

Advances on tinamou phylogeny: an assembled cladistic study of the volant palaeognathous birds

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Abstract

Tinamous are volant terrestrial birds, endemic to the Neotropics. Here, an inclusive phenotype-based phylogenetic study of the interrelationships among all extinct and living species of tinamous is conducted. In this cladistic analysis, results are compared between main character subsets and with previous molecular studies. Special attention is paid to character definition and scoring of integumentary and behavioural characters: transformation costs are applied to analyse egg coloration and plumage characters—on the basis of pigment composition and overlap of pigmentation patterns respectively—in the context of generalized (Sankoff) parsimony. Cladistic analysis recovers the traditional subdivision between those tinamous specialized for open areas (Nothurinae) and those inhabiting forested environments (Tinaminae) and support the monophyly of recognized genera. The present study demonstrates that morphological analysis yields highly congruent results when compared with previous molecular studies; thus, it provides morphological synapomorphies for clades that have been proposed by these molecular analyses. The placement of the fossil species within the open-area (Nothurinae) and the forest-dwelling (Tinaminae) tinamous is also consistent with the palaeoenvironmental conditions inferred from the associated flora and fauna.

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Tinamous include 47 ground-dwelling extant species whose habitats range from open grasslands to dense humid forest in the Neotropics (Gill and Donsker, 2015). The South American fossil record of the group is scant and goes back some 17 million years ago (Tonni, 1977; Tambussi and Tonni, 1985; Tambussi, 1987, 1989; Chiappe, 1991; Tambussi et al., 1993; Tambussi and Noriega, 1996; Bertelli and Chiappe, 2005; Picasso and Degrange, 2009; Chandler, 2012; Bertelli et al., 2014). While the monophyly of Tinamidae and their placement within Palaeognathae have been consistently accepted (Cracraft, 1974; Lee et al., 1997; Livezey and Zusi, 2007; Hackett et al., 2008; Harshman et al., 2008; Bourdon et al., 2009; Haddrath and Baker, 2012; Worthy and Scofield, 2012; Smith et al., 2013; Jarvis et al., 2014; Mitchell et al., 2014), the phylogenetic interrelationships of tinamous are still under investigation (Bertelli et al., 2002, 2014;

Porzecanski, 2003; Bertelli and Chiappe, 2005; Bertelli and Giannini, 2013). The first study of the phylogenetic interrelationships of tinamous based on external morphological characters (e.g. adult and natal plumage, ramphoteca and podoteca) was conducted by Bertelli et al. (2002). A recent re-evaluation of this external morphology-based study (Bertelli and Giannini, 2013) produced a hypothesis supporting the monophyly of the open-area tinamous, Nothurinae (*Taoniscus*, *Nothura*, *Nothoprocta*, *Rhynchotus*, *Eudromia* and *Tinamotis*), but highlighting the paraphyly of the forest tinamous, Tinaminae (*Tinamus*, *Crypturellus* and *Nothocercus*). However, a molecular study by Porzecanski (2003) using mitochondrial cytochrome *b* and nuclear RAG-2 sequences supported the monophyly of Nothurinae and Tinaminae and similar results were obtained by a recent analysis based on osteological and myological characters (Bertelli et al., 2014).

To test previously proposed hypotheses and produce a more robust reconstruction of the phylogenetic interrelationships of Tinamidae, I carried out a

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comprehensive ingroup analysis of all extant and fossil tinamous. The present study is based on a combination of several available sources of information (external and internal morphological characters), and characters of behaviour and reproduction. Most phylogenetic studies of birds that are based on morphology have almost exclusively included characters of internal anatomy (osteology and myology), while integumentary and behavioural characters have been considered as reliable only for the alpha taxonomy of birds (Sibley and Ahlquist, 1990). Moreover, even the use of morphological characters has been questioned for phylogenetic reconstruction in ornithology (Sibley and Ahlquist, 1990; Hedges, 1994; Hedges and Sibley, 1994; Johnson and Clayton, 2000a,b; Cooper et al., 2001; Johansson and Ericson, 2004; Ohlson et al., 2008). The relative importance of several types of morphological–behavioural evidence for inferring the phylogeny of the Tinamidae as well as the congruence of results from separate morphological and molecular (Porzecanski, 2003) analyses are also reported here. Special attention is paid to character definition and scoring of characters for phylogenetic reconstruction. Some of these are multistate pigmentation characters in which several conditions are related in complex form (e.g. plumage patterns, egg colours), and scheme transformation costs between states are applied (Sankoff characters). The use of generalized (Sankoff) parsimony and the consequences of applying transformation costs to multistate characters with complex costs among character states in phylogenetic analysis is evaluated by comparing the results derived from alternative methods with characters under generalized parsimony and without Sankoff matrices.

Material and methods

Characters

The dataset of the present phylogenetic analysis comprised 249 characters from the integument, osteology, myology, behaviour and breeding (Appendices 1, S1 and S2). The main subset of morphological information was composed of 113 cranial and postcranial characters used in Bertelli et al. (2014). In that paper, 40 myological characters of the cranial and appendicular musculature of tinamous were also provided. Osteological and myological characters consisted of observed variations in cranial and appendicular structures (shape, relative development, presence/absence, etc.) of both fossil and extant tinamous. However, several characters described only the presence/absence of a single condition and did not include the morphological variation enclosed in the alternative states. Thus, the information of some osteological and myological

characters was further described or modified in some cases, as detailed in Appendix S2. New character scorings for two tinamou species, *Tinamus osgoodi* and *Crypturellus atrocapillus*, were also incorporated in the current analysis. Additionally, the 74 integumentary characters contributed by Bertelli et al. (2002, see also Bertelli and Giannini, 2013) were incorporated into the morphological dataset used here. This information was further re-scored, expanded or modified (mainly the definition of character states, see comments on Appendix S2), and new scorings of an expanded outgroup taxon sampling were obtained from museum specimens.

The external morphological characters included shape and colours of the ramphoteca (horny sheath of bill), podoteca (horny scales of legs), and natal and adult plumage. For plumage character definition, the body of the bird was divided into standard topological areas (pterylae) following Clark (1993) and most characters described feather pigmentation patterns from different pterylae (feather tracts). Also, some plumage features that did not fit in this scheme were coded separately. For example, this applied to characters such as the presence of ocelli (characters 184, 186, 191, 194, 201, 214, 223 and 225), pennaceous structure of feathers (character 175), a conspicuous white rachis in the throat feathers of some *Crypturellus* species (character 192), development of rectrices (tail, character 202), and the fur-like aspect in feathers of *Nothoprocta* and *Tinamotis* (character 199). Some integumentary characters were coded to cover most of the external features seen in the group, including iris colours and absence or presence of digit I (Bertelli et al., 2002). In addition, four new structural integumentary characters were incorporated into the present analysis (e.g. development of after shaft, contour feathers around eyes modified into ‘eyelashes’, filoplumes and scale pattern of dorsal surface of tarsus; characters 245–248).

Finally, 12 new behavioural and breeding characters (songs, nidification, etc.) were added to the matrix (see characters 0–11 in Supplementary Appendices S1 and S2). Ethological characters were mainly based on the acoustic structure of songs, defined by quantitative (maximum and minimum frequency, range, etc.) and qualitative variables (syntactic structure, acoustics, modulation, etc.) that characterized each type of vocalization (Irwin, 1996; Bertelli and Tubaro, 2002). Contrary to learning capabilities and patterned song variations of derived birds (e.g. Passeriformes, Psittaciformes, Trochilidae, Rhamphastidae; Baptista, 1996; Catchpole and Slater, 2008), vocal learning is believed to be absent in basal neornithines such as tinamous (Kroodsma and Miller, 1996; McCracken and Sheldon, 1997). Moreover, vocal variation has been used to establish species limits in some tinamou species (Maijer, 1996; Laverde-R and Cadena, 2014).

According to Straneck (1990) and Hardy et al. (1993), the songs of most tinamou species are uniform across their geographical distributions. However, more recent studies on some species (e.g. *Rhynchotus rufescens*, *Crypturellus erythropus*, *Crypturellus obsoletus*) have described forms with distinctive vocalizations (Maijer, 1996; Laverde-R and Cadena, 2014).

Character coding. In the present analysis, quantitative variation observed across vocalizations was coded into states separated by gaps in some cases (e.g. number of notes; character 4). However, most quantitative continuous characters representing different values of song frequencies (Bertelli and Tubaro, 2002) were analysed using the approach of Goloboff et al. (2006), where each state is the actual numerical value observed in the species and the transformation costs are the numerical differences between these values. Continuous characters were standardized so that the full range of variation was equivalent to one step in a discrete character (see Goloboff et al., 2006). Reproductive and breeding characters (genitalia, oology, incubation) included phalli types (character 8), colours (character 9), shell variations (character 10) and incubation of eggs (character 11). Full character descriptions are provided in Appendix S2.

Most of the morphological and behavioural characters were binary, but other characters were defined with up to seven states (e.g. egg colours). In some multistate characters in which the costs of transforming from one state to another were considered different, character ordering did not conform to a lineal structure, but to a branched one (e.g. some myological and osteological characters, see Appendix S2). In those cases, the variation was re-coded into two or more characters, such that the costs between the transformations expressed the magnitudes of the observed differences (using non-redundant linear coding).

In more complex cases, step matrices were applied, in which the cost of transformation between any two states is represented as a function of the observed similarity between states. The criterion used here to determine the relative transformation costs is purely observational and does not involve evolutionary assumptions. In the step matrix, the transformations that are less costly are favoured and occur between most similar states. Other pathways are penalized but not prohibited. In this way the transformations between similar states have a lower cost than those between radically different states, which it is in agreement with the observations in the case of linear ordered characters. This approach was previously applied to the study of plumage characters (overlap of pigmentation patterns) (Bertelli et al., 2002). In tinamous, variation in plumage design is more important

than variations in colour: because different plumage patterns were more clearly recognizable than subtly graduated colour tonalities. Thus, scored variation of adult plumage characters was based mainly on the predominant design of individual feathers from each body area. 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 tinamus, so new states were added as necessary, and the states were ordered such that a Sankoff matrix of character transformation was defined (Fig. 1a).

These criteria were also applied to egg colours. Contrary to the widely distributed whitish condition of the outgroup eggshells, variation in colour was important in tinamous and included several clearly recognizable patterns that differed from species to species (Oates, 1901; Walters, 2006). Egg colours in tinamous were grouped into five main conditions (see Appendix 1, character 6). The two pigments responsible for avian egg colours are protoporphyrin and cyaninic biliverdin IX α with its zinc chelate (Kilner, 2006). Thus, two main types of egg colours were identified in tinamous based on the predominant pigment: “porphyrinic” or “cyaninic” colours (Kilner, 2006). The first included chocolates, brownish, pinkish and reddish colours, whose predominant pigment was the protoporphyrin; the second main type grouped the bluish and greenish colours derived from the biliverdin IX α (Kilner, 2006). To reflect the relative degrees of similarity between the observed conditions, transformation costs were assigned between main colours. Changes between most similar colours based on the type of predominant pigment (cyanines or porphyrines) were less costly. Bertelli (2004) discussed the use of these criteria in the study of tinamou egg colours, but its application is re-defined and scored here in the context of a comprehensive phylogenetic analysis. Thus, all varieties of porphyrinic (brownish-chocolates, pinkish-reddish) or cyaninic (bluish, greenish) colours were considered non-additive among themselves; purple–violet colours were interpreted as having both pigment types and placed at the centre in the character state tree shown in Fig. 2a.

In the Sankoff parsimony analysis, characters without complex transformation costs were given an *a priori* weight of 2 relative to characters with step matrices to compensate for effects of complex coding with relative transformation costs (e.g. some characters with more than six alternative conditions).

