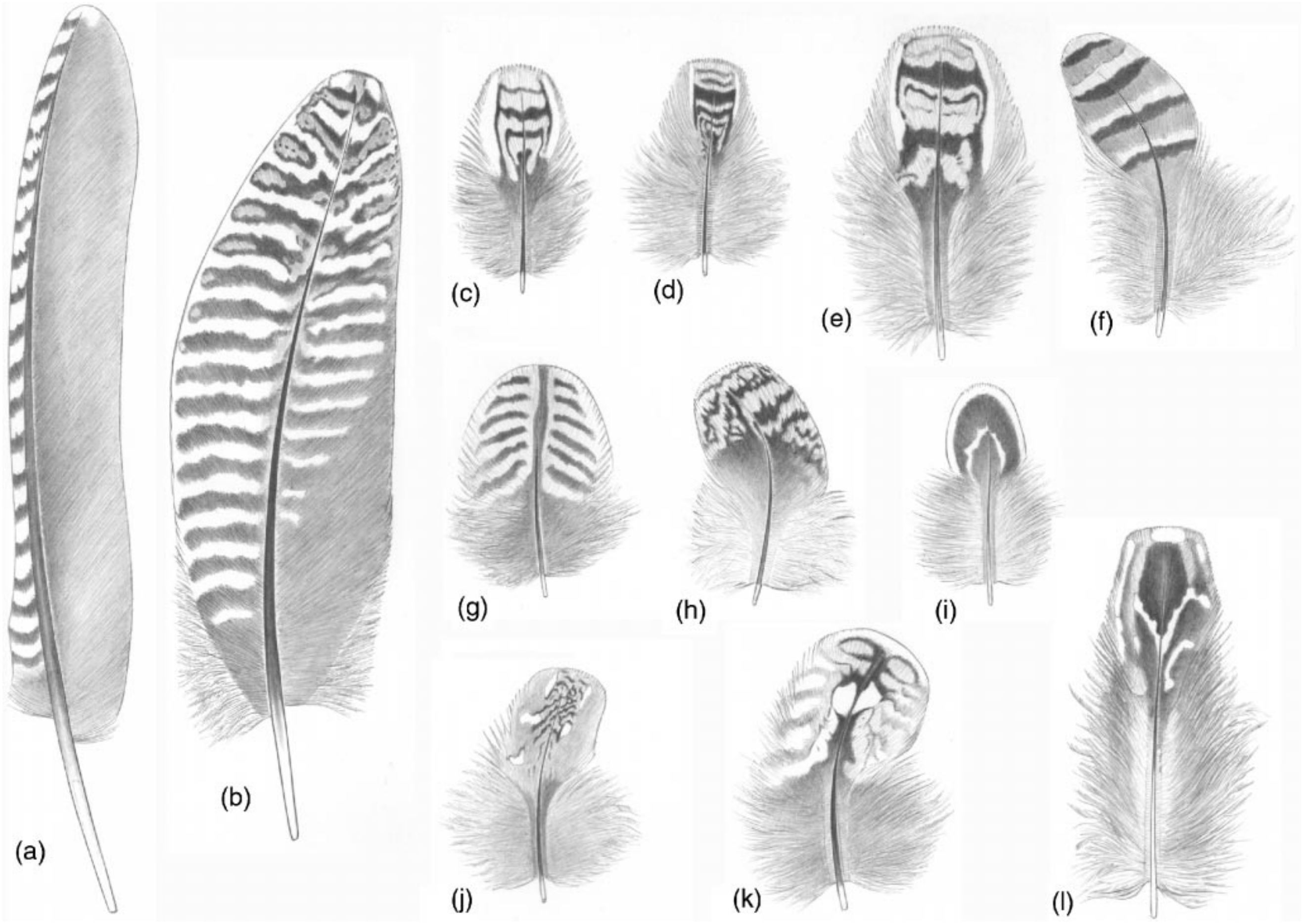

FIGURE 2. Selected wing (a, b) and contour (c–l) feathers of tinamous showing pigmentation patterns. (a) *Nothoprocta ornata* (primary remige) showing a bicolored barred outer web and immaculate inner web. (b) *Nothoprocta ornata* (secondary remige) showing both webs bicolored barred and a transition to tricolored barred near the distal part. (c) *Nothura*-like pattern in *Nothura maculosa*. (d) Same for *Nothoprocta pentlandi*. (e) Same for *Nothoprocta cinerascens*. (f) Tricolored bars in *Rhynchotus rufescens*. (g) Mixed pattern in *Eudromia elegans*. (h) Bicolored (vermiculate) bars in *Crypturellus undulatus*. (i) Scalloped feather in *C. tataupa*. (j) Rounded ocelli of *Nothoprocta pentlandi*. (k) V-shaped ocelli of *E. formosa*. (l) *Ingoufi*-like pattern of *Tinamotis ingoufi*.

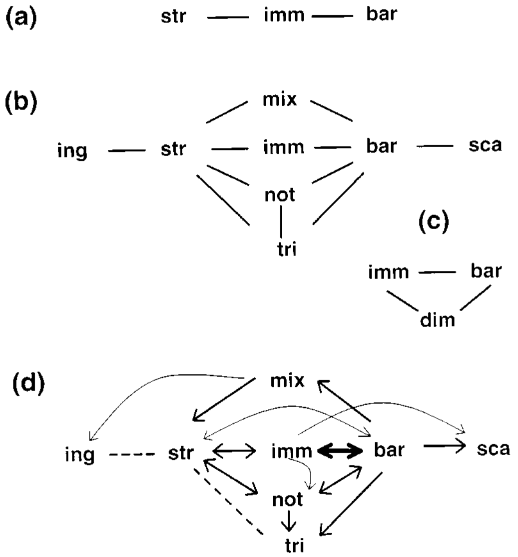

FIGURE 3. Transformations among character states in adult plumage. (a–c) Each direct connection represents one step between the two character states under the overlap criterion. (a) Relation of the three basic pigmentation elements. (b) Complete transformation scheme for all character states observed. Costs of transformation are intended to denote relative degrees of similarity between states, instead of probabilities of transformation or evolutionary pathways. (c) Additional transformation costs for the extra state in characters with sexual dimorphism. (d) Transitions implied by the results of the analysis with no step matrix characters. When different most-parsimonious reconstructions are possible, the minimum numbers of each type of transformation were used. Straight solid lines indicate transitions between more similar states; thick line indicates the most frequent transformations; thin curved lines indicate direct transitions between less similar states; dashed lines indicate transitions between similar states that never occur; arrows indicate direction of transformations. Abbreviations: str = streaked; imm = immaculate; bar = bicolored barred; ing = *ingoufi*-like pattern; mix = mixed pattern; not = *Nothura*-like pattern; tri = tricolored barred; sca = scalloped; dim = sexually dimorphic for imm-bar.

contour). *Nothura*, *Nothoprocta*, and *Taoniscus* share a common design consisting of irregular bicolored barred with two light lateral edges, which we called a *Nothura*-like pattern. All barred patterns can be derived from the basic bicolored barred by one change in feather elements: the third colored band, the marginal light stripes, or the crescentic shape.

We considered all varieties of immaculate as nonadditive among themselves. These considerations produce the complete character state tree shown in Figure 3b, where the cost of transformation between any two states equals the number of lines in the shortest path between the two states. No single character showed all the states together. In all cases, the general character state tree was replaced by a reduced one, including only the states present in the character.

Sexual dimorphism, present in only a few species (*Crypturellus boucardi*, *C. cinnamomeus*, and *C. erythropus*), was treated by adding an extra state to the relevant character. For instance, the males of *C. boucardi* are immaculate in the dorsum, whereas the females are bicolored barred (character 20). The species was coded as having state 6 (see Appendix 2), and the step matrix was modified to accommodate state 6 (male immaculate, female bicolored barred) as having one step between immaculate in both sexes (state 0) and bicolored barred in both sexes (state 1; see Fig. 3c). This approach was applied also to characters 22, 25, 28, 48, and 57.

