

Evidence for a sister group relationship between the Madagascan mesites (Mesitornithidae) and the cuckoos (Cuculidae)

(Aves)

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Abstract

The Madagascan Mesitornithidae (mesites or roatelos) are an enigmatic and poorly known group of small terrestrial birds. In this study their phylogenetic relationships are analyzed using a data set of 91 morphological characters and 29 extant avian taxa. Parsimony analysis of this data strongly supports monophyly of the taxon (Mesitornithidae + Cuculidae [cuckoos]) which has not been proposed before. Derived anatomical, parasitological, and behavioral characters are presented which support monophyly of this clade. Monophyly of the taxon (Mesitornithidae + Cuculidae) is also supported by a preliminary parsimony analysis of DNA sequences of two nuclear, protein-coding genes, RAG-1 and myoglobin intron II. In addition, sistergroup relationships of several other gruiform and non-gruiform taxa (Columbidae and Pteroclididae) are supported by derived morphological characters. Monophyly of a taxon including the remaining “Gruiformes” (i.e. excluding Mesitornithidae) is neither supported by morphological nor preliminary molecular analyses.

Key words: Aves, Mesitornithidae, Cuculidae, “Gruiformes”, phylogeny, osteology, nuclear genes

Introduction

The Mesitornithidae (mesites or roatelos) are an enigmatic group of small terrestrial birds which are endemic to Madagascar and which are among the most poorly known of all extant avian taxa (EVANS et al. 1996). According to current classifications (e.g., DEL HOYO et al. 1996), they are included in the “Gruiformes”, together with Rallidae (rails, coots, and gallinules), Heliornithidae (finfoots), Gruidae (cranes), Aramididae (limpkins), Psophiidae (trumpeters), Rhynochetidae (kagu), Eurypygidae (sunbittern), Cariamididae (seriemas), Otididae (bustards), and Turnicidae (hemipodes). Although this assemblage is probably polyphyletic (e.g., HOUDE et al. 1997, LIVEZEY & ZUSI 2001, this study), in the following

the term “Gruiformes” is used in the sense of DEL HOYO et al. (1996).

Skeletons and spirit specimens of mesites are very rare in ornithological collections and consequently there are only few studies on the anatomy of these birds (MILNE-EDWARDS 1878, FORBES 1882, LOWE 1924, LAVAUDEN & POISSON 1929). Mesites were not examined by FÜRBRINGER (1888) on whose comparative anatomical studies many classifications (e.g., WETMORE 1960) are based. LOWE (1924: 1151) concluded that the taxon “stands entirely by itself, a survival of an early group which cannot be included in any order of present-day birds”. VERHEYEN (1958), on the other hand, included mesites in his Turni-

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Tab. 1. Taxa and samples used in the molecular analysis. — Acronyms: AM: Australia Museum, Sydney; FMNH: Field Museum of Natural History, Chicago; LSUZM: Museum of Natural Science, Louisiana State University; NRM: Swedish Museum of Natural History; PFAO: Percy FitzPatrick Institute of African Ornithology, University of Cape Town; TJP: Thomas J. PARSONS; ZMCU: Zoological Museum, University of Copenhagen. — References for sequences published in GenBank: a) JOHANSSON et al. (2001); b) GROTH & BARROWCLOUGH (1999); c) JOHANSSON & ERICSON (2003), d) ERICSON et al. (2003); e) MAYR et al. (2003).