Several cases of non-comparability are indicated also in Appendix S2, and this was particularly important for the outgroup. For example, some osteological or myological elements are absent or fused in outgroup

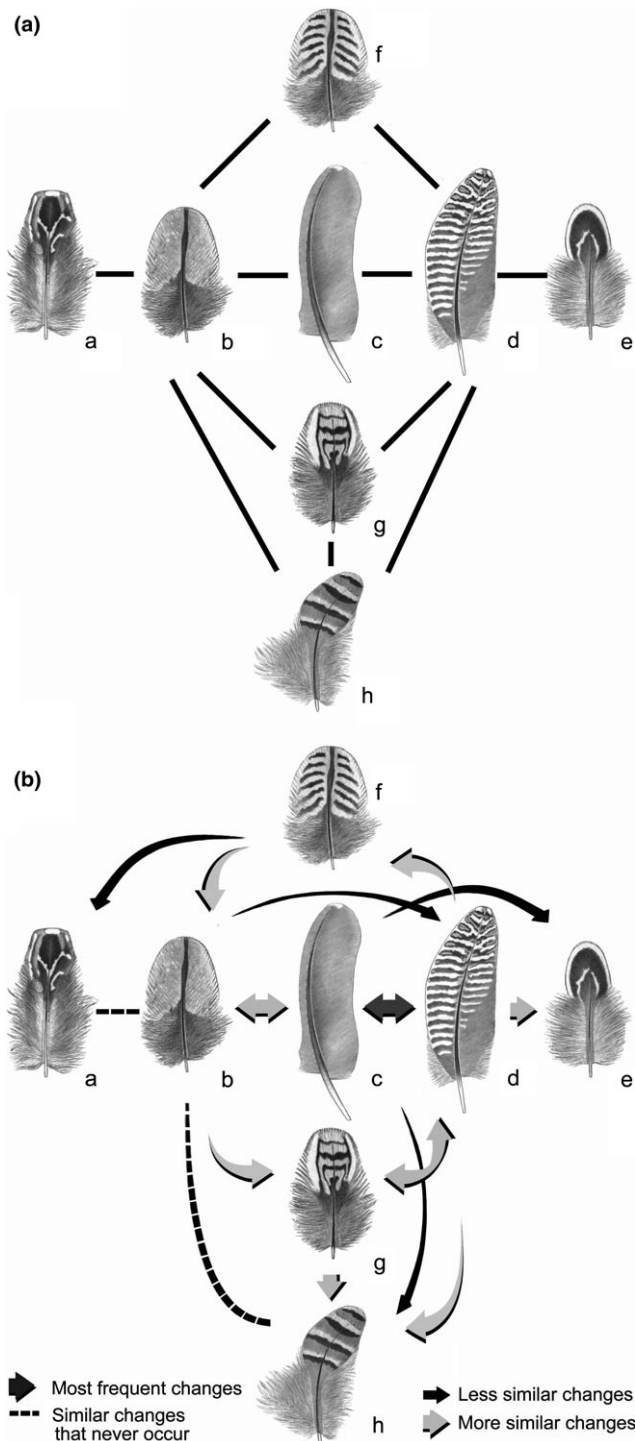


Fig. 1. (a) Transformations among states in adult plumage characters with step matrices. Each direct connection represents one step between two states. (b) State transformations of plumage characters implied by the alternative unordered analysis.

taxa, obscuring assessment of homologous conditions. Ratite plumage lacks pennaceous structure and also lacks apteria, making the primary homology of feather

pigmentation patterns uncertain (Bertelli et al., 2002). Although Galloanseres have plumage segregated into pterylae, it is uncertain whether a given plumage pattern observed in these outgroup taxa corresponds to the same condition in tinamou. For this reason, plumage characters were considered not comparable for all outgroup taxa and only integumentary characters of the ramphotheca and podotheca were scored in those terminals. Similar undetermined conditions for outgroup terminals are scored in the case of song characters; due to the substantially different acoustic structure of vocalizations in outgroup taxa, song variables could not be comparable between tinamou and outgroup taxa, and therefore these conditions were also coded as missing (see Appendix S1).

Non-comparable states were also applied for the ingroup in adult-plumage characters that described feather designs in different pterylae of the dark tinamou species (*Tinamus osgoodi*, *Crypturellus berlepschi* and *C. cinereus*). Bertelli and Giannini (2013) suggested that dark coloration of these species may represent a form of melanistic pattern in which many pterylae are affected at once (no design or pattern can be distinguishable), violating the presumed independence of characters and therefore these characters were coded as missing in these species. All remaining cases of missing entries (e.g. lack of data) are indicated explicitly in Appendix S1 for each character presenting such states.

Intraspecific variation was coded as polymorphism and this was the case of subspecies differing in some character states. However, both morphological and behavioural conditions have been actually constant in tinamou species. Only a few species have been coded as polymorphic (< 1% of the ingroup); some species of the genera *Nothura* (e.g. *N. maculosa*) and *Nothoprocta* (*N. cinerascens*) showed the higher proportion of polymorphic conditions of the ingroup (< 3% of the characters). Also sexual dimorphism was present in a few tinamou species (*Crypturellus boucardi*, *C. cinnamomeus* and *C. erythropus*). These conditions were treated by adding an extra state to some adult plumage characters, which describe the presence of more than a single state for the given character, depending on sex. Consequently, the presence of general sexual dimorphism is scored as another character state for the dimorphic *Crypturellus* species (see Appendix S1, characters 185, 187, 190, 193, 213 and 222).

Cases of repeated scoring of characters were avoided in conditions that show obvious dependence by taking some conservative decisions about character numbers and coding. For example, some integumentary characters of the bill based upon segmentation of the ramphotheca, shape, and position of nares (characters 0–4 of Bertelli et al., 2002) and the digitus pedis I (character 9 of Bertelli et al., 2002) show the same character

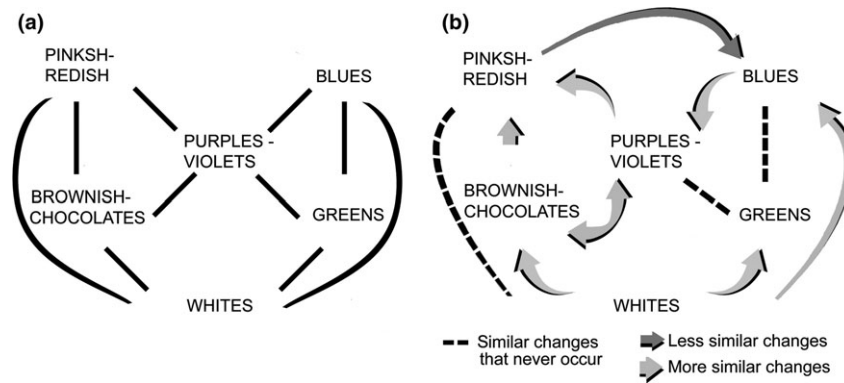


Fig. 2. (a) Transformations among character states in egg coloration. Each direct connection represents one step between two states. (b) State transformations of egg coloration characters implied by the alternative unordered analysis.

state distributions within each species as the corresponding osteological elements (characters 36, 37, 39 and 116 of Bertelli et al., 2014). Thus, integumentary and osteological characters of digit I and bill are considered correlated and the observed variations were coded jointly in characters that refer to the hallux (character 170) and both internal (mandibula) and external (ramphoteca) anatomical conditions of the bill (characters 165–169, see *Partes corporis* in Appendix S2). This was also the case of the adult plumage pattern of the dorsum, for which all principal feather tracts (pterialia scapulohumeralis and pars spinalis and pars pelvica of pterilia dorsalis) showed the same character states within each species. Thus, three pterilia sections were coded jointly in the integumentary characters 185 and 186. Another example is the presence of a fur-like feather aspect in chest, belly and under tail coverts, and therefore all feather tracts pars sternalis, pars abdominalis and pars ventis are coded together in the character 199.

Taxa

All currently recognized extant and extinct representatives of Tinamidae were included in this analysis (Appendix S1). Species status may be controversial in some forms. Ward (1957) reviewed the history of species number in the family, which varied (in different periods) from 33 to 73. As Ward stated, ‘these discrepancies may often be attributed to various interpretations of species definition by different authors in different periods of time’. As many as 140 subspecies have been described (Ward, 1957). More recently, Gill and Donsker (2015) recognized 47 tinamou species while Remsen et al. (2015) identified 45 extant forms. Nevertheless, for the reconstruction of the higher tinamou relationships, each terminal that could be scored unambiguously in the context of the present study was included and thus all main forms are represented. Within species, usually the nominate subspecies was

included plus forms in some taxa that scored distinctly in some integumentary and behavioural characters. For instance, three forms of *Rhynchotus*, formerly treated as either different species (Maijer, 1996; Gill and Donsker, 2015; Remsen et al., 2015) or as subspecies (Peters, 1931; Blake, 1977, 1979), two subspecies of *Nothoprocta ornata* (*kalinowskii* and *ornata*) (Blake, 1977; Fjelså and Krabbe, 1990; Gill and Donsker, 2015; Remsen et al., 2015), and two of the seven known forms of *Eudromia elegans* (*E. e. elegans* and *E. e. albida*) (Olrog, 1959; Navas and Bo, 1981) are represented as terminals. This was also the case of the oldest extinct tinamous (Bertelli and Chiappe, 2005; Bertelli et al., 2014) that have been scored as four different terminals based on differences between the character-states coded for the fossil tinamous. The fossil tinamous included were the extinct species *Eudromia olsoni*, *Eudromia* sp., *Nothura parvula*, *Nothura* sp., *Crypturellus reai*, and the early Miocene fossils MACN-SC-T, MACN-SC-H, MACN-SC-3610 and MACN-SC-3613. The final matrix therefore included 60 ingroup terminals comprising all extinct (nine fossil terminals) and living (47 species rank forms after Gill and Donsker, 2015) recognized tinamou taxa (see Appendix S1).

Outgroup comparisons were made with members of Palaeognathae: *Apteryx australis*, *Rhea americana* and the fossil *Lithornis*. Codings from two species of *Lithornis* (*L. celetius* and *L. vulturinus*) were combined to form a single supraspecific terminal (*Lithornis*) representing Lithornithidae. Additionally, galliform (*Megapodius flavirostris*, *Ortalis canicollis*, *Odontophorus capueira*) and anseriform (*Chauna torquata*, *Mergus serrator*, *Anas flavirostris*) taxa were added to the taxonomic sample because these birds are widely accepted as early divergences of Neognathae (e.g. Ericson et al., 2006; Livezey and Zusi, 2007; Hackett et al., 2008; Jarvis et al., 2014; Mitchell et al., 2014). The root was placed on the Mesozoic non-neornithine bird

Ichthyornis dispar (Clarke, 2004). The specimens examined are listed in Appendix S4.

Cladistic analysis

Tree searches were conducted using standard parsimony and Sankoff parsimony (Sankoff and Rousseau, 1975) analyses in TNT v. 1.0 (Goloboff et al., 2008a, b). The latter is a generalized parsimony approach that allows for inclusion of characters for which the costs of transformation between states are defined by the researcher and step matrices are applied after defining the cost of transformation among states according to their perceived similarity (Sankoff and Rousseau, 1975; Goloboff, 1998). Sankoff parsimony analyses were performed under equally and implied character weighting to assess the effects of weighting against homoplasy. Character weights are not given *a priori* but are assigned during tree search, so weighting depends only on the homoplasy inherent to the characters themselves (Goloboff 1993). Herein, the effects of *K*-values of 3, 4, 6, 9 and 12 are tested, representing moderate to mild weighting against homoplasy, given the size of the dataset and its degree of homoplasy (Mirande, 2009).

The alternative unordered analysis (with transformation costs among states set equal) was carried out for comparative purposes, i.e. to assess the consequences of applying transformation costs to those characters in which the states are related in a complex way (Bertelli et al., 2002). Transformations of both plumage and egg coloration characters without step-matrices were examined in the resulting optimal trees to determine the extent to which penalized transformations under Sankoff parsimony were actually recovered in the analyses using unordered characters.

All analyses included 1000 replicates of Wagner trees (using random addition of sequences), followed by tree bisection reconnection (TBR) branch swapping, keeping up to ten trees per replica. The best trees obtained at the end of the replicates were subjected to a final round of TBR branch swapping. Zero-length branches were collapsed if they lacked support under any of the most parsimonious reconstructions. The support for the groups was calculated using both jackknife resampling and Bremer supports (Bremer, 1994). Following Goloboff et al. (2003), results from a jackknife resampling of characters using GC frequencies in 1000 replicates of symmetric resampling (*K* = 3) are here reported to examine the most-parsimonious trees (MPTs) in which the monophyly of a given group is rejected (Fig. 3). The suboptimal trees used to calculate Bremer supports were searched in seven successive stages to prevent overestimation of support values (Goloboff and Farris, 2001; Giannini and Bertelli, 2004). Thus, the absolute Bremer support values were

calculated on the basis of a sample of $\geq 14\,000$ suboptimal trees up to seven steps longer than the optimal trees. In that way, many nearly optimal trees that could be overlooked in a less careful selection of suboptimal trees were calculated, which would lead to overestimated support values.

To improve consensus tree resolution, unstable taxa were identified over the entire set of MPTs (Pol and Escapa, 2009). These problematic taxa were pruned from the MPTs (*a posteriori* of the heuristic tree searches) to construct a reduced strict consensus, provide diagnosis of some relevant clades that collapsed in the complete strict consensus, and evaluate nodal support (i.e. alternative positions of the unstable taxa create a minimal bound for the support of several tree nodes; see Fig. 3). The exclusion of these taxa therefore allowed a comparison of differences in branch support irrespective of their alternative positions within Tinamidae. Because the fossils feature many missing entries, several derived character states optimized as synapomorphies in the consensus of the extant species were not unambiguously optimized in the set of MPTs. Thus, to summarize the results of the phylogenetic study, diagnosis and support values are calculated both including and excluding fossil taxa (Fig. 3). All analyses were run in TNT (Goloboff et al., 2008a,b).

Results and discussion

General topology and supports

Generalized (Sankoff) parsimony analyses under equal weights yielded 860 MPTs trees of 1880.616 steps found in 781 of the 1000 replicates (results discussed here) and tree searches under implied weights resulted in 960 optimal trees of fit 147.937 (*K* = 4); as an average, each character has 1.144 extra steps (i.e. homoplastic steps), having between 72.4 and 91.3% of the fit of a character without homoplasy in the explored range of *K*-values, which corroborates that those values imply moderate to mild weighting against homoplasy (Mirande, 2009). Analysis under standard parsimony (unordered characters in equal weights) recovered 110 MPTs trees of 998.967 steps found in 781 of the 1000 replicates.