The pattern in different parts of the body was remarkably constant in all species studied; very few species have been coded as polymorphic (<1% of all the ingroup entries). Although each feather tract is remarkably constant within a species, different consecutive feather tracts often exhibit differences within specimens that provide actual examples of the transformations we postulated. Transitions from immaculate to bicolored barred to scalloped are present in the flanks and legs of some *Crypturellus*, such as *C. casiquiare*. Transitions from tricolored barred to bicolored are present in *Rhynchotus* and *Nothoprocta*. Transitions from bicolored barred to *Nothura*-like are readily observable in the collar and dorsum of many *Nothura* and *Nothoprocta*. Additionally, there are examples of transitions from *Nothura*-like or tricolor to streaked. In *Rhynchotus rufescens maculicollis*, the streaked design of the dorsal neck gradually transforms into the tricolored barred of the dorsum. In the same body areas, streaked transforms into *Nothura*-like pattern in several *Nothoprocta* and *Nothura*. The mixed, tricolored barred, and *Nothura*-like patterns each show an observed one-step transition to both bicolored barred and streaked. The last transition observed was between *Nothura*-like pattern and tricolored barred in *Nothoprocta ornata* (see Fig. 1b).

Adult plumage, other characters.—We observed two types of light-colored ocelli superimposed over almost any kind of feather pattern in different pterylae. Ocelli were either rounded spots or paired V-shaped marks. When present, the patches tended to cover several feather tracts, e.g., in the dorsum or the upper wing (see Appendix 2, characters 19 and 49), or were restricted to a single feather tract (characters 21, 26, 29, 36, 50, 58, and 60).

Two feather traits do not refer directly to color patterns of the vexillum. A conspicuous white rachis is found in the throat feathers of *Crypturellus cinereus* and *C. berlepschi* (character 27). A furlike structure appears in the feathers of *Nothoprocta* and *Tinamotis* (character 34).

To achieve a better cladistic resolution of some groups (e.g., *Crypturellus*), a more detailed definition of character states (including degrees of tonalities or development of bars) may be required. However, the present coding scheme seems to provide sufficient resolution for a first approximation of the general relationships within Tinamidae.

Natal plumage.—We scored the information provided by Jehl (1971), who studied the natal plumage (down feathers or neossoptilus, characters 69–80) of 17 species of all genera except *Taoniscus*. We coded each of Jehl's distinct descriptive statements for each body area he recognized. Some ambiguous characterizations were pooled into more comprehensive concepts (see character 69, Appendix 2). We proceeded accordingly with the chick of *Taoniscus nanus* described by Teixeira and Nacinovic (1990). By examining specimens of *Tinamus solitarius*, we confirmed the similarity of *Tinamus major* and *T. solitarius*, assumed by Jehl (1971) after Salvadori (1895). We also examined chicks of *Nothoprocta cinerascens*. Data on natal plumage were thus available for a total of 20 species.

Cladistic Analysis

Our resultant tree is unrooted because the placement of the root taxa was weakly determined by the data, mostly because most integumentary characters (62 of 80) are noncomparable between ratites and tinamous. The ratites, however, were not physically excluded from the entire analysis, only from the consensus, so that their character states could still influence the way in which tinamous are related among themselves.

The basic searches were done using SPA, a program for Sankoff parsimony analysis (Goloboff, 1998). This generalized parsimony approach allows for inclusion of characters for which the costs of transformation between states are defined by the researcher (Sankoff and Rousseau, 1975), as in our plumage characters. We did 20 iterations of parsimony ratchet (Nixon, 1999), saving a single tree per iteration and using TBR branch swapping (Swofford and Olsen, 1990) for each of 50 random addition sequence Wagner trees (thus totalling 1,000 ratchet iterations). Half the runs used 1 as random seed; the other half used 2. This strategy is most likely to find all the islands of optimal trees. The trees produced by the ratchet were submitted to TBR branch swapping to find all equally parsimonious trees. The results were finally exported to TNT (Goloboff et al., 2000) for diagnosis/summary.

The support for the groups was calculated using both resampling and Bremer supports. The resampling used the equiprobable model of Goloboff et al. (unpubl.), which is itself a modification of parsimony jackknifing (Farris et al., 1996). Only approximate searches were done for each of 500 replications, with 5 random addition sequences followed by TBR (saving a single tree per addition sequence). The best three of those five trees were selected, the branches with only ambiguous support were collapsed (i.e., rule 1 was used; see Coddington and Scharff, 1994), and the strict consensus of those three trees (without considering the outgroup, *T. osgoodi*, or the new species) was calculated. The support was estimated both as the absolute frequency and as the difference in frequency between the group and the most frequent contradictory group (Farris et al. *in* Horovitz, 1999; Goloboff et al., unpubl.). The trees used to calculate Bremer supports, both absolute (Bremer, 1994) and relative (Goloboff and Farris, 2001), were found by computing 20 random addition sequence Wagner trees followed by SPR (Swofford and Olsen, 1990), keeping no more than 2 trees per replication and retaining all trees found. These trees, together with the optimal trees, were used as the starting point for TBR branch swapping, sequentially saving up to 2,000, 4,000, 6,000, and 10,000 trees within one, two, four, and six steps, respectively, of the best. Many more than 10,000 trees within six steps of the best trees exist, but these provide a basis for estimating the Bremer supports. The absolute Bremer support values so calculated could thus be slight overestimations of the actual values. The relative support values were calculated considering only those trees within the absolute Bremer support for each group, which produces better support estimates (Goloboff and Farris, 2001). By using only the trees within absolute Bremer supports, the values for the relative supports could be either slightly over- or underestimated.

We compared the results of the present analysis with those of Bertelli (unpubl.), which is the only cladistic analysis of tinamou relationships and includes 26 taxa scored for a partial set of osteological characters. Those results were combined with the present ones by the semistrict supertree method implemented in TNT (Goloboff et al., 2000; Goloboff and Pol, in press). The method displays a group in the output tree only when it is supported by some combination of trees and contradicted by none. Goloboff and Pol (in press) warned against possible problems with supertrees created from input trees with very different taxon sets. The present case involves two trees, and the taxa in one of the trees are essentially a subset of the taxa in the other. Thus, the problems pointed out by Goloboff and Pol cannot occur under these circumstances. To determine whether the number of observed compatible groups could be achieved by chance alone, the number of nodes in the combined tree was compared with the number of nodes in 10,000 random pairs of trees (of 26 and 50 taxa, with proportions of polytomies similar to the ones observed in the real data sets). The comparisons between the real data sets involve rerooting on *Nothocercus* the tinamid subtree in the integumentary tree (the unambiguous root for the tinamid subtree in the osteological dataset). To take this result into account in our test, for each pair of trees, we rerooted the 26-taxon tree in order to have the largest possible number of nodes in the resulting supertree (thus making the test more conservative).

RESULTS AND DISCUSSION

Searches, Topology, and Support

The searches produced 36 trees (distinct under rule 4; see Coddington and Scharff, 1994) of length 444. Of the 50 independent starting points, 48 produced trees of this length (in 977 of the 1,000 ratchet iterations), thus increasing the confidence that the trees are indeed optimal.

The strict unrooted consensus of the 36 trees is shown in Figure 4. The two most likely placements for the root are indicated with dots. Rooting at the branch leading to *Tinamus osgoodi* is suggested (weakly so) by the integumentary data, whereas rooting at *Nothocercus* is suggested unambiguously by osteology (Bertelli, unpubl.). This last possibility requires two extra steps for the integumentary data (characters 2 and 68). In both rootings, only the group of steppe tinamous (Miranda-Ribeiro's Nothurinae) is recovered; the forest dwelling Tinaminae are paraphyletic for both of these rootings.

Values of support are shown on the branches (Fig. 4). The first line shows values of frequencies/frequency differences under the modified jackknife procedure. Those values are calculated without considering the positions of the root taxa, *T. osgoodi*, or the new species, which are weakly determined by the data. Because the searches were approximate, some of the values may be biased (see Goloboff et al., unpubl.); some partitions were more frequently contradicted than supported (the corresponding values are then indicated in brackets). The second line shows the absolute/relative Bremer supports (again, without considering those problematic taxa). There is a high correlation between the Bremer support and the jackknife values. The third line (included for completeness) shows the absolute/relative Bremer supports including all the taxa. A comparison of the values in the second and third line gives an indication of possible alternative placements of the conflictive taxa (root, *T. osgoodi*, and the new species).

For both possible rootings, Nothurinae is well supported. The new species and *Taoniscus nanus* are successive sister groups to all the other steppe tinamous. *Nothura* is paraphyletic because *N. boraquira* and *N. minor* are the sister group of the rest of the *Nothura* plus *Nothoprocta*, *Rhynchotus*, *Eudromia*, and *Tinamotis*. The monophyly of *Nothura*, however, is only weakly contradicted, and the genus becomes monophyletic in only slightly longer trees. *Nothoprocta* is fully resolved and well supported; within this genus, only the group formed by *N. ornata* and *N. kalinowskii* is well supported.