Species	Family	Sample no.	Origin	GenBank accession numbers	
				RAG-1	Myoglobin
<i>Mesitornis unicolor</i> (DES MURS 1845)	Mesitornithidae	FMNH 345610	Madagascar	AY756082	AY756085
<i>Turnix varia</i> (LATHAM 1801)	Turnicidae	AM LAB1062	Australia	AY756083	AY756086
<i>Afrotis atra</i> (LINNAEUS 1766)	Otididae	LSUMZ B-8672	Captive	AY339100 ^d	AY339073 ^d
<i>Grus canadensis</i> (LINNAEUS 1758)	Gruidae	TJP	unknown	AY339110 ^d	AY339083 ^d
<i>Aramides ypecaha</i> (VIEILLOT 1819)	Rallidae	NRM 937389	Paraguay	AY756084	AY756087
<i>Larus fuscus</i> LINNAEUS 1758	Laridae	NRM 946538	Russia	AY339113 ^d	AY339086 ^d
<i>Stercorarius macormicki</i> SAUNDERS 1893	Stercorariidae	NRM 896303	Antarctica	AY339105 ^d	AY339078 ^d
<i>Arenaria interpres</i> (LINNAEUS 1758)	Scolopacidae	NRM 946593	Russia	AY339102 ^d	AY339075 ^d
<i>Gallinago gallinago</i> (LINNAEUS 1758)	Scolopacidae	NRM 20016235	Sweden	AY339109 ^d	AY339082 ^d
<i>Jacana jacana</i> (LINNAEUS 1766)	Jacanidae	NRM 937364	Paraguay	AY339112 ^d	AY339085 ^d
<i>Charadrius collaris</i> VIEILLOT 1818	Charadriidae	TJP	unknown	AY339106 ^d	AY339079 ^d
<i>Haematopus ater</i> VIEILLOT & OUDART 1825	Haematopodidae	TJP	unknown	AY339111 ^d	AY339084 ^d
<i>Burhinus bistriatus</i> (WAGLER 1829)	Burhinidae	LSUMZ B-19210	Captive	AY339103 ^d	AY339076 ^d
<i>Pterocles gutturalis</i> SMITH 1836	Pteroclididae	PFAO 37 YtS	South Africa	AY339116 ^d	AY339089 ^d
<i>Scardafella squammata</i> (LESSON 1831)	Columbidae	NRM 956728	Paraguay	AY339121 ^d	AY339094 ^d
<i>Corythaixoides leucogaster</i> (RÜPPELL 1842)	Musophagidae	ZMCU P509	Kenya	AF294654 ^a	AY233368 ^e
<i>Opisthocomus hoazin</i> (MÜLLER 1776)	Opisthocomidae	LSU B-10753	Peru	AY233357 ^e	AY233363 ^e
<i>Cuculus canorus</i> LINNAEUS 1758	Cuculidae	NRM 996341	Sweden	AF294655 ^a	AY165808 ^c
<i>Chauna torquata</i> (OKEN 1816)	Anhimidae	TJP	unknown	AF143728 ^b	AY165805 ^c
<i>Alectura lathamii</i> GRAY 1831	Megapodiidae	LSUMZ B-20851	Captive	AF294687 ^a	AY165801 ^c

ciformes, together with Turnicidae, Thinocoridae (seed-snipe), and Pteroclididae (sandgrouse). OLSON (1979) and some earlier authors (e.g., MILNE-EDWARDS 1878, FORBES 1882) suggested affinities to the Eurypygidae, Rhynchotidae, and Ardeidae (herons), whereas HESSE (1990) considered mesites to be the sister taxon of the Rallidae. A cladistic analysis of the interrelationships between anseriform, “ciconiiform”, “gruiform”, and charadriiform birds by ERICSON (1997) did not support “gruiform” affinities of the Mesitornithidae but showed these to be basal to the aforementioned taxa. A study of “gruiform” phylogeny by LIVEZEY (1998) also resulted in a basal position of the Mesitornithidae, although this analysis was mainly focused on the relationships within the Rallidae and the ingroup included only gruiform birds. A preliminary analysis of skull and vertebral characters by LIVEZEY & ZUSI (2001) showed the Mesitornithidae to be the sister taxon of a clade including Turnicidae, Columbidae (doves), Pteroclididae, and charadriiform birds but the results were explicitly considered preliminary by the authors.

The Mesitornithidae are among the few avian taxa that were not included in the egg white protein and

DNA-DNA hybridization studies of SIBLEY & AHLQUIST (1972, 1990). The only molecular study that has been carried out so far is by HOUDE et al. (1997) who analyzed the 12 S rDNA but also could not conclusively resolve the position of the Mesitornithidae (which were shown in different positions depending on the weighting scheme applied to the data sets). Because of unusually large genetic distances to the other ingroup taxa, HOUDE et al. (1997: 141) concluded that mesites “either represent an ancient lineage, unrelated to Gruiformes, or an unusually rapid rate of evolution has erased any evidence of that relationship in their 12 S rDNA.”

A major shortcoming of most of the above cited analyses is that no derived characters were given which establish the relationships of the Mesitornithidae, and that comparisons were mainly restricted to other “gruiform” birds. Here we present morphological and preliminary molecular evidence that supports a sister group relationship between Mesitornithidae and Cuculidae (cuckoos). Analysis of the morphological data was completed by one of us (G.M.) before the molecular data was analysed, and the results of both analyses were obtained independently.