The strict consensus tree including extinct tinamous exhibits a large polytomy involving all species of Tinamidae. This is mainly due to the highly unstable behaviour of some fossil taxa (MACN-SC-T, MACN-SC-H, *Nothura* sp.). In addition, the unstable taxa *Crypturellus reai* and *Eudromia olsoni* also took alternative positions within their respective genera. Therefore, the consensus tree of the heuristic searches was calculated excluding *a posteriori* (i.e. from the

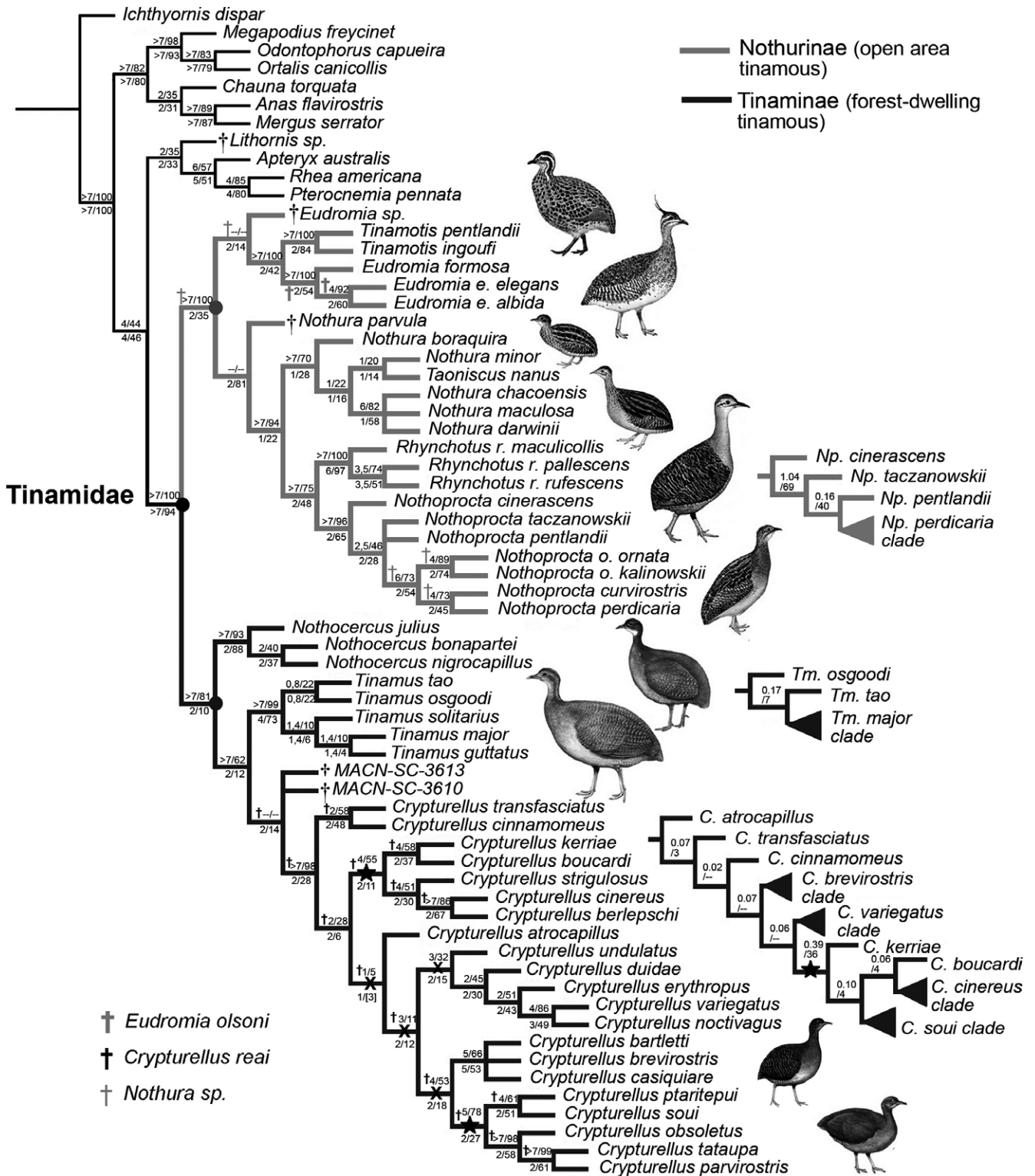


Fig. 3. Reduced strict consensus of the phylogenetic analysis of fossils and living tinamous using TNT. Topologies in the insets were recovered with implied character weights ($K = 4$). Differences between topologies under non-ordered versus Sankoff analyses are marked with an "x". Possible equally parsimonious positions for the fossil taxa are denoted with daggers "†". Species of the genus *Crypturellus* that exhibit dark plumage coloration are indicated with stars. Support values (jackknife resampling and Bremer) of the phylogenetic analysis including extant species and fossils are given above and below branches, respectively.

consensus) these unstable fossils by a procedure that tests the interrelationships of tinamous (living and fossil taxa), comparing sets of phylogenetic trees inferred from all the available data (i.e. including those fossils of ambiguous positions; Pol and Escapa, 2009). After the identification and exclusion of the unstable fossil species, an almost fully resolved reduced consensus tree was recovered with nearly identical topologies under Sankoff and unordered analyses (see strict consensus in Fig. 3). Most of the nodes were compatible across alternative analyses and differences between alternative trees were groupings with low stability within some areas of the *Crypturellus* clade (Fig. 3, non-congruent nodes marked with an X). The resulting ingroup topology was well resolved, except for one trichotomy in *Crypturellus*, *Nothura* and *Nothoprocta*.

Extant taxa. In the consensus topology, a monophyletic Tinamidae and almost all currently recognized polytypic tinamou genera were recovered with high support: only *Nothura* was paraphyletic in terms of *Taoniscus* (Fig. 3). However, that rejection was not strong as searches constrained to recover a monophyletic group yielded optimal trees only one step longer than the unconstrained trees. Nothurinae and Tinaminae were well supported and thus Tinamidae was subdivided into two groups: the forest-dwelling Tinaminae (*Crypturellus*, *Tinamus*, *Nothocercus*) and the steppe, or open area, Nothurinae (*Taoniscus*, “*Nothura*”, *Nothoprocta*, *Eudromia*, *Tinamotis*, *Rhynchotus*; Fig. 3). The monophyly of the open area and forest-dwelling tinamous was well supported [bootstrap support (BS) > 7/Group present/contradicted (GC) > 81]. Trees depicting Nothurinae and Tinaminae as non-monophyletic required as many as seven extra steps.

A well-supported *Nothocercus* (BS > 7/GC 93) was the earliest diverging taxon of the forest-dwelling tinamous. *N. julius* was the sister taxon to other two species (*N. bonapartei* and *N. nigrocapillus*) (BS 2/GC 40). Next, *Tinamus* and *Crypturellus* grouped together with relatively good support (BS > 5/GC 62). The monophyly of these genera was recovered with good support (BS > 7/GC > 98), but relationships within the taxa were generally weakly supported (with exception of the dark-coloured, relatively unpatterned species, see Fig. 3). Within *Tinamus*, relationships were weakly supported (BS > 0, 8/GC > 10), *T. osgoodi* and *T. tao* formed a group, and *T. solitarius* was the sister taxon to the clade (*T. major* + *T. guttatus*). Although interrelationships were mostly unresolved in the non-additive consensus (with the exception of the clade *T. osgoodi* + *T. tao*), groups recovered by the Sankoff analyses appeared in trees from the optimal set (Fig. 3). Within *Crypturellus*, relationships were almost fully resolved (except for a trichotomy formed by

C. casiquiare, *C. barletti* and *C. brevirostris*). Most *Crypturellus* groupings recovered in the standard parsimony analysis were obtained in the Sankoff consensus (Fig. 3). Differences between analyses (four incongruent nodes) included the poorly supported positions of species such as *C. undulatus* and *C. atrocapillus* and major groupings with low stability (marked with an “x”, see Fig. 3). The main differences between unweighted and weighted Sankoff analyses include some clades of *Crypturellus*; for example, no matter which *k*-values are used (moderate to mild), a clade grouping species of the genus that exhibit dark plumage coloration was recovered across weighted analyses (Fig. 3, inset). However, the support for most clades was low (with the exception of the greyish unpatterned *Crypturellus* species), implying from one to four extra steps when depicted as non-monophyletic (Fig. 3). In the equally weighted Sankoff analysis, the clade (*C. transfasciatus* + *C. cinnamomeus*; BS 2/GC 58) was recovered as the sister to all other *Crypturellus* species. In turn, the unpatterned species formed relatively well-supported groupings (BS > 4/GC > 51), including the clade (*C. kerriae* + *C. boucardi*) that grouped together with (*C. cinereus* + *C. berlepschi*) + *C. strigulosus*). Next, *C. atrocapillus* was the sister taxon (but poorly supported) to a large clade composed of the remaining species of the genus (BS 3/GC 11). Within the latter group, *C. undulatus* was the sister taxon to the clade (*C. duiade* + (*C. erythropus* + (*C. noctivagus* + *C. variegatus*))), and those relationships were relatively well supported (BS > 2/GC > 32). Next, *C. brevirostris*, *C. bartletti* and *C. casiquiare* formed a well-supported group (BS 5/GC 66), but with unresolved interrelationships, and this was the sister taxon to a well-supported greyish coloured tinamous clade (BS 5/GC 78). Within the latter, two well-supported groups were recovered: (*C. tepui* + *C. soui*) (BS 4/GC 61) and (*C. obsoletus* + (*C. tataupa* + *C. parvirostris*)) (BS > 7/GC > 98).

In the open area subtree, (*Tinamotis* + *Eudromia*) grouped together with high support (GC 100/BS > 7) and the monophyly of these genera was also highly supported (BS > 7/GC 100). The included subspecies of *E. elegans* (*E. elegans elegans* + *E. elegans albida*) formed a clade (BS 4/GC 92) that was sister to *E. formosa*. Next, the suprageneric group consisting of (*Taoniscus* + *Nothura* + *Nothoprocta* + *Rhynchotus*) was recovered with high support (BS > 7/GC 94). In turn, the clade diverged into two well-supported suprageneric groups, (*Nothoprocta* + *Rhynchotus*) and (*Taoniscus* + *Nothura*) (BS > 7/GC 70). Within the latter, *Nothura boraquira* was the sister taxon to the other species, *Taoniscus nanus* was recovered within a paraphyletic *Nothura* as the sister taxon to *Nothura minor*, and this clade was related to the group formed by the species *N. maculosa*, *N. darwinii* and *N. chacoensis*

(with unresolved relationships). With the exception of the last clade (BS 4/GC 82), groupings within *Nothura* were poorly supported and suboptimal, implying from one to two extra steps when it was depicted as non-monophyletic (Fig. 3). Next, the monophyly of *Rhynchotus* and the relationships within the genus were highly well supported (BS > 7/GC 100), with *R. rufescens maculicollis* as the sister taxon to the other forms: *R. r. rufescens* and *R. r. pallescens* (BS 3/GC 74). *Nothoprocta* was also recovered with high support (BS > 7/GC 96) and *N. cinerascens* was the sister taxon of all other species of the genus (BS 2/GC 46); the phylogenetic positions of *N. taczanowski* and *N. pentlandi* were unresolved, forming a trichotomy consisting of these species and a clade composed of the remaining species of the genus. Within the latter, two groups of two taxa each were recovered: (*N. ornata* + *N. kalinowski*) and (*N. curvirostris* + *N. perdicaria*), both of which were well supported (BS > 4/GC > 73). A fully resolved *Nothoprocta* is recovered under the Sankoff analysis with implied character weighting (Fig. 3, inset); however, this topology also appeared in trees from the equally weighted optimal set.

Extinct taxa. The fragmentary earliest known tinamous MACN-SC-T and MACN-SC-H were identified as responsible for the great deal of instability: MACN-SC-T fell in multiple positions within the ingroup subtree while MACN-SC-H fell in alternative positions within the forest-dwelling Tinaminae. An additional unstable fossil was the Pleistocene *Nothura* sp. that took multiple positions within the open-area group Nothurinae. The generic allocation of the extinct species *Crypturellus reai* and *Eudromia olsoni* was confirmed, and they showed a more local unstable behaviour within their respective genera. The instability of the fragmentary Early Miocene remains was exclusively caused by the lack of information (i.e. missing data) whereas a mixture of missing data and character conflict was the case for *Nothura* sp., *C. reai* and *E. olsoni*.