Rhynchotus + *Tinamotis* + *Eudromia* is a strongly supported group (absolute Bremer

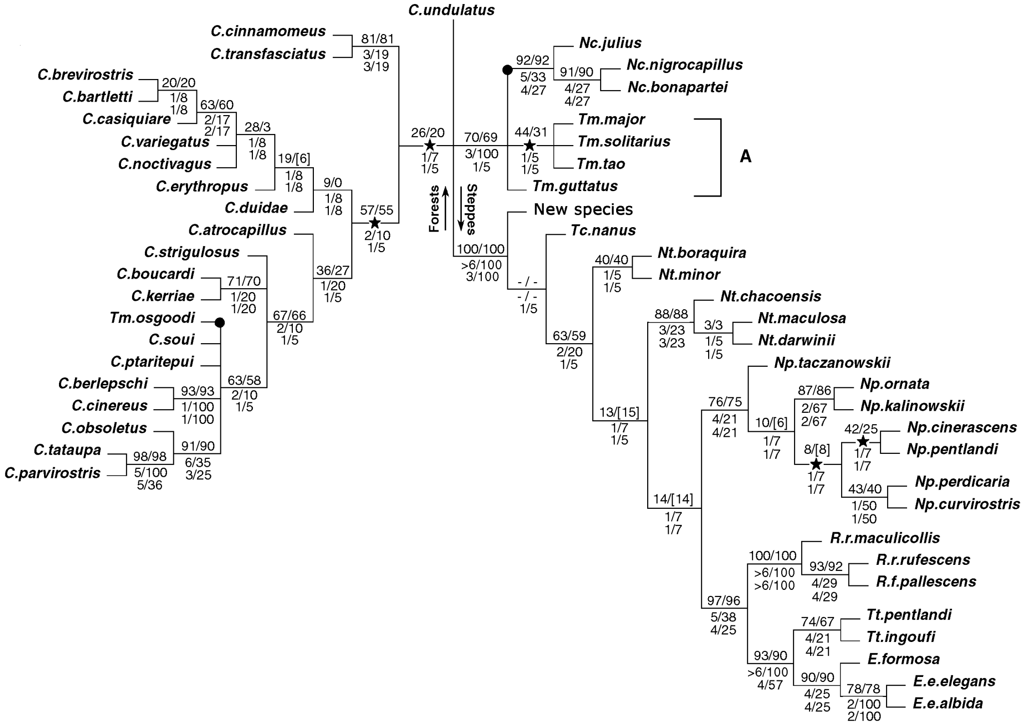

FIGURE 4. Consensus obtained under Sankoff parsimony analysis of the matrix in Appendix 3. The two most likely points of attachment of the root to this network are shown with dots. Values of support are given at each branch. The first line shows values of frequencies/frequency differences under jackknife (se brackets indicate partitions more frequently contradicted than supported), when the position of problematic taxa (root taxa, *Tinamus osgoodi*, and the new species) is not considered; the second line shows the absolute/relative Bremer supports (not considering problematic taxa); the third line shows the absolute/relative Bremer supports including all the taxa. The branches that collapse in the supertree (osteology + integument) are marked with a star; group A is gained in the supertree (*Tinamus* except *T. osgoodi*). Genus abbreviations: *C* = *Crypturellus*; *E* = *Eudromia*; *Nc* = *Nothocercus*; *Tm* = *Tinamus*; *Tc* = *Taoniscus*; *Nt* = *Nothura*; *Np* = *Nothoprocta*; *R* = *Rhynchotus*; *Tt* = *Tinamotis*. The labeled arrows indicate the regions of the network that comprise steppe and forest-dwelling tinamous.

support = 5) but with considerable character conflict (relative Bremer support = 38%). Within the monospecific *Rhynchotus*, the relationships among subspecies are clear, with *R. rufescens maculicollis* as sister to the other two subspecies. Therefore, our results support the separation of *Rhynchotus maculicollis* (monotypic) and *Rhynchotus rufescens* (which includes the subspecies *R. rufescens rufescens* and *R. rufescens pallescens*) recomended by Maijer (1996) on the basis of song structure.

The sister group to *Rhynchotus* is Salvadori's (1895) Tinamotidinae (*Tinamotis* + *Eudromia*). Each genus is monophyletic. The two forms of *Eudromia elegans* included in our study (*E. elegans elegans* and *E. elegans albida*) form a group, with *E. formosa* as its sister.

Within the forest-dwelling tinamous, the support for most of the groups is weak. The only well-supported groups are the genus *Nothocercus*, the sister relationship of *N. bonapartei* and *N. nigrocapillus*, the groups formed by *Crypturellus cinnamomeus* + *C. transfasciatus*, *Crypturellus obsoletus* + *C. tataupa* + *C. parvirostris*, and the sister relationship of *C. tataupa* + *C. parvirostris* (the two alternative rootings do not involve changes in the monophyly of any of these four groups). There is also the group *C. cinereus* + *C. berlepschi* with support values of 1 but without character conflict (relative Bremer support-100%). However, *Tinamus* is not present as a group in our consensus; four of its species form a polytomy with *Nothocercus*, whereas *T. osgoodi* appears within *Crypturellus* as sister of *C. cinereus* and *C. berlepschi*. The monophyly of *Crypturellus* would require rerooting with *Nothocercus* as sister of the other tinamids, including *T. osgoodi* in the genus, and probably excluding *C. undulatus*.

Congruence

Most of the nodes of our integumentary analysis are compatible with those in the osteological phylogeny of Bertelli (unpubl.); the semistrict supertree has 33 nodes. Some of the differences in the two trees are the result of differences in how the root attaches to the tinamids; if the tree for the integumentary characters is rerooted on *Nothocercus* (as in the osteological tree), the combined tree has 38 nodes. Semistrict supertrees (being a kind of consensus) may be poor indicators of (lack of) congruence when they have very few resolved nodes; however, because almost every group is shared (or compatible) between the two trees, the conclusion of a high degree of congruence does follow. The trees for the integumentary and osteological data sets are much more congruent ($P = 0.0001$) than expected by chance alone; no single case in the simulations had >25 compatible nodes (the test was conservative in choosing the rooting that produced more nodes).

The most widely used supertree technique is matrix representation with parsimony or (MRP; Baum, 1992; Baum and Ragan, 1993). However, MRP may create spurious groups, i.e., groups that are not actually supported by any of the input trees (or combination of input trees; these are the "novel clades" of Bininda-Emonds and Bryant, 1998). The MRP supertree for the osteology and integument data sets has no spurious groups, although it does have a group (all of *Crypturellus* except *C. undulatus*) that is supported in the integument tree and contradicted by the osteology tree.

The supertree differs from the consensus in Figure 4 in having one additional group and missing five. The additional group (A, Fig. 4) comprises all of *Tinamus* except *T. osgoodi*; this group is actually resolved in some of the optimal integumentary trees. The five nodes lost when combining the trees (star, Fig. 4) are all within *Nothoprocta*, *Tinamus*, and *Crypturellus*. These five nodes are poorly supported anyway, and thus the incongruence between the two data sets seems trivial.

Even when a robust phylogenetic hypothesis would require combining different data sets rather than analyzing them separately, establishing that different sources of evidence agree as to the relationships within a given group increases the confidence that (at least some of) the groups recovered are indeed monophyletic.

Alternative Cost Regimes

We also conducted an alternative parsimony analysis considering those characters with complex transformation costs as nonadditive. The consensus of the 522 trees (425 steps long, from 100 replications of random addition sequence Wagner trees, 81 of which were of minimum length, followed by global TBR branch swapping) was much less resolved than the consensus obtained under Sankoff parsimony. However, the lack of resolution was caused by the instability of the root taxa, *T. osgoodi*, and the new species. If the consensus is calculated without considering those taxa, nine of the nodes in Figure 4 collapse (five are within *Crypturellus*, and two are within *Nothoprocta*) and no new nodes appear; all the nodes that collapse under the nonadditive regime are those nodes with the lowest support in the Sankoff analysis.

Using the trees produced in this search, we examined character-state transformations to see whether transformations not occurring in the Sankoff analysis (by virtue of their high cost) could occur if those transformations were less penalized. Among the 522 trees, we selected the ones that were shorter under Sankoff parsimony (70 trees 445 steps long, i.e., 1 step longer than the optimal Sankoff trees). All the transformations implied by the nonadditive regime are transformations between states that, in the more complex cost regime, are either "adjacent" or separated by one "intermediate" state (i.e., with transformation costs either 1 or 2; see Fig. 3d). These same changes also occur, with about the same proportions, for the optimal Sankoff trees. Thus, in the Sankoff trees, the reduced numbers of transformations between more different states are not a consequence of the penalty imposed on them but rather a consequence of the interaction with other characters.