Support values for the placements of extinct tinamous were low, even when ignoring the alternative positions of the unstable fossil terminals (BS 2; Fig. 3). This is not unexpected given the ambiguity resulting from the limited evidence provided by the incomplete fossils. In contrast, and spite of the high percentage of missing data of the fragmentary early Miocene tinamous MACN-SC 36 10 and MACN-SC 3613, the placement of these fossils was well resolved as related to the extant forest genus *Crypturellus* (Fig. 3). This was also the case of the late Miocene *Eudromia* sp. (recovered outside the clade *Eudromia* + *Tinamotis*), and the Pliocene tinamou species *Nothura parvula* positioned outside the remaining open-area clades (*Taoniscus* + *Nothura* + *Nothoprocta* + *Rhynchotus*) (Fig. 3).

In summary, with the exception of the early Miocene specimens, most Tertiary fossil tinamous were recovered within the open-area Nothurinae in the optimal trees by the cladistic analyses.

Alternative cost regime

Most of the nodes of the Sankoff analyses (93%) were compatible with those recovered in the standard parsimony consensus tree. Step matrices and transformation costs effects were minimal, affecting only few poorly supported groupings within *Crypturellus* and thus the incongruence between alternative analyses was limited (lost nodes in the unordered analysis are marked with an X in Fig. 3). Furthermore, there was considerably higher congruence between the Sankoff and non-ordered optimal topologies in the current analysis compared with those results obtained from the integumentary data set alone of Bertelli et al. (2002). The low level of conflict found here (with and without step-matrices) is an indication that the interaction among characters is maintained regardless of whether character-state transformations are penalized or not.

Previous results of the integumentary analyses of tinamous have suggested that more frequent changes occur between most similar states (see Bertelli et al., 2002). State transformations of plumage and egg coloration characters were also re-evaluated here on the unordered optimal trees (in which all state changes were equally costly) to determinate whether transformations never implied in the Sankoff analyses (as a result of their high cost) did occur if those transformations were less penalized (Figs 1 and 2). In the shortest trees produced by the combined analysis, most of the transformations implied by the unordered regime were also low-cost transformations between states in the more complex cost regime (Figs 1b and 2b). Furthermore, egg colour and plumage design transformations that were penalized under generalized (Sankoff) parsimony were obtained only rarely under standard parsimony. The same state changes were also observed, with approximately the same frequency, in the Sankoff optimal trees. This is interpreted as additional evidence that the reduced number of transformations between several non-related states is not a consequence of the imposed penalty but in fact emerges from the interaction with other characters.

Thus, results were congruent with the observation and description of characters coded with costs in plumage and egg coloration features with step matrices. Even when it was assumed that all state transformations are equally costly, the current results suggest, in agreement with Bertelli et al. (2002), that some transformations were more expected than others and those transformations occurred between most similar states (Figs 1b and 2b).

Influence and congruence of characters

The combined analysis of integumentary, osteological, myological and behavioural–breeding characters recovered a tree structure similar to the recently evaluated internal anatomy phylogeny by Bertelli et al. (2014) and previous molecular analysis of Porzecanski (2003).

The monophyly of the open-area tinamous has been consistently supported by morphological (Bertelli et al., 2002, 2014; Bertelli and Chiappe, 2005; Bertelli and Giannini, 2013), and molecular (Porzecanski, 2003) data sets. By contrast, the forest-dwelling genera were placed at the base of the tinamou tree and form a paraphyletic clade by the inclusion of the Nothurinae by integumentary data (Bertelli et al., 2002; Bertelli and Giannini, 2013). Thus, the main differences between diverse phylogenetic analyses (Bertelli et al., 2002; Bertelli and Giannini, 2013) resolve exclusively around the ingroup rooting. In the integument-based tree (i.e. using traditional characters of bird systematics), *Nothocercus* is the basal taxon, sister to all other tinamous; next, *Tinamus* is paraphyletic, and the next clade recovered is *Crypturellus* sister to the Nothurinae. By contrast, the internal anatomy and molecular analyses recovered two clades: forest-dwelling Tinaminae (*Nothocercus*, *Tinamus*, *Crypturellus*) and open-area Nothurinae (*Taoniscus*, *Nothura*, *Nothoprocta*, *Rhynchotus*, *Tinamotis*, *Eudromia*); rooting on *Nothocercus* as suggested by recent integumentary analysis (Bertelli and Giannini, 2013) required more than seven extra steps on the internal anatomy data (Fig. 3).

In the combined analysis, osteological and myological data allowed the recovery of Tinaminae albeit with considerable conflict with integumentary data. The internal anatomy data (osteology and myology), however, were insufficient to resolve interrelationships of some genera (e.g. *Crypturellus*, *Tinamus*) and other areas of the tinamou sub-tree. It was the combination of the different morphological data subsets and behavioural characters that resolved the internal branching and decreased the ambiguity in the placement of the ingroup subtree root.

Only the group of steppe tinamous (Nothurinae) is recovered with both internal and external morphology rooting. No matter which type of evidence is used, the open-area tinamous are recovered as monophyletic with good support in both alternative analyses. Additional differences are observed within Nothurinae: the integumentary–behavioural results differs from the internal anatomy consensus in having *Taoniscus* as sister to all other Nothurinae, next *Nothoprocta*, and a paraphyletic *Nothura* are successive sister taxa to *Rhynchotus* and the clade (*Eudromia* + *Tinamotis*). By contrast, the osteology–myology tree recovered the clade (*Eudromia* + *Tinamotis*) as sister to all other open-area groups.

Most incongruent nodes across the main analyses subsets were in fact groups with relatively low stability and alternative results may not be in real conflict. After including all available evidence in the present comprehensive analysis, both absolute and relative supports increased in three of the polytypic genera (e.g. *Tinamus*, *Nothoprocta*, *Nothocercus*). Second, suprageneric clades either maintained or increased their support values, for instance in the clade *Tinamus* + *Crypturellus*. Only relationships within *Nothura* decreased their support values. This means that the new combined data brought a considerable amount of evidence for well-established clades but conflict within the *Nothura* subtree (although minimally supported). Therefore, the congruence between internal and external morphological characters and together with the present combined morphological analysis was considerably high.

Internal anatomy (osteology and myology) versus other character types (integument and behaviour) used for bird systematics were also evaluated separately to compare the degree of homoplasy of these sources [i.e. estimated by the consistency index (CI)] and their influence considering all available evidence. Although the number of taxa was lower for the internal anatomy analysis, the results obtained demonstrated that levels of homoplasy of the integument + behaviour dataset (CI 44; 60 terminal taxa) were similar to those of the osteology + myology dataset (CI 45; 53 terminal taxa). Furthermore, this value was generally maintained in the total analysis (CI = 41 for the shortest tree including the 70 terminals). Thus, behavioural and integumentary characters have similar levels of homoplasy in relation to those of internal anatomy. When these types of characters were analysed separately, both types of data presented similar degrees of homoplasy, indicating that traditional characters used in bird systematics (e.g. integument, song characters) were as reliable as other types of evidence.

Character performance

The information coded in an extensive dataset of morphological and behavioural characters provided an almost fully resolved phylogeny of Tinamidae with 75% of ingroup clades having good support (BS > 4/GC > 50, Fig. 3). Unambiguous (ingroup) apomorphies of the recovered clades are discussed in Appendix S3.

The distribution of synapomorphies from various character types (integument, internal anatomy, breeding, song structure, etc.) showed hierarchical structure with different characters having high performance at various hierarchical levels (Fig. 4). For example, internal anatomy characters were important at several nodes but were mainly the primary source of

synapomorphies for Tinamidae. Thus, 16 morphological changes that supported this clade were osteological and myological features, which together with one reproductive synapomorphy contributed to the monophyly of Tinamidae. However, it should be stressed that most external morphological and behavioural characters (pigmentation patterns, songs) have been considered non-comparable for the outgroup and thus relationships of the tinamous with other birds (supported on these character types) were mainly based on a few breeding, podotheca and bill characters.

Osteological and myological characters were not only diagnostic at higher hierarchical levels but also provided evidence at lower levels (see Appendix S3). A conservative condition of the osteology and myology seems not to occur in tinamous and considerable morphological variation was observed in the cranium and postcranial elements of the group. Furthermore, in the optimization of the MPTs, modifications of the osteological features were distributed at almost all hierarchical levels, with the exception of a few areas such as some interrelationships of *Crypturellus* species and within the genera *Tinamus* and *Nothura*. Myological characters also provided support for Tinamidae, Nothurinae, four suprageneric clades and five genera, but myological synapomorphies at intrageneric level

were not recovered in the current analysis. This correlated in part with the fact that osteological and myological character coding for several species within *Crypturellus* and *Nothoprocta* were unknown, which produce ambiguity in character optimizations, and thus it was not possible to determine the level at which these characters represent synapomorphies of the groups. Generally, the total number of clades recovered by the internal anatomy characters was lower than those recovered by the external morphology (Fig. 4). Note also that some of these differences (proportion of recovered nodes by different evidence types) were associated with the more extensive taxon sampling of skin specimens: this type of character is easier to preserve in museum material as the bulk of ornithological specimens were primarily conserved as dry skins. These characters also have the advantage (with respect to internal anatomy, or molecular characters) of being thoroughly known for practically all species of birds.

Suprageneric and generic groups are supported by all character types but the integumentary and behavioural changes are clearly more important than others (e.g. in clades within polytypic genera, see Fig. 4). Although integumentary and behavioural characters were infrequently used for phylogeny reconstruction in

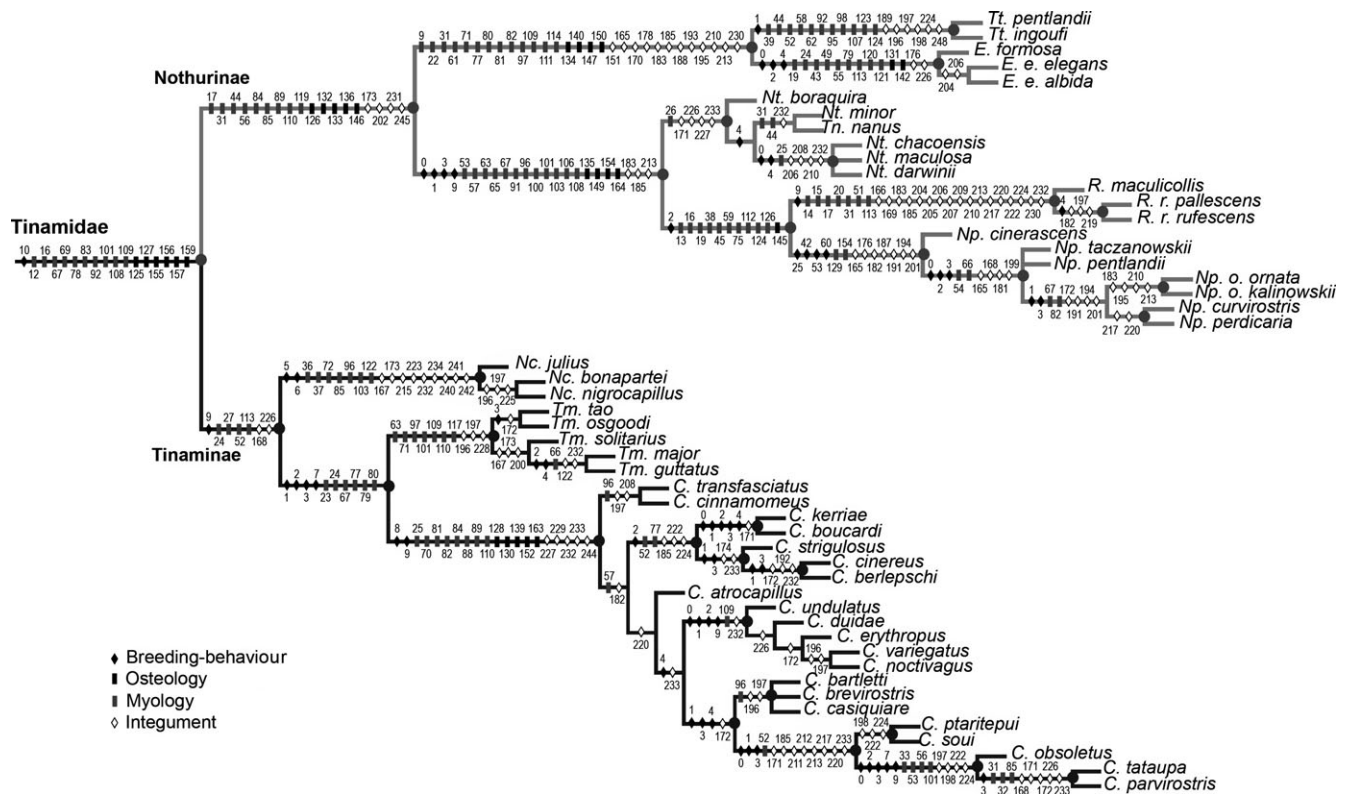


Fig. 4. Distribution of unambiguous synapomorphies recovered in the current character analyses. See Appendix S2 for details on character descriptions and Appendix S3 for a discussion on the groups recovered.

birds (Livezey, 1991, 1995, 1997, 1998; Chu, 1998; Bertelli et al., 2002, 2006; Giannini and Bertelli, 2004; Bertelli and Giannini, 2005, 2013; Ksepka et al., 2006, 2012; Clarke et al., 2007, 2010; Livezey and Zusi, 2007; Ksepka, 2009), the current analysis showed that they are capable of providing synapomorphies for nodes in almost every level of the ingroup subtree, thus confirming their value as a source of useful phylogenetic information. Furthermore, breeding and behavioural characters (despite the fact that they comprise a minor fraction of the total character set: 12 out of 249 characters) have been determinant in some areas of the tree, providing synapomorphies in 29 of the 48 ingroup nodes, which characterized four suprageneric clades (e.g. Rhynchotinae, Tinamotidinae, *Rhynchotus* + *Nothoprocta*, *Tinamus* + *Crypturellus*), five of the seven recovered genera, as well as 17 internal nodes (see above). In particular, song characters showed good performance at different hierarchical levels, but mainly were informative within *Crypturellus* (11 of 19 nodes supported by continuous characters of vocalizations).

Outgroup–ingroup relationships based on integumentary characters of tinamous relied mostly on bill and leg characters, and also a few external structural characters coded as non-comparable for the outgroup (Fig. 4). Nevertheless, these characters of external morphology provided unambiguous synapomorphies such as those supporting the monophyly of the subfamilies Nothurinae and Tinaminae and thus decreasing the ambiguity in recovering these groups. Previous integumentary studies (Bertelli et al., 2002; Bertelli and Giannini, 2013) strongly supported Nothurinae with numerous synapomorphies of adult and natal plumage characters. However, note that several of these plumage characters that supported the open-area group in previous analyses when rooting on *Nothocercus* (as suggested by previous integumentary analyses; Bertelli et al., 2002; Bertelli and Giannini, 2013) under current optimal topologies have not been optimized as synapomorphies for the steppe tinamous group. Other integumentary and behavioural characters used traditionally in bird systematics for contrasting groups or species (forest vs. open-area tinamous; Tinamotidinae vs. Tinaminae; *R. rufescens* vs. *R. maculicollis*) were informative at the expected nodes (e.g. position of nares, presence/absence of the first toe, bill plates, arrangement of foot scutes, acoustic structure of songs). Finally, some integumentary characters (e.g. colour variations) have been less informative, requiring many extra steps and several independent origins or reversals.

Changes and phylogeny

The MPTs resulting from the present analysis suggested one major divergence within Tinamidae forming

two groups: a group of forest-dwelling taxa and an open-area clade (Fig. 3). Two alternative patterns in several osteological changes can be interpreted in the context of the current phylogenetic hypothesis (Figs 5 and 6). For example, morphological features of the skull such as the lacrimal–ectethmoid plate, mandibular articular areas and modifications of the quadrate (reverted in *Tinamotis*) are conspicuously developed in the open-area groups (e.g. characters 31, 53 and 56) (Fig. 5). Regarding the postcranium, the marked increase in the size of the processus lateralis of the coracoid (reverted in *Taoniscus*) and the processus craniolateralis of the sternum were also notable changes in the pectoral girdle of the open-area tinamous (e.g. character 85) (Fig. 5). The postacetabular pelvis of the forest-dwelling tinamous was similar or more developed than the praeacetabular area, as opposed to the markedly longer praeacetabular pelvis (and tuberculum praeacetabulare) of most open-area groups (reverted in Tinamotidinae) (e.g. characters 101 and 108) (Fig. 5). Another interesting feature was the degree of the hypotarsal sulcus aperture, from a nearly closed canal in the forest groups to a broader, plantar open sulcus in the open-area species (character 120). These anatomical modifications are also noted by Bertelli et al. (2014) and may be related to feeding adaptations, flight and/or terrestrial locomotion.

The adult plumage of tinamous is rather simple in forest-dwelling species compared to the complex patterns of open-habitat relatives. Although Miranda-Ribeiro (1938) stated that these feather patterns support the traditional subfamilial division, the modest adult plumage of the forest-dwelling tinamous is plesiomorphic in the context of the current phylogenetic hypothesis (Fig. 6). The distribution of state characters in the consensus tree allowed the interpretation of these change transformations; for example, a general trend in plumage changes of the dorsum that includes several pteryxae (pars spinalis + pars pelvica + pteryxa scapulohumeralis; dorsum, mantle and rump) can be interpreted (character 185) as indicating the basic pattern was bicoloured barred, from which two main types derived: the mostly immaculate patterns of some *Crypturellus*, and the complex variations of the open-area tinamous (*Nothura*-like, tricoloured, mixed, etc.; Fig. 6), all of which can be directly related to crypsis in specific dark (forest) versus luminous (steppe) environments. Within the forest tinamous, changes toward simpler designs seem to occur independently in two areas of the *Crypturellus* subtree: the *C. kerriae* group (including the dimorphic *C. boucardi*) and the *C. tataupa* group with scalloped barred patterns that are acquired always from bicoloured barred patterns, without reversal. By contrast, changes from the basic barred toward the mostly immaculate patterns seem to occur directionally in the analysis under implied

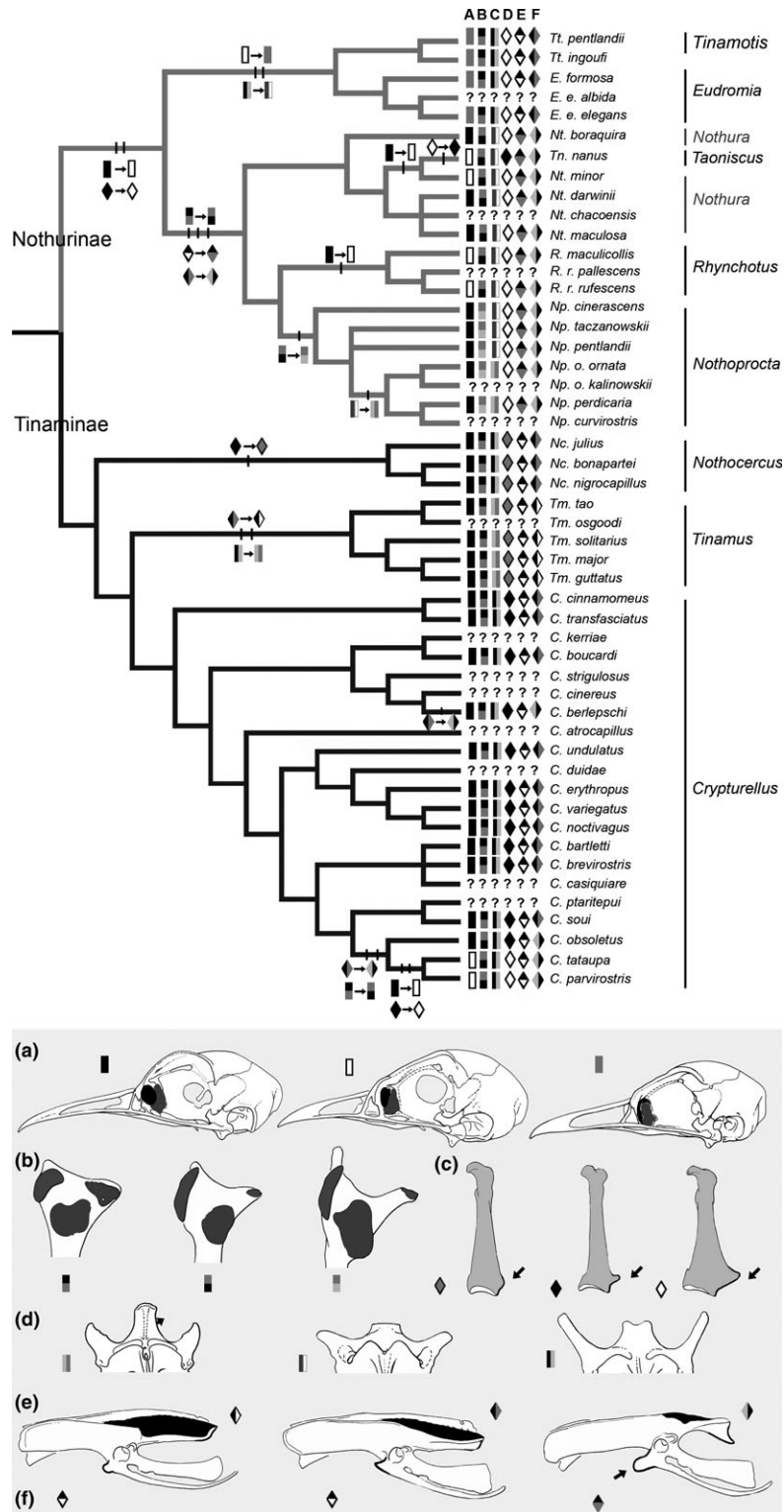


Fig. 5. Taxonomic distribution and optimization of six selected osteological characters described in more detail in Appendix S2. (a) Lacrimal-ectethmoid complex (character 31); (b) mandibula, cotyla medialis (character 53); (c) coracoid, processus lateralis (character 85); (d) sternum, cranial projection of the spina interna rostri (character 71); (e) ilium, dorsal surface, relative length of cranial and caudal portions (character 101); and (f) pubis, tuberculum praeacetabulare (character 108). For the data matrix, see Appendix S1. Further discussion is provided in the text.

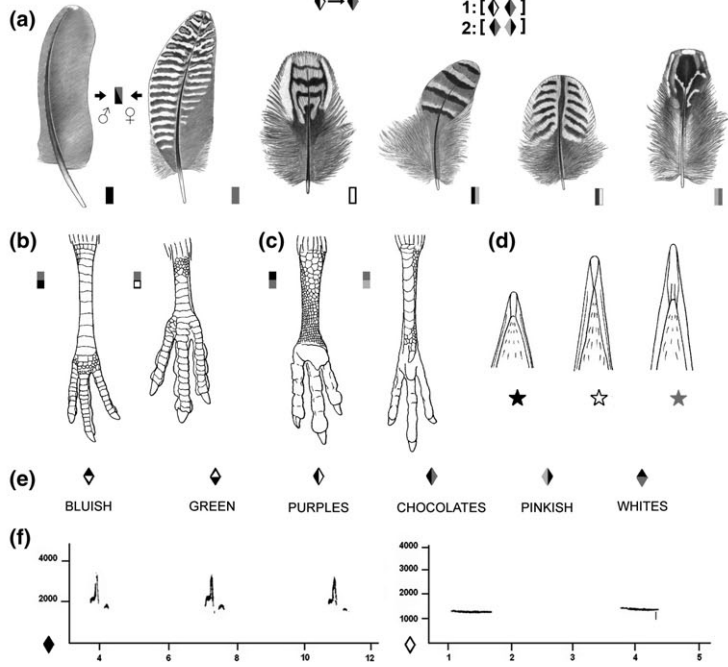
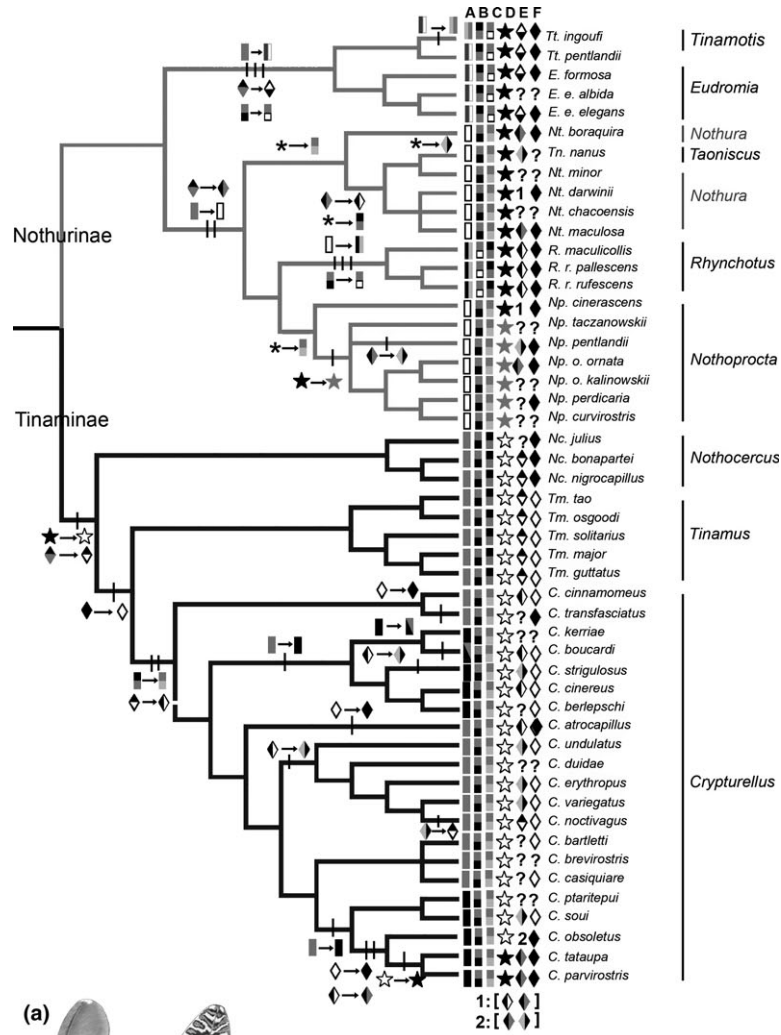


Fig. 6. Taxonomic distribution and optimization of six selected breeding–behavioural and integumentary characters described in more detail in Appendix S2. (a) Pars spinalis + pars pelvica + pteryla scapulothoracalis (dorsum + mantle + rump), feather pattern (character 185); (b) acrotarsium, dorsal–tarsi scutes, pattern (character 230); (c) podoteca ventralis (plantar–tarsi scutes), scale pattern (character 229); (d) rostrum mandibulare + ramphoteca, ventral plate, lateral grooves (character 168); (e) oology, egg colours (character 9); and (f) songs, frequency modulation (character 7). Asterisks (*) indicate ambiguous transformations that occur in that node. For the data matrix, see Appendix S1. Further discussion is provided in the text.

weights (Fig. 3, inset). Within the Nothurine, more complex designs such as the tricolour barred pattern derived from either the *Nothura*-like pattern or the *ingoufi*-like pattern that derived from the mixed pattern, never reverted (Fig. 6).