Relationships

No matter which rooting is chosen, the monophyly of the steppe tinamous (Nothurinae) is recovered and well supported. All the four character groups studied in the integumentary system contributed to the monophyly of the steppe tinamous (see Appendix 4):

1. Ramphoteca. The steppe tinamous have the anterior dorsal plate longer than the posterior plate (character 2), with the nares placed proximally in the bill, in contact with the head feathers (character 7). The grooves of the mandible are parallel, and the maxilla color is brown (characters 3 and 5).
2. Adult plumage. The feather pattern of the upper parts, which is rather simple in the forest-dwelling tinamous (immaculate or barred), becomes complex, first *Nothura*-like and then, from this, tricolored, mixed, or *ingoufi*-like (characters 12, 18, 20, and 48). The facial lines appear (moustachial and auricular stripes, characters 14 and 15), and the rectrices become rudimentary, indistinct from upper tail coverts (character 37). The feathers of underparts are furlike (character 34).
3. Podoteca. In the distal end of the acrotarsium, the bases of both the third and fourth toe are covered by a single scute (character 66).
4. Natal plumage. Five characters (71–74, 78) are unambiguous synapomorphies of the steppe tinamous, and their character states are complementary in all the forest-dwelling tinamous. One (character 78) is the development of the rachis and aftershaft; the others (characters 71–74) are design patterns of the head plumage (including forehead indistinct from the crown and three facial lines).
5. The color of iris changes to yellowish (character 8).

In contrast to the monophyly of Nothurinae, the subfamily Tinaminae is not recovered. Thus, rather than dividing the Tinaminae into several monophyletic groups, it seems best to simply eliminate subfamilial divisions within Tinamidae.

Integumentary Characters and Phylogeny

The consensus allows the interpretation of two alternative general trends in plumage changes. With the root placed at *Tinamus osgoodi*, the main trend in pigmentation pattern is the transformation from basically immaculate to bicolored barred to more complex variations involving extra feather elements (*Nothura*-like, tricolored barred, mixed, *ingoufi*-like). If the root is placed at *Nothocercus*, the basic pattern is now the bicolored barred, from which two main types derive: the mostly immaculate pattern of some *Crypturellus* (e.g., the *tataupa* group) and the complex variations of the steppe tinamous. Changes toward more complex states seem to occur directionally in terminal groups (see Fig. 3d, arrows). The scalloped pattern present in several characters in *Crypturellus obsoletus* + *C. tataupa* + *C. parvirostris* is acquired from either immaculate or bicolored barred but never reverts; tricolor barred derives from either *Nothura*-like pattern or bicolored barred in *Rhynchotus* and in some *Nothoprocta* and is never lost; and *ingoufi*-like pattern only derives from the mixed pattern and never reverts. The streaked pattern appears first in the throat of the new species and in the dorsal neck of *Taoniscus nanus* and gradually becomes more widespread in other steppe tinamous.

The natal plumage is highly informative. Chicks of most forest-dwelling tinamous share a dark general pattern with a distinct forehead, whereas chicks of the steppe tinamous are lighter in color and show several head stripes. Although Jehl (1971) thought that this finding supported the traditional subfamilial division, the natal plumage of the forest-dwelling tinamous is plesiomorphic and not evidence of monophyly.

Both the position of nares (traditionally used for contrasting steppe and forest-dwelling tinamous) and the presence/absence of the first toe (Salvadori's Tinaminae vs. Tinamotidinae, respectively) appeared informative at the levels at which they had been hypothesized. Other bill and leg characters used here (including divisions and relative proportions of bill plates and number and arrangement of foot scutes) also were useful at different levels. Of the characters involving coloration of nonfeathered parts, only the iris was reasonably informative (although it still required six extra steps). The colors of maxilla, mandible, and feet required many more independent origins and reversals, showing little congruence with the best cladograms.

Habitats

According to our phylogenetic reconstruction (and for each of the two possible rootings), tinamous plesiomorphically inhabited forests (a habitat type retained by the species now in *Nothocercus*, *Tinamus*, and *Crypturellus*), and a single lineage spread to steppes. This result is congruent with the results of Bertelli (unpubl.), who also postulated (on the basis of fossil evidence and a more reduced data set) that the tinamous invaded the steppes during the Miocene.

CONCLUSIONS

Chu (1998) emphatically defended and recommended the use of integumentary characters in systematic ornithology. We included all the integumentary characters used in classical taxonomy of tinamous and added many new ones. The classical characters performed very well in the context of the total data set structure. Integumentary characters produced ca. 55% of nodes with absolute Bremer supports of ≥ 2, and >30% of nodes have both absolute Bremer supports ≥ 2 and relative Bremer supports >30%. Jackknife estimations show a proportion of well-supported groups (>60% of the nodes with frequency >50%) much higher than indicated by Chu (1998; about 17% of the groups with bootstrap frequency >50%). Our data support integumentary characters even more forcefully than do the data of Chu (1998), because we have about three times as many well-supported groups.

Additionally, there is high congruence with Bertelli's (unpubl.) osteological data. The number of nodes shared or compatible between the two analyses was much higher than expected by chance. Both the degree of congruence with a previous analysis and the internal consistency of the data set, contradict once again the "perception among ornithological systematists that integumentary features are too labile to be historically informative" (Chu, 1998:000). In our analysis, even higher level relationships were depicted clearly and provided a reasonable basis for systematic conclusions. It seems illogical to accept that bill, leg, and plumage traits are reliable characters for bird alpha taxonomy but not for establishing higher level relationships.

Our crucial difficulty in using integumentary characters, i.e., the lack of comparability of feather patterns with respect to the outgroup, is inherent to our study group. In our data set, even when it is assumed that all state transformations are equally likely, the results of the analysis suggest that some transformations are more likely than others, and those transformations are the ones between the most similar states. Some authors have strongly argued for routinely or initially using nonadditive characters in the belief that assigning costs to some transformations implies strong evolutionary assumptions (e.g., Scotland and Williams, 1993). The alternative position was defended by Lipscomb (1992), who suggested that the information on relative degrees of similarity, whenever available, should be used to decide relative costs between different states, just as it is used to decide primary homology. If the cladogram implies transformations between more similar states, it is simply in agreement with the observations, which is precisely what happens when transformation costs based on the overlap criterion is used. The criterion of overlap of pigmentation elements used here can probably be extended to many other groups of birds in which barred, ocellate, or streaked feather patterns are common.

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APPENDIX 1

Comparative material examined in the construction of the data set of 47 recognized species plus a new undescribed species. In the analysis we usually included the nominate subspecies. Abreviations of institutions: AMNH- American Museum of Natural History, New York; COL-Colección Ornitológica Lillo, Facultad de Ciencias Naturales e IML, Tucumán, Argentina; LACMNH-Natural Museum of Los Angeles County; MACN-Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina.

Apteryx australis australis (AMNH 202963, 408894). *Rhea americana albescens* (COL 648, 5943, 7479, 7480, 7481, 11280, 11354). *Pterocnemia pennata garleppi* (COL 700); *Pterocnemia pennata pennata* (COL 12019, 576). *Tinamus guttatus* (AMNH 270403, 272134, LACMNH 37843); *Tinamus major major* (LACMNH 42107, 42108); *Tinamus major robustus* (AMNH 101060, 233290, 468924, 468925, 468926); *Tinamus osgoodi osgoodi* (AMNH 763823); *Tinamus solitarius solitarius* (AMNH 139901, 272026, 468920, 468921, 468923; COL 514a, 514b; LACMNH 28514, 46501, 46502, 46503, 46504, 46505, 46506; MACN 3530, 34089, 34090, 34093, 34094, 36566); *Tinamus tao tao* (AMNH 277444, 277446, 288122, 408891, 429001; LACMNH 42103). *Nothocercus bonapartei bonapartei* (AMNH 1156020, 1156030, 132201, 176517); *Nothocercus julius* (AMNH 55329, 111255, 35595, 468947, 468948); *Nothocercus nigrocapillus* (AMNH 136764). *Crypturellus atrocapillus atrocapillus* (AMNH 819597, 819789); *Crypturellus bartletti* (AMNH 230472, 239610, 525515, 824044); *Crypturellus berlepschi* (AMNH 230459, 468976, 468977, 468978, 819167); *Crypturellus boucardi boucardi* (AMNH 10342, 10346, 11020, 34502, 106196; LACMNH 24389); *Crypturellus brevirostris* (AMNH 203471, 233702, 239611, 469113); *Crypturellus casiquiare* (AMNH 434024); *Crypturellus cinnamomeus cinnamomeus* (AMNH 55335, 813097; LACMNH 77810); *Crypturellus cinereus* (AMNH 221110, 254826, 281109, 468965, 468967; LACMNH 36103, 42104, 42105, 42106); *Crypturellus duidae* (AMNH 272157, 273139); *Crypturellus erythropus erythropus* (AMNH 120285, 283052, 283053, 469628, 469129); *Crypturellus kerriae* (AMNH 123204); *Crypturellus noctivagus noctivagus* (AMNH 313713, 313714, 317184, 469092; LACMNH 59478, 60000, 60001); *Crypturellus obsoletus obsoletus* (AMNH 53331, 313706, 313711, 317185, 313903; COL 361a, 361b, 4872, 6224, 6225, 6226, 6227; LACMNH 27765, 37848, 46511, 46512, 46513, 46514, 46515, 46516, 46517, 46518, 46519, 46520, 46521, 46522, 46523, 46524, 46525, 46526, 46527; MACN 31740, 34080, 34081, 34084, 34451, 36565, 38172); *Crypturellus parvirostris* (COL 6222, 7848; LACMNH 26743, 27421, 27422, 28390, 31344, 32282, 32286, 42072, 42073, 42074, 42075, 42076, 42077, 42078, 42079, 42080, 44149, 101690; MACN 8560, 33241, 38183, 38184, 39188); *Crypturellus ptaritepui* (AMNH 831256); *Crypturellus soui albigularis* (LACMNH 32274, 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* (LACMNH 36102); *Crypturellus soui caucae* (LACMNH 36100, 36101); *Crypturellus soui harterti* (LACMNH 31097); *Crypturellus soui inconspicuus* (LACMNH 110165); *Crypturellus soui modestus* (LACMNH 16466, 16467, 16468, 16469); *Crypturellus soui mustelinus* (LACMNH 41864, 41865); *Crypturellus soui panamensis* (LACMNH 30310); *Crypturellus soui soui* (AMNH 129302; COL 1739); *Crypturellus strigulosus* (AMNH 238770, 238772, 238773, 285466, 430138; LACMNH 26744, 26745, 26746, 34337, 37847, 42102); *Crypturellus tataupa tataupa* (COL 48, 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; LACMNH 28191, 35337, 35338, 46507, 58482; MACN 31217, 33453, 34088, 38174, 38178); *Crypturellus transfasciatus* (AMNH 119535, 119538, 154696, 154697, 170771); *Crypturellus undulatus undulatus* (AMNH 34880, 127223a, 127223b, 469089, 819154; COL 1722, 1723, 1724, 1725, 1726; MACN 2055, 4109, 8979, 37393, 42394); *Crypturellus variegatus* (AMNH 125255, 469101, 804359, 804360, 804361; LACMNH 42094, 42095, 42096, 42097, 42098, 42099, 42100, 42101, 59479, 60002). *Rhynchotus rufescens catingae* (LACMNH 26735, 26736); *Rhynchotus rufescens maculicollis* (COL 362a, 362b, 967, 974, 1052, 1053, 6649, 7175, 7840, 9816, 9817, 9818, 10861, 10862, 12192, 15218; MACN 2300, 8148, 32836, 42312); *Rhynchotus rufescens pallescens* (COL 9986, 14017; LACMNH 104785; MACN 2177, 2526, 40339, 40340, 40981); *Rhynchotus rufescens rufescens* (COL 363a, 363b, 7122; LACMNH 32287, 32288; MACN 4579, 39192, 52681). *Nothoprocta cinerascens cinerascens* (COL 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; MACN 8148, 8428, 409806); *Nothoprocta curvirostris curvirostris* (AMNH 166330, 866315, 469156, 469157, 469155); *Nothoprocta kalinowskii* (AMNH 169176); *Nothoprocta ornata rostrata* (COL 358a, 358b, 964, 969, 973, 5173, 5243, 5416, 5417, 5655, 6024, 6026, 10872, 12011, 12193, 12194, 12195; MACN 8502, 35871, 42306, 42308, 42311); *Nothoprocta pentlandi pentlandi* (COL 359a, 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; MACN 8148, 9648, 32837, 42310); *Nothoprocta perdicaria perdicaria* (LACMNH 25239, 25240); *Nothoprocta perdicaria sanborni* (COL 364, 3986, 4024, 4026, 4027, 4028, 4029, 4030, 4037, 4043, 4094, 7826, 7828, 7830, 7832, 7833, 7834, 7837; LACMNH 25241, 25242, 25243, 25244, 25245, 25246; MACN 2398, 4312, 4453, 4604, 4605, 4608, 4809); *Nothoprocta taczanowskii* (AMNH 169552). *Nothura boraquira* (AMNH 24001, 240990, 240991, 240995, 241002; COL 11497, 11500, 11498, 11499; LACMNH 26737, 26738, 26739, 31345); *Nothura chacoensis* (MACN 42899); *Nothura darwinii darwinii* (COL 7478, 14550, 14551; MACN 8339, 31516, 35038, 412040); *Nothura darwinii salvadorii* (COL 365, 1727, 1728, 1729, 1808, 2222, 9059, 9496, 9498, 10029, 10432, 10867, 11022, 11025, 11397, 11398, 11399); *Nothura maculosa annectes* (COL 7838, 7839, 8778); *Nothura maculosa maculosa* (COL 364, 1687, 2779, 4889, 4988, 4990, 4991, 5120, 7120, 7151, 15235; LACMNH 28466, 28914; MACN 601a, 6169, 8314, 51469, 52173, 52366, 53027, 53028, 53270, 53480, 142988); *Nothura maculosa nigroguttata* (COL 914); *Nothura maculosa major* (LACMNH 32281, 32283, 32284); *Nothura maculosa pallida* (COL 1497, 1543, 5295, 7965, 10149, 12211); *Nothura maculosa paludivaga* (COL 5515, 5555, 5558, 9984, 9985); *Nothura minor* (AMNH 348095, 348096, 28913). *Taoniscus nanus* (AMNH 237448, 261898; MACN 53007). *Eudromia elegans albida* (COL 5946); *Eudromia elegans elegans* (COL 942, 14459, 14460, 14462, 14469; MACN 471, 9631, 35468, 5325, 52463, 52665, 52141, 53256, 53274); *Eudromia elegans intermedia* (COL 465a, 465b, 465c, 465d, 465e, 965, 975, 5665, 7841, 8415, 8446, 8448, 11119, 11120, 11121, 11122); *Eudromia elegans magnistriata* (COL 7475, 7477, 11780); *Eudromia elegans multiguttata* (COL 966); *Eudromia elegans patagonica* (COL 583a, 583b, 10995, 12036, 12037, 12041, 13117, 13710, 14458, 14461, 14464, 14465, 14466, 14467, 14468, 14470, 14471; LACMNH 54426, 54427); *Eudromia elegans riojana* (COL 10245, 10246, 10247, 10248, 10249, 10250, 11287, 11288, 11289, 11290, 11291, 11292, 11294, 11295, 11296, 11337, 11342, 11343, 11344, 11345, 11346); *Eudromia formosa formosa* (COL 970, 972, 11107, 11108, 12849, 13048; MACN 2497a, 2497b, 32232, 4664, 4693, 8148, 9451, 40240, 40985, 41056, 52831); *Eudromia formosa mira* (MACN 41056). *Tinamotis ingoufi* (COL 8027, 12038, 13303, 13711; MACN 142, 159, 2736, 2773, 29289, 52250, 52296, 52478, 52748); *Tinamotis pentlandi* (COL 698; MACN 33922). *Undescribed species* (MACN 30a, 3101a).

APPENDIX 2

Description of the 80 integumentary characters (Anatomia Topographica Externa) used in the present study. The terminology follows Clark (1993). All characters that could be arranged in a morphological series were coded as additive (characters 2, 3, 7, 12, 13, 22, 23, 25, 33, 34, 45, 61–63, 67, 69, 78, and 79). Sankoff transformation costs were defined for characters 0, 9, 12, 16–18, 20, 22, 25, 28, 30–32, 35, 37, 44, 46–48, 57, and 59.

Caput

Rostrum

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; Fig. 1c); similar (1; Fig. 1b); shorter (2; Fig. 1a).
3. Rostrum mandibulare (lower mandible), ventral plate, lateral grooves: posteriorly convergent and contacting each other (0; Fig. 1d); parallel (1; Fig. 1e); posteriorly divergent (2; Fig. 1f).
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). This is the single character in which *Crypturellus boucardi* and *C. kerriae* differ.