Other characters used in traditional systematics (including divisions and relative proportions of bill plates, and the number and arrangement of foot scutes) were reasonably useful at the different levels at which they had been hypothesized to support, allowing the interpretation of general trends in these integumentary characters. For example, changes in the ramphoteca included the transformation from a basic design of the bill with similar plates and parallel lateral grooves, from which derived an open-area bill type with naris placed proximally, longer proximal plates (and posteriorly divergent lateral grooves), and the forest-dwelling bill pattern with medial/posterior naris, convergent lateral grooves and shorter proximal plate relative to the distal one (e.g. characters 167 and 168) (Fig. 6). The basic arrangement of the tinamou foot scutes is the juxtaposed pattern of dorsal–tarsi scales with numerous and reticulated plantar tarsi scutes that becomes imbricated in some steppe tinamous (*Tinamotis*, *Rhynchotus*) and organized in a transverse pattern of one row (*Crypturellus* and some steppe tinamous) to several rows of plantar scales (e.g. *Nothoprocta*) (Fig. 6). Chicks of most forest-dwelling tinamous share a dark general design, whereas chicks of the steppe tinamous have lighter plumage colours with several head stripes. These plumage character conditions have been hypothesized to be related to camouflage advantages in different habitat types (Sick, 1984; Cabot, 1992; Davies, 2002; see above). Other integument coloration characters (e.g. colours of the maxilla, mandible, feet and iris) require many more extra steps, showing little congruence with the obtained optimal trees.

Regarding reproductive characters, the non-intromittent phallus that remains attached to the wall of the cloaca present in *Crypturellus* derives from the intromittent-type condition widely distributed among basal birds. The basic eggshell coloration is whitish, from which alternative general trends can be interpreted. In the open-area groups, two main types derive from the whitish eggs: the cyaninic green shell colours of Tinamotidinae and the mostly porphyritic colours (brownish, pinkish) of other steppe tinamous (reverted in *Rhynchotus*). Within the forest-dwelling tinamous, the main trend in pigment egg colours was the

transformation from the cyaninic bluish to transitional purple–violet to the more porphyritic egg colours (brownish, pinkish). Changes toward porphyritic colours seemed to occur directionally in terminal *Crypturellus* groups and the brownish–pinkish egg colours were acquired from the purple–violet eggshell conditions (Fig. 6). Behavioural changes such as the acoustic structure of songs also occur directionally in some forest-dwelling groups and never reverted. For example, songs with generally constant frequencies along time present in *Crypturellus* and *Tinamus* were acquired from vocalizations with high-frequency variations (Fig. 6); habitat–song relationships in tinamous suggested that song structures could be related to different habitat conditions for long-range communication between species (Bertelli and Tubaro, 2002).

Conclusions

In light of the highly resolved and supported results, highly congruent with other sources of evidence (particularly DNA sequences), morphology proved to be a rich source of phylogenetic characters in tinamous, insofar as the ratio of characters to taxa is large (4:1 here) with all known species, both extant and fossil, included in the analyses. Previous attempts have used more restricted datasets that served the purpose of exploring the performance of a particular external (Bertelli et al., 2002; Bertelli and Giannini, 2013) or internal (Bertelli and Chiappe, 2005; Bertelli et al., 2014) anatomical system. The present study provided the most comprehensive phylogenetic analysis incorporating different sources of anatomical information along with newly developed behavioural and reproductive characters, translated into scorings that in some cases represented more complex observations (e.g. step matrices for state transformation costs). In addition, the incorporation of different sources of information contributed new synapomorphies for clades, corroborated some of the synapomorphies already proposed and allowed study of the evolution of different structures in tinamous (cranial and postcranial features, plumage, etc.). Dense taxonomic sampling was also a primary aim here and all extant and fossil species of the group are included. The addition of fossils was a particular need to understand the evolution of the diversity of tinamous as a group, and thus all tinamou fossil taxa that have been described to date were included (see Bertelli et al., 2014).

The traditional subdivision between tinamous specialized for open areas, or steppe tinamous (Nothurinae), and those inhabiting forested environments (Tinaminae) was supported by the present analyses, confirming the traditional classification of the family into two subfamilies originally proposed by Miranda-Ribeiro (1938). The monophyly of most traditional genera (with the exception of *Nothura*) and the tree structure recovered here (*Nothocercus* (*Tinamus* + *Crypturellus*) and ((*Eudromia* + *Tinamotis*) ((*Taoniscus* + *Nothura*) (*Nothoprocta* + *Rhynchotus*))) is also congruent with the previous internal anatomy and molecular studies (Porzecanski, 2003; Bertelli et al., 2014). By contrast, the monophyly of *Nothura* has only been recovered by molecular evidence (Porzecanski, 2003) and so the status of *Taoniscus* (here nested in *Nothura*) remains an open question that awaits a total-evidence analysis.

The known fossil record of tinamous is contained within the early Miocene–Quaternary interval of southern South America. The earliest tinamous are about 16.5 million years old and are placed within both the open-area and the forest groups. The early divergence between forest and arid land taxa and the placement of the known fossil tinamous is also congruent with previous results obtained by Bertelli et al. (2014). The oldest extinct tinamous existed at a time when the early Miocene subtropical forested landscapes of southern South America were transitioning into the open-area environments that characterize most of the region today (Bown and Larriestra, 1990; Genise and Bown, 1994; Vizcaíno et al., 2012). With the exception of these early–middle Miocene fossils, most of the younger records of tinamous are more closely related to the steppe Nothurinae (Fig. 1). Thus, according to the present phylogenetic reconstruction, the placement of the oldest fossil tinamous within the open-area (Nothurinae) and the forest-dwelling (Tinaminae) groups (and the position of younger records more closely related to the open-area Nothurinae) is consistent with the inferred palaeoenvironmental conditions and the habitat type of the closest living relatives.

Results of the alternative non-ordered analysis, in which all state transformations were equally likely, suggest that transformation costs, as observed and coded in step matrices, were not analytical artefacts and that character-state transformations indeed occurred more frequently between most similar states. The current analysis showed that using Sankoff cost matrices representing more complex observations (such as overlap in feather design analysis and egg pigment composition) resulted in a better fit between the observations and the transformations among more similar states implied in the cladogram. Thus, the present analysis supports the tenet that information on relative degrees of similarity, whenever available, should be

used to decide relative costs between different states for character description in the same way as it is used to decide in hypotheses of the primary homology of characters (Lipscomb, 1992). The egg colour and feather pigmentation patterns described in tinamous are common to many other group of birds; the results suggest that a similar criterion could be used to assign costs to state transformations in birds generally.

The present phylogenetic analysis suggests that all types of characters were informative, contributing evidence at various hierarchical levels of the tree. Both the compatibility between the analysis of partial data and their internal consistency contradict the perception among ornithological systematics that integumentary and behavioural features are too labile to be historically informative. Behavioural, breeding and integumentary characters (songs, plumage, bill morphology, scales of the legs, etc.) are not frequently used as a source of corroboration for phylogenetic hypotheses, in spite of the fact that these types of characters were extensively used to differentiate species, and many such characters contributed to higher-order groupings of traditional diagnoses in birds. However, recent examples show that, just as in the case of tinamous, integumentary and behavioural characters are as reliable as other types of phenotypic evidence, and that with the proper coding, most of the expected groups (i.e. those erected by the traditional systematics, including subfamilies, genera, tribes, etc.) are actually recovered (Chu, 1998; Bertelli et al., 2002, 2006; Giannini and Bertelli, 2004; Bertelli and Giannini, 2005, 2013; Ksepka et al., 2006, 2012; Clarke et al., 2007, 2010).

The combined morphological analysis also improved the support of most groups, including the above-mentioned Tinaminae, most genera and suprageneric clades, also decreasing the level of conflict in the first case. It is also worth noting that nodal support varies throughout the recovered intra-relationships of major groups in the optimal trees, with areas of conflict among the different types of characters visible as areas of particularly low branch support; that is, weakly supported clades were located within *Tinamus*, *Nothura* and some groupings of *Crypturellus* species. These areas of the tree will require further study, and future investigations of the phylogeny of tinamous should contribute to a more robust hypothesis in these conflicting areas of the tree. As discussed above, there is a high level of congruence with previous studies of DNA sequences but also some groupings that emerged here are in partial or complete contradiction with molecular results (Porzecanski, 2003). As taxonomic conclusions should be made in groupings with good support from several sources of data, a simultaneous analysis of all the evidence (morphological and molecular) is the next step to test the current hypothesis of the phylogenetic relationships of tinamous.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Dataset in the present analysis.

Appendix S2. Description and discussion of the morphological and behavioural characters used in the cladistic analysis.

Appendix S3. Systematic results and discussions for each recovered clade.

Appendix S4. Comparative material used in construction of the data matrix.

Appendix 1

List of morphological and behavioural characters used in the cladistic analysis. Characters whose states could be arranged in a linear transformation series were coded as additive (non-additive and additive characters are indicated by “–” and “+”, respectively). Characters with complex costs among states (Sankoff characters) were coded using step matrices and indicated by “*”. Full character descriptions and discussion of sources are provided in Appendix S2.

Behaviour and reproductive characters

Characters 0–3 represent continuous measurements on each tinamou songs of the following variables: maximum and minimum frequencies (characters 0 and 1), bandwidth (character 2), and emphasized frequency (frequency with the higher amplitude in the song; character 3).

4) + Songs, numbers of syllables produced: one (0); two (1); three–four (2); seven (3); nine to 11 (4); more than 12 but < 20 (5); long songs, between 30 and 40 syllables (6); very long songs, more than 80 syllables (7).

5) – Acoustic structure of song: pure sinusoidal modelling of syllables (0); harmonics (1).

6) – Syntactic structure of songs: absence of a sequential arrangement (0); constant trill (1); accelerated trill (2); fast trill (3).

7) – Songs, frequency modulation: constant or slightly modulated (0); distinctly modulated (1).

8) – Genitalia, phallus: protrudens (0); nonprotrudens (1).

9) * Oology, egg colours: bluish (0); greens (1), purples (2); brownish chocolates (3); pinkish (4); whites (5).

10) – Oology, external surface of the eggshell: dull to slightly glossy (0); highly glossy (1).

11) – Incubation, parental care: biparental or female-only (0); male only (1).

Osteología

12) – Os supraoccipitale, position of foramen v. occipitalis externa relative to the prominentia cerebellaris: ventral of the prominentia (0); dorsal, proximal of the crista nuchalis transversa (1).

13) – Os supraoccipitale, development of sulcus v. occipitalis externa: short grooves (0); ventrally extended and curved grooves (1).

14) – Os supraoccipitale, crista nuchalis sagittalis: absent (0); present (1).

15) – Os exoccipitale, processus paroccipitalis: not developed, flat or poorly developed as a wing-like projection, approaching but not extending below the ventral margin of the otic cavity (0); distinctly prominent, projecting ventrally (1).

16) – Os exoccipitale, foramen n. vagi, position: nearer to the foramen n. hypoglossum than to foramen n. ophthalmici (0); nearer to the foramen n. ophthalmici than to foramen n. hypoglossum (1).

17) + Fossa temporalis: small temporal notch, smaller than otic cavity, not extending caudally beyond the cotyla quadratica squamosi (0); larger than or about the same size as otic cavity, caudal extension about or beyond the position of the cotyla (1).

18) – Os squamosum, prominentia supraneaica developed as a distinct crest: absent (0); present (1).

19) – Os squamosum, processus zygomaticus: absent or vestigial (0); present, variably developed (1); present, laterally compressed (2).

20) – Os squamosum, ventral margin of the processus zygomaticus: straight (0); notched (1).

21) – Sutura frontoparietalis: absent (0); present (1).