Regio Nasalis

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). Character state 3 applies only to *Apteryx*, which has nostrils at the tip of its elongated bill.

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). Salvadori (1895) first used this trait to define the subfamilies Tinaminae (posessing hallux) and Tinamotidinae (lacking hallux).

Pennae

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

Pterylae

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). We joined the three parts of the dorsum in a single character because feather pattern covaries in these three parts without exception, i.e., they scored the same for all taxa. Therefore, we considered them mutually dependent.
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: bicolored 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). This line runs from the head as a continuation of the eyeline to the base of the neck.
24. Pars cervicalis (lateral neck), ventral light stripe: absent (0); present (1). This line runs ventral and in paralel to the dorsal light stripe of the lateral neck (character 23).
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). Fjelsa and Krabbe (1990:58) noted that in some andean *Nothoprocta* species "the rear of the body has an exceptionally fur-like plumage." We observed that in *Nothoprocta ornata*, *N. kalinowski*, *N. taczanowski*, *N. pentlandii*, and *N. perdicaria* furlike feathers extend up to the chest (state 2). The two species of *Tinamotis* also bear these feathers but restricted to the pars abdominalis and pars venti (state 1).

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). The tail in Tinamidae comprises 10 weak and short feathers hidden under the rump. The genera *Tinamus*, *Nothocercus*, and *Crypturellus* have a distinct tail.

Pteryla alae (wing feathers)

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 pattern: 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); tricolored barred (3); rufous immaculate (4).
60. Pars cruralis (thigh), rounded ocelli: absent (0); present (1).

Podoteca

61. Podoteca lateralis, lateral-tarsi scutes, general aspect on medial view: one row (0); two or three rows (1; Figs. 1i, 1k); more than three rows (2); without longitudinal array (3; Fig. 1m).
62. Podoteca ventralis, plantar-tarsi scutes, number: numerous scutes (0; Fig. 1n); two or three rows of medium-sized scutes (1; Fig. 1j); one row of large scutes (2; Fig. 1l).
63. Podoteca ventralis, plantar-tarsi scutes, surface aspect: relatively smooth (0; Fig. 1l); relatively roughened (1); distinctly rasplike (2; Fig. 1j).
64. Podoteca ventralis (plantar-tarsi scutes), scale pattern: transverse scutes (0; Fig. 1l); reticulate scutes (1; Figs. 1j, 1n). As already noted by Blake (1977), in *Pterocnemia pennata* the plantar surface in the upper tarsus is reticulate, whereas the lower half of the tarsus has transverse scutes. Accordingly, we coded *P. pennata* as having both states.
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; Fig. 1g); base of the third and fourth toe covered by a single scute (1; Fig. 1h).
67. Acropodium, scute number on hind toe: one (0); two (1); three (2); four or five (3). Because *Tinamotis* and *Eudromia* lack a hallux, we scored these taxa as noncomparable.
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. Polymorphisms are indicated as A = {01}, B = {02}, C = {03}, D = {12}, E = {13}, F = {14}, G = {15}, H = {34}, I = {50}, J = {123}, K = {56}.

Apteryx	1100123400	0---------	----------	----------	----------	----------	-301100A0-	----------
Pterocnemia	0111123101	0---------	----------	----------	----------	----------	-301A00-0-	----------
Rhea	0111123101	0---------	----------	----------	----------	----------	-221010-0-	----------
Tm. solitarius	1120100300	1021014100	1001000000	0231000111	1120202210	0131111101	010210021?	0001111100
Tm. major	1120157300	1021010100	1001000000	2231000111	1120202210	0131111101	0102100110	0001111100
Tm. tao	111010K200	1021014110	1001000000	0231010111	1100002210	0011111101	010210021?	??????????
Tm. guttatus	11201??300	1020010100	1000000000	0000000111	1122202210	1011111101	010210014?	??????????
Tm. osgoodi	1110105200	1020012000	0010000000	0001000111	1100001100	0011111000	010210021?	??????????
Nc. bonapartei	1120107300	1010001110	1010010000	2231010101	0022212210	1133333111	1101100312	1001100000
Nc. julius	1120101300	1010000110	1000000010	0001011111	1120202210	1011111111	0101100312	1001100010
Nc. nigrocapillus	112010I300	1010000010	1010010000	0231000111	1120202110	1011111111	110110031?	??????????
C. undulatus	1110107200	1020000110	1000000010	0001010111	1120002210	0021121101	01200001F1	1001111101
C. soui	111012G210	1010000000	0010010000	0000000111	1100001100	0011111000	01200000H2	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. cinereus	1110105220	1010001000	0010010100	0001000111	1100001100	0011111000	012000010?	??????????
C. boucardi	111012L200	1010000000	6010010000	0001000111	1120202260	0011111500	0120000020	1001111101
C. kerriae	111012?200	1010002000	0010010000	0001000111	1120202210	0011111000	0120000020	1001111101
C. cinammomeus	1110107200	1021000100	1030030050	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. berlepschi	1110105220	1010001000	0010010100	0001000111	1100001100	0011111000	022000010?	??????????
C. casiquiare	11101??2?0	1010000000	1010010000	111?010111	1100002210	00?11?1101	012000003?	??????????
C. strigulosus	1110107220	1010001000	0010010000	0001000111	1120002200	0021111000	012000000?	??????????
C. transfaciatus	11101072?0	1021000100	10000000A0	1111010111	1122202210	0021121101	012000002?	??????????
C. ptaritepui	1110121230	1010002000	0010010000	0000000111	1100000000	0011111000	012000114?	??????????
C. brevirostris	11101052?0	1010000000	1010010000	0111010111	1100002210	0021121101	012000001?	??????????
Nt. minor	1101127010	1030110320	2020020020	00011100A1	0A2B2A2220	0??????100	012000113?	??????????
Nt. maculosa	11011230A0	1030110320	2020020020	00011E000A	0022212220	011311110A	0120001330	1110011120
Nt. chacoensis	11011230A0	1030110320	2020020000	00011E0000	0022212220	0113111100	0120001330	1110011120
Nt. boraquira	1101127010	1030110320	2020020020	0001110001	0120202220	0131333100	0120001D3?	??????????
Nt. darwini	1101123000	1030110320	2020020020	00011E0001	0A22212220	011311110A	012000133?	??????????
Np. ornata	31021010A0	1130114230	2000000010	2001210001	0120212130	0133333000	0210001DE0	1110011120
Np. kalinowski	31021??0?0	1120114230	2000000010	2001210001	0121212130	0133333101	0210001D??	??????????
Np. cinerascens	2101155000	1130110220	2000001011	0001141001	01202021J0	0131333100	0210001D10	1110011120
Np. pentlandi	3102103000	1130114220	20000A1001	0001231001	0120202120	0011111010	0110001210	1110011120
Np. perdicaria	3102105000	1130114210	2000000000	0001230001	0110102220	010C303100	0210001230	1110011120
Np. taczanowski	3102103000	1130114220	2000011011	0000211001	0022212220	0133333101	021000133?	??????????
Np. 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	012B212141	01EE333101	0300111-1?	??????????
R. r. pallescens	100-005010	1000110030	3010010010	2031040002	2212322230	0103003303	02001113E0	1110011120
R. r. macullicollis	100-005010	1000110330	3020020010	2201040022	2211322230	0100300303	0200111310	1110011120
R. r. rufescens	100-005010	1000111030	3010010000	0031040022	2212322230	0103003303	02001113E0	1110011120
T. tinapentlandi	2101123001	1002110340	4022120030	2223110001	0120212140	0131333104	0200111-F?	????011120
T. inagoufi	2101144011	1002113351	5122120022	2223110022	2212112251	0133333104	0200111-1?	??????????
Tc. nanus	1101127010	1030110320	2000000010	0001110011	11000022D0	0022222100	0120001130	1?10011120
New species	1101123010	1020113120	20000B0040	3351130011	1122212220	0131??1401	012000130?	?1????????

Appendix 4

List of unambiguous synapomorphies, based on 36 optimal trees. Groups are listed with the root placed at *Nothocercus* (Fig. 4). Direction of changes are indicated by arrows. Double arrows indicate cases in which direction of change depends on whether the root is placed at *Nothocercus* or at *Tinamus osgoodi*.