- 22) – Os frontale, dorsal surface, distinct fossa at midline: absent (0); present (1).
- 23) – Orbita, margo supraorbitalis, glandular depressions (fossae glandularum nasales): absent (0); present (1).
- 24) + Orbita, ossiculi supraorbitales: absent (0); incomplete row of ossicles (1); paired complete row, forming a robust supraorbital layer surrounding the fossae glandularum nasales (2).
- 25) – Orbita, interorbital area (os frontale), dorsal surface: broader than or of similar width as the internarial area (0); narrower (1).
- 26) – Orbita, fonticuli orbitocraniales: vestigial or absent (0); present, large foramina present (1).
- 27) – Orbita, sulcus and foramen n. olfactorii forming a wide transversal fenestra, which perforates the septum interorbitale: yes (0) no (1).
- 28) – Orbita, septum interorbitale: extensively ossified (0); well-developed fonticuli interorbitales (1).
- 29) + Os mesethmoidale: does not reach rostrally beyond nasal-frontal hinge (0); extends rostrally immediately beyond the nasal-frontal hinge (1); extends far rostrally (2).
- 30) – Os ectethmoidale: separated from os lacrimale (0); contacting or fused to os lacrimale, forming a lacrimal–ectethmoid complex (1); extensively fused with os lacrimale and nasal capsule (2).
- 31) + Lacrimal–ectethmoid complex: narrow plate on ventromedial part of the antorbital wall, enclosing a wide and circular opening (foramen orbitonasale laterale) (0); plate and enclosed foramen with triangular outline (1); wide plate that covers most of the antorbital wall (foramen orbitonasale laterale narrow (2).
- 32) – Os lacrimale, dorsal surface of the head: expanded (0); very narrow (1).
- 33) – Os lacrimale, lacrimal duct perforating the lacrimal: as a foramen or almost complete foramen (0); forming a wide notch (incisura ductus lacrimonalis) (1).
- 34) – Os parasphenoidale, processus basiptyergoideus, developed as a large and ovoid facet for articulation with the pterygoid: no (0), yes (1).
- 35) – Os parasphenoidale, processus basiptyergoideus: stout process (0); elongated (1).
- 36) + Os parasphenoidale, processus parasphenoidalis medialis, aspect in caudal view: absent (0); weakly developed ventrally as a low bump (1); prominent, developed as a conspicuous bony knob (2).
- 37) – Os parasphenoidale, lamina parasphenoidalis (basitemporal platform), marked medial crest: absent (0), present (1).
- 38) – Os parasphenoidale, lamina parasphenoidalis, bony lateral projection directly rostral of ostium canalis carotici: absent (0); present (1).
- 39) – Os parasphenoidale, ostium canalis carotici: opens on each side of lamina parasphenoidalis, close to the eustachian tube openings (0); more caudally placed, at about the middle of the lamina parasphenoidalis (1).
- 40) – Tuba auditiva: open rostral, close to midline (0); open laterally, widely separated (1).
- 41) – Os palatinum, rostrocaudally wide pars choanalis: present (0); absent (1).
- 42) – Os palatinum, processus maxillaris: gradually curved from pars choanalis, facing obliquely ventromedially (0); contact distinctly curved, processes facing ventrally (1).
- 43) Os palatinum, jugamentum maxillopalatinum: absent (0); present (1).
- 44) – Processus maxillares of the ossa palatina and processus maxillopalatini of the ossa maxillaria: mediolaterally wide plates (wider than fossa choanalis) (0); mediolaterally narrow plates (same width or slightly narrower than fossae) (1); distinctly narrower than fossae (2).
- 45) – Os quadratojugale, dorsal process: absent or vestigial (0), present (1).
- 46) + Maxilla, rostrum maxillare, length with respect to the cranio-caudal length of the external nares in lateral view: shorter (0); equal or longer (1); distinctly longer (2).
- 47) – Mandibula, rostrum mandibulare, dorsal surface: symphysis concave (0); symphysis flat (1).
- 48) – Mandibula, dentary: unforked in lateral view, or with weakly developed dorsal ramus (0); strongly forked having well-developed dorsal rami (1).
- 49) + Mandibula, processus retroarticularis: absent (0); poorly projected, as a small and rounded tubercle (1); distinctly projected, as a short and stout process (2); long and compressed blade-like process, strongly projected (3).
- 50) – Mandibula, cotyla caudalis and lateralis: separated (0); confluent (1).
- 51) + Mandibula, cotyla lateralis and caudalis: short, kidney-shaped articular surface (0); elongate (1) long and strongly curved (2).
- 52) – Mandibula, processus medialis mandibularis, facies articularis parasphenoidalis: vestigial or not developed (0); distinct (1).
- 53) + Mandibula, cotyla medialis: shallow and somewhat round facet (0); distinct facet, extending to the medial border of the articular surface of the articular mandible (1); deep and cranio-caudally elongated facet, protruding beyond the medial border of the mandible (2).
- 54) – Mandibula, processus medialis mandibularis, aspect in dorsal view: triangular (0); long and narrow (1).
- 55) – Quadratum, processus mandibularis medialis, medial area (between articular condylae) in ventral view with a swollen aspect, inflated: absent (0); present (1).
- 56) + Quadratum, processus mandibularis, prominentia submeatica, dorsal projection in lateral view: absent or slightly developed (0); dorsally projected relative to the edge of the processus orbitalis (1); markedly more projected than the processus, with a marked ridge (2).
- 57) – Quadratum, shape of the processus orbitalis: curved and flaring out at its tip (0); almost straight, distal expansion less developed or absent, subequal in proportion to the rest of the process (1); wide and robust, distal expansion vestigial (2); wide at its base with pointed tip (3).
- 58) – Axis, lateral sides of corpus, pneumatic foramina: absent (0), present (1).
- 59) – Axis, processus spinosus: blunt processes (0), blade-like and curved (1).
- 60) – Axis, processus ventralis, distinct blade-like and curved projection: absent (0); present (1).
- 61) – Axis, processus costalis: absent or vestigial (0), present, well developed (1).
- 62) – First series of vertebrae cervicales (from third vertebra cervicalis), processus costales: absent or poorly projected (0), well developed (1).
- 63) + Synsacrum, aspect of centrum and processus costales in ventral view: centrum with a flat aspect and wide processus costales, not completely fused to the lamina (0); most vertebrae with compressed centrum; relatively narrow processes, fused to the lamina; caudal-most elements with morphology similar to condition 0 (1); vertebrae with compressed centrum; relatively narrow processus, fused to the lamina, processus costales gradually shorter towards caudal end of synsacrum (or caudal most absent, angular aspect of the caudal end of synsacrum) (2).
- 64) – Synsacrum (vertebrae lumbicales), vertebral arches, dorsal swell of praecetabular portion adjacent to the medial confluence of ilia: absent (0); present (1).
- 65) + Synsacrum, dorsal surface of postacetabular area, distinctly depressed: absent (0); present (1); with marked muscular impressions (2).

66) + Thoracic vertebrae, fusion: all unfused, notarium absent (0); three vertebrae fused (1); four vertebrae fused (2); five vertebrae fused (3).

67) – Sternum, processus craniolateralis, dorsal view: short, widely spaced (0); variably developed, craniolaterally orientated, less projected than the spina interna (1); greatly elongated cranially, more projected (or reaching) than the spina interna (2); projecting laterally (3).

68) – Sternum, rostrum, spina externa: absent (0); present (1).

69) – Sternum, rostrum, spina interna: absent (0); present (1).

70) – Sternum, rostrum, relative width of spina interna rostri: slender, rostral end narrower than craniolateral process (0); wide, broader than craniolateral process (1).

71) + Sternum, cranial projection of the spina interna rostri: markedly elongate, markedly protruding cranially (0); variably developed (1); significantly short, measuring less than half the length of the processus craniolateralis (2).

72) – Sternum, spina interna in ventral view, strongly concave cranial edge: absent (0); present (1).

73) – Sternum, carina: absent (0); present (1).

74) – Clavicles fused to form a furcula: absent (0); present (1).

75) – Furcula: robust and thick sternal end (0); weak and thin sternal end (1).

76) – Scapula: separated from coracoid (0); fused to coracoid (1).

77) – Scapula, caudal half of blade: expanding distally, with a blunt club-like extremity (0); distal expansion reduced, generally broadest at midline and tapering distally (1).

78) + Coracoid, omal end, dorsal foramen below cotyla scapularis: not excavated (0); vestigial, poorly developed (1); well developed, large opening (2).

79) – Coracoid, shape of the facies articularis clavicularis in medial view: circular to ovate (0); crescent-shaped with overhanging tuberculum brachiale protruding ventromedially (1).

80) – Coracoid, groove for origin of ligamentum acroracohumerale, confluence with facies articularis clavicularis: separated (0); confluent (1).

81) – Coracoid, distinctly protruding processus acroracoides (cranial projection relative to the facies articularis humeralis): present (0); absent (1).

82) – Coracoid, proximal margin of cotyla scapularis with pneumatic openings: absent or few small foramina (0); perforated with large foramina (1).

83) – Coracoid, facies articularis scapularis: shallow (0), excavated and cuplike (1).

84) – Coracoid, base of processus procoracoides, medial edge, distinctly projected crest: absent (0); present (1).

85) + Coracoid, processus lateralis, dorsal view: poorly developed or absent (0); developed, shorter or similar than sternal facet (1); well-developed, distinctly longer than sternal facet, three-pointed sternal end (2).

86) + Coracoid, dorsal surface of distal end, impression for the m. sternocoracoides: not pneumatized (0); only few openings developed (1); strongly pneumatized (2).

87) – Humerus, ulna, radius and carpometacarpus: well-developed separate elements (0); reduced or vestigial (1).

88) – Humerus, incisura capitis obstructed by a tubercle projecting from the border of humeral head: absent (0); present (1).

89) + Humerus, crista bicipitalis, aspect in caudal view: rounded, continuously curving (0); intermediate between squared off and rounded (1); distinctly squared off (generally with a hook-shaped extension) (2).

90) – Humerus, pneumatic foramina at bottom of fossa pneumotricipitalis (or corresponding area in taxa without such fossa): absent (0), present (1).

91) – Humerus, osseous ring or muscular scar surrounding the foramen pneumaticum: absent (0); present (1).

92) – Humerus, ventral condyle, length of main axis relative to that of dorsal condyle, cranial aspect: shorter or subequal (0); longer (1).

93) – Humerus, shallow and crescent-like impression for insertion of musculus brachialis: no (0); yes (1).

94) – Humerus, processus supracondylaris dorsalis developed as a rounded and compact tubercle: absent (0); present (1).

95) – Humerus, position of processus supracondylaris ventralis: on ventral surface or cranioventral margin (0); more cranially located (1).

96) – Humerus, processus flexorius, distal prolongation viewed cranioventrally: absent (0), projects beyond the ventral condyle or moderate, as far as the ventral condyle (1).

97) + Ulna/humerus proportions: ulna distinctly longer than humerus (0); about the same length (1); ulna shorter than humerus (2).

98) – Radius, distal end, expansion in ventral view: distal end with curved aspect, one side more projected than the other (0); distal end wide, both sides expanded (1).

99) – Carpometacarpus, fossa on ventral surface of proximal end, caudal to pisiform process: absent or shallow (0) very deep (1).

100) – Carpometacarpus, trochlea carpalis: caudal rim of ventral portion with deep notch, shallow fossa infratrochlearis (0); caudal rim of ventral portion weakly notched or notch absent, deep and well-defined infratrochlear pit (1).

101) + Ilium, dorsal surface, relative length of cranial and caudal portions, separated by the crista dorsolateralis ilii in dorsal view, and by the acetabular area in lateral view: cranial portion shorter than caudal portion (0); portions approximately of similar length or subequal (1); praeacetabular region distinctly longer than caudal portion but less than twice the length of the latter (2); praeacetabular region around twice or more than twice the length of the postacetabular portion (3).

102) – Pelvis, shape of the crista iliaca dorsalis at the acetabular area, dorsal view: straight line or only slightly curved (0); markedly curved (1).

103) – Pelvis, ala praeacetabularis ilii, cranial end rounded and markedly expanded laterally: absent (0); present (1).

104) + Pelvis, ilium and ischium: broadly fused, small fenestra present (0); fused over only a short distance, large fenestra present (1); not fused, fenestra open (2).

105) – Pelvis, ventral surface of postacetabular ilium: ilioischiatric membrane attaches to ventrolateral edge of ilium (0); ridge for attachment of ilioischiatric membrane inset medially from lateral edge of ilium (1).

106) – Ilium pars postacetabularis, caudal end markedly extended with “tail”-like aspect: absent or poorly developed (0); present (1).

107) – Pelvis, maximum width (measurement at level of the acetabular area related to the cranial end of the praeacetabular area in dorsal view): slightly wider (0); or nearly twice as wide as the praeacetabular width (1).

108) + Pubis, tuberculum praeacetabulare: absent or poorly developed, length shorter than acetabulum size (0); developed, approximately the same size or slightly larger than the acetabulum (1); well projected, distinctly larger than acetabulum (2).

109) + Femur, development of the crista trochanteris: little or no cranial projection (0); somewhat projected, but curved and medially directed, shallow fossa trochanteris (1), projects markedly, deep fossa (2).

110) + Femur/tarsometatarsus proportions: tarsometatarsus significantly longer than femur (0); about the same length as the femur (1); shorter than the femur (2); significantly shorter than the femur, distally does not reach the articular area (3).