Tinamidae

All trees.—Color of mandible (6): brownish (3) → grayish (5); Feather structure (10): absent (0) → present (1); Lateral-tarsi scutes (61): more than three rows (2) or without longitudinal array (3) → two or three rows (1).

Some trees.—Color of maxilla (5): brownish (2) → blackish (0).

Tinamidae (Except *Tinamus osgoodi)*

All trees.—Plantar-tarsi scutes (62): numerous (0) ↔ large (2); Plantar-tarsi scutes (63): roughened (1) ↔ smooth (0).

Nothocercus

All trees.—Crown + nape (12): bicolored barred (2) → immaculate (1); Flanks, ocelli (58): absent (0) → present (1); Hind toe, number of scutes (67): two (1) or three (2) → four or five (3).

Some trees.—Auricular stripe (15): present (1) → absent (0); Pattern of dorsum, natal plumage (69): brown or straight (0) → barret with black (2); Postorbital line, natal plumage (75): present (1) → absent (0); Malar line, natal plumage (76): present (1) → absent (0); Auricular line, natal plumage (77): present (1) → absent (0).

Nothocercus bonapartei + N. nigrocapillus

All trees.—Lateral neck (22): bicolored barred (0) → immaculate (1); Ventral neck (25): bicolored barred (0) → immaculate (1); Thigh, ocelli (60): absent (0) → present (1).

Some trees.—Abdomen (31): brownish or rufous immaculate (0) → bicolored barred (2); Belly (32): brownish immaculate (0) → bicolored barred (3).

Tinamus solitarius + T. major + T. tao

All trees.—Eyebrow + postocular eyeline (13): absent (0) → slightly marked (1); Lateral neck, dorsal light stripe (23): absent (0) → present (1).

Some trees.—Abdomen (31): brownish or rufous immaculate (0) → bicolored barred (2); Belly (32): brownish immaculate (0) → bicolored barred (3).

*Nothocercus + Tinamus (*Except *T. osgoodi)*

All trees.—Median underwing coverts (55): whitish immaculate (2) ↔ brownish immaculate (1); Plantar-tarsi scutes (62): large (1) ↔ numerous (0); Plantar-tarsi scutes (63): smooth (0) ↔ roughened (1) or rasplike (2); Plantar-tarsi scutes (64): transverse pattern (0) ↔ reticulate (1).

Some trees.—Maxilla, relative length of proximal versus distal plate (2): similar (1) ↔ shorter (2); Nostrils (7): medial (1) ↔ anterior (3); Median underprimary coverts (52): whitish immaculate (2) ↔ brownish immaculate (1).

*Crypturellus (*Except *C. undulatus) + Tinamus osgoodi*

All trees.—Color of tarsi (68): pinkish to reddish (2) ↔ grayish (1) or greenish to olive (4).

Some trees.—Dorsal collar (18): immaculate (0) ↔ bicolored barred (1).

Crypturellus cinnamomeus + C. transfasciatus

All trees.—Eyebrow + postocular eyeline (13): absent (0) → slightly marked (1); Belly (32): brownish immaculate (0) → whitish immaculate (1); Inner vane of outer secondary remiges (43): brownish immaculate (0) → bicolored barred (2).

*Crypturellus (*Except *C. undulatus, C. cinnamomeus, C. transfasciatus) + Tinamus osgoodi*

All trees.—Crown + nape (12): immaculate (1) ↔ bicolored barred (2); Dorsal neck (17): immaculate (0) ↔ bicolored barred (1); Lateral neck (22): immaculate (1) ↔ bicolored barred (0); Ventral neck (25): immaculate (1) ↔ bicolored barred (0).

Some trees.—Outer vane of inner secondary remiges (44): brownish immaculte (0) ↔ bicolored barred (2).

Crypturellus duidae+ C. erythropus + C. noctivagus + C. variegatus + C. casiquiare + C. brevirostris + C. bartletti

All trees.—Lateral-tarsi scutes (61): two or three rows (1) → 1 row (2).

Crypturellus erythropus + C. noctivagus + C. variegatus + C. casiquiare + C. brevirostris + C. bartletti

All trees.—Color of mandible (6): yellowish (7) → horn (6).

Crypturellus noctivagus + C. variegatus + C. casiquiare + C. brevirostris + C. bartletti

All trees.—Abdomen (31): brownish or rufous immaculate (0) → whitish immaculate (1); Belly (32): brownish immaculate (0) → whitish immaculate (1); Color of tarsi (68): pinkish to reddish (2) → yellowish (3).

Crypturellus casiquiare + C. brevirostris + C. bartletti

All trees.—Outer vane of outer secondary remiges (42): bicolored barred (2) → brownish immaculate (0); Lateral-tarsi scutes (61): one row (2) → two or three rows (1); Scute number on hind toe (67): two (1) → one (0).

Crypturellus brevirostris + C. bartletti

All trees.—Color of tarsi (68): yellowish (3) → grayish (1).

Crypturellus atrocapillus + C. strigulosus + C. boucardi + C. kerriae + C. soui + C. ptaritepui + C. berlepschi + C. cinereus + C. obsoletus + C. tataupa + C. parvirostris + Tinamus osgoodi

All trees.—Flank, upper side (35): immaculate (0) ↔ bicolored barred (1). Some trees: Chin (16): brownish-rufous immaculate (1) ↔ whitish immaculate (0).

Crypturellus strigulosus + C. boucardi + C. kerriae + C. soui + C. ptaritepui + C. berlepschi + C. cinereus + C. obsoletus + C. tataupa + C. parvirostris + Tinamus osgoodi

All trees.—Dorsum + mantle + rump (20): immaculate (0) ↔ bicolored barred (1); Median underwing coverts (55): brownish immaculate (1) ↔ whitish immaculate (2); Flank, lower side (57): immaculate (0)

↔ bicolored barred (1); Thigh (59): brownish immaculate (0) ↔ bicolored barred (1).

Crypturellus boucardi + C. kerriae

All trees.—Outer vane of inner secondary remiges (44): brownish immaculate (0) → bicolored barred (2).

Some trees.—Color of maxilla (5): blackish (0) → brownish (2).

Crypturellus soui + C. ptaritepui + C. berlepschi + C. cinereus + C. obsoletus + C. tataupa + C. parvirostris + Tinamus osgoodi

All trees.—Color of mandible (6): grayish (5) ↔ yellowish (7); Outer vane of outer secondary remiges (42): brownish immaculate (0) ↔ bicolored barred (2); Outer vane of greater primary coverts (46): brownish immaculate (1) ↔ bicolored barred (2); Inner vane of greater primary coverts (47): brownish immaculate (1) ↔ bicolored barred (2).

Some trees.—Scute number on hind toe (67): two (1) ↔ one (0); Color of tarsi (68): greenish to olive (4) ↔ pinkish to reddish (2); Pattern of dorsum, natal plumage (69): lightly barred (1) ↔ brown or straight (0).

Crypturellus berlepschi + C. cinereus

All trees.—Throat, white rachis (27): absent (0) → present (1).

Some trees.—Color of maxilla (5): brownish (2) → blackish (0); Color of iris (8): brownish (2) → reddish (2); Chin (16): grayish immaculate (2) → brownish-rufous immaculate (1).

Crypturellus obsoletus + C. tataupa + C. parvirostris

All trees.—Belly (32): brownish immaculate (0) → scalloped (4); Undertail coverts (33): immaculate (0) or bicolored barred (1) → scalloped (2); Flank, lower side (57): immaculated (0) → scalloped (2); Thigh (59): brownish immaculate (0) → scalloped (2).

Crypturellus tataupa + C. parvirostris

All trees.—Mandible, lateral grooves of ventral plate (3): convergent (0) → parallel (1); Color of maxilla (5): brownish (0) → reddish (3); Color of mandible (6): grayish (5) → pinkish to reddish (2); Lateral-tarsi scutes (61): two or three rows (1) → one row (0).

Some trees.—Chin (16): grayish immaculate (2) → whitish immaculate (0); Color of tarsi (68): greenish to olive (4) → pinkish to reddish (2).

Steppe Tinamous

All trees.—Maxilla, relative length of proximal versus distal plate (2): similar (1) → longer (0); Mandible, lateral grooves of ventral plate (3): convergent (0) → parallel (1); Color of maxilla (5): blackish (0) → brownish (2); Nostrils (7): medial (1) → posterior (0); Color of iris (8): brownish (0) → yellowish (1); Moustachial stripe (14): absent (0) → present (1); Dorsal collar (18): bicolored barred (1) → *Nothura*-like pattern (2); Dorsum + mantle + rump (20): bicolored barred (1) → *Nothura*-like pattern (2); Chest + belly + undertail coverts, furlike aspect (34): absent (0) → present in belly (1); Tail (37): poorly developed (1) → rudimentary (0); Lesser and median dorsal secondary coverts (48): bicolored barred (1) → *Nothura*-like pattern (2); Dorsal-tarsi scutes (66): separate scutes covering digits III and IV (0) → a single scute covering both digits (1); Rachis and aftershaft of dorsal feathers, natal plumage (71): rudimentary (0) → developed (1).

Some trees.—Auricular stripe (15): absent (0) → present (1).

Steppe Tinamous (Except the New Species)

All trees.—Crown + nape (12): bicolored barred (2) → *Nothura*-like pattern (3); Dorsal neck (17): bicolored barred (1) → streaked (3); Thigh (59): bicolored barred (1) → brownish immaculate (0).

Steppe Tinamous (Except the New Species and *Taoniscus nanus)*

All trees.—Lateral neck (22): bicolored barred (0) → streaked (2); Ventral neck (25): bicolored barred (0) → streaked (2); Outer vane of bastard wing (38): brownish immaculate (1) → bicolored barred (0); Outer vane of primary remiges (40): brownish immaculate (1) → bicolored barred (0); Median secondary underwing coverts (55): whitish immaculate (2) → bicolored barred (3).

Nothura minor + N. boraquira

All trees.—Breast (28): immaculate (0) or bicolored barred (1) → streaked (2).

Nothura chacoensis + N. maculosa + N. darwinii + Nothoprocta + Rhynchotus + Tinamotis + Eudromia

All trees.—Color of mandible (6): yellowish (7) → brownish (3); Color of iris (8): yellowish (1) → brownish (0); Inner vane of outer secondary remiges (43): brownish immaculate (0) → bicolored barred (2); Inner vane of inner secondary remiges (45): immaculate (0) → bicolored barred (1); Greater underprimary coverts (53): brownish immaculate (1) → bicolored barred (3); Scute number of hind toe (67): two (1) or three (2) → four or five (3).

Nothura chacoensis + N. maculosa + N. darwinii

All trees.—Inner vane of primary remiges (41): brownish immaculate (1) → bicolored barred (0); Median underwing primary coverts (52): bicolored barred (3) → brownish immaculate (1); Median underwing secondary coverts (55): bicolored barred (3) → brownish immaculate (1).

Nothura maculosa + N. darwinii

All trees.—Breast (28): immaculate (0) → streaked (2).

Nothoprocta + Rhynchotus + Tinamotis + Eudromia

All trees.—Color of maxilla (5): brownish (2) → blackish (0); Lateral-tarsi scutes (61): two or three rows (1) → more than three rows (2); Plantar-tarsi scutes (62): large (2) → medium-sized (1).

Nothoprocta

All trees.—Bill shape (0): slightly decurved (1) → strongly decurved (3); Mandible, lateral grooves of ventral plate (3): parallel (1) → divergent (2); Occipital feathers (11): indistinct (0) → forming a crest (1); Chin (16): whitish immaculate (0) → bicolored barred (4); Dorsal neck (17): streaked (3) → *Nothura*-like pattern (2); Lateral neck (22): streaked (2) → bicolored barred (0); Ventral neck (25): streaked (2) → immaculate (1); Chest + belly + undertail coverts, furlike aspect (34): belly (1) → chest to belly (2).

*Nothoprocta (*Except *N. taczanowskii)*

All trees.—Ventral neck (25): immaculate (1) → bicolored barred (0); Inner vane of outer secondary remiges (43): bicolored barred (2) → brownish immaculate (0); Scute number on hind toe (67): four or five (3) → three (2).

Nothoprocta ornata + N. kalinowskii

All trees.—Dorsal collar (18): Nothura-like pattern (2) → tricolored barred (3); Breast (30): brownish or rufous immaculate (0) → bicolored barred (2); Lesser and median dorsal secundary coverts (48): *Nothura*-like pattern (2) → tricolored barred (3).

Nothoprocta pentlandi + N. cinerascens + N. perdicaria + N. curvirostris

All trees.—Flank, upper side (35): bicolored barred (1) → *Nothura*-like pattern (3); Inner vane of inner secondary remiges (45): bicolored barred (1) → immaculate (0).

Nothoprocta pentlandi + N. cinerascens

All trees.—Throat, rounded ocelli (26): absent (0) → present (1); Ventral collar, ocelli (29): absent (0) → light spots (1); Flank, upper side, rounded ocelli (36): absent (0) → present (1); Color of tarsi (68): yellowish (3) → grayish (1).

Nothoprocta perdicaria + N. curvirostris

All trees.—Median underprimary coverts (52): bicolored barred (3) → rufous immaculate (0); Median underwing coverts (55): bicolored barred (3) → rufous immaculate (0).

Rhynchotus + Tinamotis + Eudromia

All trees.—Crown + nape (12): *Nothura*-like pattern (3) → streaked (0); Breast (30): brownish or rufous immaculate (0) → bicolored barred (2); Plantar-tarsi scutes (62): medium-sized (1) → numerous (0); Plantar-tarsi scutes (64): transverse pattern (0) → reticulate pattern (1); Dorsal-tarsi scutes (65): juxtaposed (0) → imbricated (1); Color of tarsi (68): yellowish (3) → grayish (1).

Rhynchotus

All trees.—Maxilla, lateral grooves of dorsal plate(1): present (1) → absent (0); Mandible, lateral grooves of ventral plate (4): present (1) → absent (0); Color of mandible (6): brownish (3) → grayish (5); Color of iris (8): brownish (0) → yellowish (1); Flank, upper side (35): bicolored barred (1) → tricolored barred (4); Inner vane of bastad wing (39): brownish immaculate (1) → rufous immaculate (2); Outer vane of primary remiges (40): bicolored barred (0) → rufous immaculate (2); Inner vane of primary remiges (41): brownish immaculate (1) → rufous immaculate (2); Outer vane of outer secondary remiges (42): bicolored barred (2) → rufous immaculate (1); Outer vane of inner secondary remiges (44): bicolored barred (2) → tricolored barred (3); Inner vane of inner secondary remiges (45): bicolored barred (1) → tricolored barred (2); Median underprimary coverts (52): bicolored barred (3) → rufous immaculate (0); Median underwing coverts (55): bicolored barred (3) → rufous immaculate (0); Flank, lower side (57): bicolored barred (1) → tricolored barred (3); Thigh (59): bicolored barred (1) → tricolored barred (3).

Rhynchotus r. pallescens + R. r. rufescens

All trees.—Dorsal neck (17): streaked (3) → immaculate (0); Lateral neck (22): streaked (2) → immaculate (1); Ventral neck (25): streaked (2) → immaculate (1); Belly (32): brownish immaculate (0) → bicolored barred (3); Lesser underwing coverts (54): bicolored barred (3) → rufous immaculate (0).

Tinamotis + Eudromia

All trees.—Bill shape (0): slightly decurved (1) → decurved toward tip (2); Hallux (9): present (0) → absent (1); Eyebrow + postocular eyeline (13): absent (0) → strongly marked and white (2); Dorsal collar (18): bicolored barred (1), *Nothura*-like pattern (2), or tricolored barred (3) → mixed pattern (4); Dorsum + mantle + rump (20): bicolored barred (1), *Nothura*-like pattern (2), or tricolored barred (3) → mixed pattern (4); Lateral neck, dorsal stripe (23): absent (0) → strongly marked (2); Breast (28): bicolored barred (1) → mixed pattern (3); Lesser and median dorsal secondary coverts (48): bicolored barred (1), *Nothura*-like pattern (2), or tricolored barred (3) → mixed pattern (4).

Tinamotis

All trees.—Lateral neck, ventral stripe (24): absent (0) → present (1); Abdomen (31): brownish or rufous immaculate (0) → bicolored barred (2); Belly (32): brownish immaculate (0) → rufous immaculate (2); Undertail coverts (33): bicolored barred (1) → rufous immaculate (3); Thigh (59): bicolored barred (1) → rufous immaculate (4).

Eudromia

All trees.—Color of mandible (6): brownish (3) → blackish (0); Occipital feathers (11): indistinct (0) → long and filamentous (2); Lateral-tarsi scutes (61): → more than three (2) → without longitudinal array (3).

Eudromia e. elegans + E. e. albida

All trees.—Inner vane of bastard wing (39): brownish immaculate (1) → bicolored barred (0); Inner vane of primary remiges (41): brownish immaculate (1) → bicolored barred (0).