111) – Femur, condylus medialis, articular surface in medial view: proximal terminus of cranial rim much farther proximal than proximal terminus of caudal rim (0); proximal terminus of cranial rim subequal to proximal terminus of caudal rim (1).

112) – Femur, markedly bowed: absent (0); present (1).

113) – Tibiotarsus, condylus lateralis and medialis, relative length: condylus lateralis distinctly longer (0); condylus lateralis subequal or slightly longer than medialis (1).

114) – Tibiotarsus, crista cnemialis cranialis: distinctly longer in proximodistal direction than crista cnemialis lateralis (0); short, similar distal projection relative to the crista cnemialis lateralis (1).

115) – Tibiotarsus, sulcus extensorius, distinct medial location: absent (0); present (1).

116) – Tibiotarsus, pons supratendineus: absent (0), present (1).

117) – Tibiotarsus, condylus lateralis, shape in cranial view: proximal margin angular, widens distally (0); elongated with rounded proximal end (1); short with a more rounded aspect (2).

118) – Tarsometatarsus, hypotarsus, general shape and distal extension of hypotarsal ridges relative to foramina vascularia proximalia: truncated and squared off, ending approximately at level of or proximal to foramina (0); acuminated, ending markedly distal to foramina (1).

119) – Tarsometatarsus, hypotarsus: with several well-developed cristae intermediae (0); one well-developed, proximally prominent crista (and a low ridge, if present) (1).

120) + Tarsometatarsus, hypotarsus, hypotarsal sulcus/canal for m. flexor digitorum longus, proximal view: developed as a broad, plantary open sulcus, without medially bordering cristae (0); developed as a broad, plantary open sulcus that is separated by distinct cristae (1); nearly enclosed canal (2); fully enclosed canal (3).

121) – Tarsometatarsus, hypotarsus, sharp medial ridge at cotyla medialis: present (0), absent (1).

122) – Tarsometatarsus, fossa parahypotarsalis lateralis: shallow (0), marked and deeply excavated (1).

123) – Tarsometatarsus, foramen vasculare distale: well developed (0); vestigial, almost completely closed (1).

124) + Tarsometatarsus, distal trochleae, relative distal extension of trochleae metatarsorum II and IV: trochlea metatarsi II more distally projected than trochlea metatarsi IV (0); both trochleae about equally projected distally, distal ends of incisurae intertrochleares lateralis medialis et lateralis levelled (1); trochlea metatarsi II slightly less distally projected than trochlea metatarsi IV, but reaching distally beyond proximal margin of incisura intertrochlearis lateralis (2); trochlea metatarsi II much less distally projected than trochlea metatarsi IV, without reaching proximal margin of incisura intertrochlearis lateralis (3).

Arthrologia and myologia

125) – Ligamentum orbitoquadratum: absent (0); present (1).

126) – Ligamentum postorbitale, origin: frontal part of the process postorbitalis (0); pleurosphenoid part of the process (1); ossiculus postorbitalis (covers the frontal and pleurosphenoid parts of the process) (2).

127) – Ligamentum jugomandibulare internum: absent (0); present (1).

128) – Ligamentum jugomandibulare externum, insertion: undivided (0); bipartite (1).

129) – Ligamentum quadratomandibulare rostrale: absent (0); present (1).

130) + Ligamentum quadratomandibulare rostrale: extensive, not divided (0); bipartite, with medial and lateral parts (1); only medial part present (2).

131) – Ligamentum sphenomandibulare: absent (0); present (1).

132) + Aponeurosis parabasalis, attachment: to postmeatic area (0); to both the postmeatic area and lamina basitemporalis (1); to lamina basitemporalis (2).

133) – M. adductor mandibulae externus, pars caudalis: absent (0); present (1).

134) – M. adductor mandibulae externus, origin on temporal fossa: absent (0); present (1).

135) – M. adductor mandibulae externus, parajugal branch of pars profunda: absent (0); present (1).

136) + M. adductor mandibulae externus, pars profunda and superficialis: fused (0); partially separated (1); separated (2).

137) – M. intramandibularis: absent (0); present (1).

138) – M. pseudotemporalis, ventral temporal portion: absent (0), present (1).

139) – M. pseudotemporalis, attachment to os suprangulare: absent (0); present (1).

140) – M. pseudotemporalis and m. quadratomandibularis, complete or almost complete separation: absent (0); present (1).

141) – M. quadratomandibularis, insertion: beyond the dorsal margin of the mandible (0); does not extend so far dorsally (1).

142) – M. quadratomandibularis, aspect at origin: thin, superficial aponeurosis (0); strong aponeurotic sheet (1).

143) – M. pterygoideus, pars medialis: separated into three unipennate portions (0); complex multipennate system (1).

144) – M. pterygoideus, fasciculus caudalis: absent (0); present (1).

145) – M. pterygoideus, pars medialis enclosed in aponeurotic sheath: absent (0); present (1).

146) – M. protractor pterygoidei et quadrati: undivided (0); bipartite (1).

147) – M. depressor mandibulae externus, insertion: on fossa caudalis mandibularis (0); extending beyond fossa caudalis (1).

148) – M. columellae, perforated by n. glossopharyngealis et vagi: absent (0); present (1).

149) – M. levator palpebrae dorsalis, muscular portion: well developed (0); poorly developed, thin layer (1).

150) – M. levator palpebrae dorsalis, origin from os ectethmoidale: absent (0); present (1).

151) – M. orbicularis palpebrarum, morphology: muscular fibres (0); ligament (1).

152) – M. orbicularis palpebrarum, origin from ossiculi supraorbitales: absent (0); present (1).

153) – M. depressor palpebrae ventralis: well developed (0); vestigial (1).

154) + M. obliquus dorsalis, origin: muscle undivided (0); divided into two parts (1); divided into three parts (2).

155) – M. coracobrachialis cranialis, enormously developed: absent (0); present (1).

156) – M. deltoideus, pars minor, caput ventrale fused to m. supracoracoideus: absent (0); present (1).

157) + M. latissimus dorsi, pars caudalis, origin extensive: absent (0), present, attachment to 2 ribs (1); very extensive, attachment to four ribs (2).

158) – M. latissimus dorsi, pars metapatagialis, relative position to the m. serratus superficialis: over dorsal surface (0); adjacent (1).

159) – M. interosseus dorsalis, insertion: undivided (0); divided (1).

160) + M. ulnometacarpalis dorsalis, origin: only dorsal head present (0); bipartite, small ventral head (1); bipartite, large ventral and dorsal head (2).

161) M. supinator, distinctly longer: absent (0); present (1).

162) – M. ilirotrochanterici cranialis and medius: separated (0); fused (1).

163) – *M. fibularis longus*, sesamoid: absent (0); present (1).

164) – *M. flexor hallucis longus* and *m. flexor digitorum longus*: not fused (0); fused (1).

Partes corporis (skeletal and integumental parts)

165) – Rostrum + rhamphoteca, bill shape: straight (0); slightly decurved (1); decurved toward tip (2); strongly decurved (3).

166) – Rostrum maxillare + rhamphoteca, dorsal plate, lateral grooves: absent (0); present (1).

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

168) + Rostrum mandibulare + rhamphoteca, ventral plate, lateral grooves: posteriorly convergent and contacting each other (0); parallel (1); posteriorly divergent (2).

169) – Rostrum mandibulare + rhamphoteca, ventral plate, lateral grooves: absent (0); present (1).

170) + Hallux, development (Mayr 2011: character 110 modified): absent (0); greatly reduced, measuring less than half the length of the proximal phalanx of third toe (1); long (2).

Integument

171) – Ramphoteca, colour of maxilla: blackish (0); horn (1); brownish (2); reddish (3); olive (4); greyish (5); yellowish (6).

172) – Ramphoteca, colour of mandible: blackish (0); pale with dark tip (1); pink to reddish (2); brownish (3); olive (4); greyish (5); horn (6); yellowish (7).

173) + 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).

174) – Colour of iris: brownish (0); yellowish (1); reddish (2); whitish (3).

175) – Vexillum, pars pennacea, feather structure: absent (0); present (1).

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

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

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

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

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

181) * Jugulum (chin), feather pattern: whitish immaculate (0); brownish-rufous immaculate (1); greyish immaculate (2); streaked (3); bicoloured barred (4).

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

183) * Pars interscapularis (dorsal collar), feather pattern: immaculate (0); bicoloured barred (1); *Nothura*-like (2); tricoloured barred (3); mixed (4); *ingoufi*-like (5).

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

185) * Pars spinalis + pars pelvica + pteryla scapulothoracalis (dorsum + mantle + rump), feather pattern: immaculate (0); bicoloured barred (1); *Nothura*-like (2); tricoloured barred (3); mixed (4);

ingoufi-like (5); dimorphic: male immaculate, female bicoloured barred (6).

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

187) * Pars cervicalis (lateral neck), feather pattern: bicoloured barred (0); immaculate (1); streaked (2); dimorphic: male immaculate, female bicoloured barred (3).

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

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

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

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

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

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

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

195) – Pars sternalis, superior (breast), feather pattern: dark colours, greyish, brownish or rufous immaculate (0); whitish immaculate (1); bicoloured barred (2).

196) – Pars sternalis, inferior (abdomen): brownish or rufous immaculate (0); whitish immaculate (1); bicoloured barred (2).

197) * Pars abdominalis (belly), feather pattern: brownish or greyish immaculate (0); whitish immaculate (1); rufous immaculate (2); bicoloured barred (3); scalloped (4).

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

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

200) * Pteryla lateralis (flank, upper side), feather pattern: immaculate (0); bicoloured barred (1); *Nothura*-like (2); tricoloured barred (3).

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

202) + Rectrices (tail): rudimentary, indistinct from upper tail coverts (0); poorly developed but distinct from upper tail coverts (1); well developed (2).

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

204) – Remiges alulae (bastard wing), vexillum pennae internum (inner vane), feather pattern: bicoloured barred (0); brownish immaculate (1); rufous immaculate (2).

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

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

207) – Remiges secundarii externa (outer secondary remiges, i.e. the secondaries adjacent to primaries), vexillae pennae externum (outer vane), feather pattern: brownish to greyish immaculate (0); rufous immaculate (1); bicoloured barred (2).

208) – Remiges secundarii interna (inner secondary remiges, i.e. the secondaries adjacent to primaries), vexillae pennae internum (inner vane), feather pattern: brownish to greyish immaculate (0); rufous immaculate (1); bicoloured barred (2).

209) * Remiges secundarii interna (inner secondary remiges, i.e. the secondaries next to the body), vexillae pennae externum (outer vane), feather pattern: brownish immaculate (0); rufous immaculate (1); bicoloured barred (2); tricoloured barred (3).

210) * Remiges secundarii interna (inner secondary remiges, i.e. the secondaries next to the body), vexillae pennae internum (inner vane), feather pattern: immaculate (0); bicoloured barred (1); tricoloured barred (2).

211) – Tectrices primariae dorsales (greater primary coverts), vexillae pennae externum (outer vane), feather pattern: rufous immaculate (0); brownish immaculate (1); bicoloured barred (2).

212) – Tectrices primariae dorsales (greater primary coverts), vexillae pennae externum (inner vane), feather pattern: rufous immaculate (0); brownish immaculate (1); bicoloured barred (2).

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

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

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

216) – Tectrices primariae ventrales minores (lesser under primary coverts), feather pattern: rufous immaculate (0); brownish immaculate (1); whitish immaculate (2); bicoloured barred (3).

217) – Tectrices primariae ventrales mediae (median under primary coverts), feather pattern: rufous immaculate (0); brownish immaculate (1); whitish immaculate (2); bicoloured barred (3).

218) – Tectrices primariae ventrales majores (greater under primary coverts), feather pattern: rufous immaculate (0); brownish immaculate (1); whitish immaculate (2); bicoloured barred (3).

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

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

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

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

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

224) * Pars cruralis (thigh), feather pattern: brownish immaculate (0); bicoloured barred (1); scalloped (2); tricoloured barred (3); rufous immaculate (4).

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

226) + 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).

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

228) + Podoteca ventralis, plantar-tarsi scutes, surface aspect: relatively smooth (0); relatively roughened (1); distinctly rasp-like (2).

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

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

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

232) + Acropodium, scute number on hind toe: one (0); two (1); three (2); four or five (3); six or more (4).

233) – Tarsi, colour pattern: brownish (0); greyish (1); pinkish to reddish (2); yellowish (3); greenish to olive (4).

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

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

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

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

238) – Preorbital line: absent (0); present (1).

239) – Supraorbital line: absent (0); present (1).

240) – Postorbital line: absent (0); present (1).

241) – Malar line: absent (0); present (1).

242) – Auricular line: absent (0); present (1).

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

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

245) + Aftershaft of adult feathers: present, shorter than main shaft length (greater than half main shaft length) (0); present, significantly shorter than main shaft (less than half length of main shaft) (1); absent (2).

246) – Contour feathers around eyes modified into ‘eyelashes’: absent (0); present (1).

247) – Filoplumes: present (0); absent (1).

248) – Dorsal surface of tarsus, scale pattern: transverse scales (0); upper tarsus reticulated scales, lower half of tarsus transverse scales (1).