Material and methods

Analysis of the morphological data

Apart from representatives of all other higher avian taxa, skeletons of the following taxa have been examined in the collections of Forschungsinstitut Senckenberg, the Museum für Naturkunde, Berlin, and the Swedish Museum of Natural History: Mesitornithidae: *Mesitornis* (partial skeleton), *Monias*. Tinamidae: *Crypturellus*, *Nothura*, *Rhynchotus*, *Tinamus*. Cracidae: *Crax*, *Nothocrax*, *Penelope*, *Pipile*. Phasianidae: Tetraoninae: *Bonasa*, *Dendragapus*, *Lagopus*, *Lyrurus*, *Tetrao*, *Tetrastes*; Phasianinae: *Alectoris*, *Catreus*, *Chrysolophus*, *Coturnix*, *Crossoptilon*, *Gallus*, *Lophophorus*, *Lophura*, *Pavo*, *Phasianus*, *Polyplectron*, *Syrmaticus*, *Tragopan*; Numidinae: *Acryllium*, *Numida*; Meleagrinae: *Meleagris*. Turnicidae: *Turnix*. Gruidae: *Anthropoides*, *Balearica*, *Bugeranus*, *Grus*. Aramidae: *Aramus*. Psophiidae: *Psophia*. Rhynochetidae: *Rhynochetos*. Eurypygidae: *Eurypyga*. Cariamidae: *Cariama*, *Chunga*. Otididae: *Choriotis*, *Otis*, *Tetrastes*. Rallidae: *Amaurornis*, *Aramides*, *Crex*, *Fulica*, *Gallinula*, *Gallirallus*, *Himantornis* (few postcranial elements), *Laterallus*, *Limnocorax*, *Pardirallus*, *Porphyrio*, *Porphyriops*, *Porphyrola*, *Porzana*, *Rallus*. Heliornithidae: *Heliornis*. Jacanidae: *Actophilornis*. Haematopodidae: *Haematopus*. Thinocoridae: *Thinocorus*. Charadriidae: *Charadrius*, *Pluvialis*, *Squatarola*, *Vanellus*. Scolopacidae: *Actitis*, *Calidris*, *Gallinago*, *Limosa*, *Numenius*, *Scolopax*, *Tringa*. Recurvirostridae: *Himantopus*, *Recurvirostra*. Burhinidae: *Burhinus*. Glareolidae: *Cursorius*, *Glareola*, *Pluvianus*. Laridae: *Larus*, *Sterna*. Alcidae: *Aethia*, *Alca*, *Alle*, *Cephus*, *Cyclorhynchus*, *Fratercula*, *Ptychorhamphus*, *Uria*. Opisthocomidae: *Opisthocomus*. Musophagidae: *Corythaixoides*, *Crinifer*, *Musophaga*, *Tauraco*. Cuculidae: *Carpococcyx*, *Centropus*, *Ceuthmochares*, *Chrysococcyx*, *Clamator*, *Coccyzus* (skull), *Coua*, *Crotophaga*, *Cuculus*, *Eudynamis*, *Geococcyx*, *Guira*, *Rhamphococcyx*, *Saurothera*. Pteroclididae: *Syrhaptus*, *Pterocles*. Columbidae: *Calaenas*, *Chalcophaps*, *Columba*, *Ducula*, *Galliolomba*, *Geopelia*, *Goura*, *Ocyphaps*, *Oena*, *Oreopelia*, *Ptilinopus*, *Streptopelia*, *Treron*, *Trugon*, *Turtur*, *Zenaidra*. Ardeidae: *Agamia*, *Ardea*, *Ardeola*, *Botaurus*, *Butorides*, *Cochlearius*, *Egretta*, *Ixobrychus*, *Nycticorax*.

Nomenclature of the extant genera and species follows MORONY et al. (1975). Information on the osteology of charadriiform birds was further taken from STRAUCH (1978).

All non-osteological characters were taken from the literature. Anatomical terminology follows BAUMEL & WITMER (1993), VANDEN BERGE & ZWEERS (1993), and BREAZILE & KUENZEL (1993).

91 characters of 27 ingroup taxa were coded for the phylogenetic analysis with PAUP 3.1 (SWOFFORD 1993) (see character matrix in Appendix II). The shortest tree was found with the heuristic search option, and character transformation was

evaluated with the accelerated transformation (ACCTRAN) mode. Four characters were coded as ordered. The consistency index (CI), retention index (RI), and rescaled consistency index (RC) were calculated. The robustness of the tree was tested with a bootstrap analysis of 1000 replicates.

Outgroup comparisons were made with the palaeognathous Tinamidae and with representatives of the Galliformes which were shown to be the most basal neornithine taxa in recent phylogenetic analyses (e.g., SIBLEY & AHLQUIST 1990, GROTH & BARROWCLOUGH 1999, LIVEZEY & ZUSI 2001).

Analysis of the molecular data

In order to compare the morphological results with those obtained from analyses of molecular data, we performed a phylogenetic analysis of sequence data obtained from two nuclear genes (see below). We have used one representative each of 18 families of Neoaves (sensu SIBLEY & MONROE 1990) (Table 1). As outgroups we used a screamer (*Chauna torquata*, Anhimidae) and a megapode (*Alectura lathami*, Megapodiidae), i.e. two representatives of Galloanseres, the sister group to Neoaves (GROTH & BARROWCLOUGH 1999, VAN TUINEN et al. 2000).

DNA was extracted from tissue or blood specimens using the QIAamp[®] DNA Mini Kit (QIAGEN[®]) following the manufacturer's recommendations. Laboratory procedures for amplifying and sequencing the RAG-1 and myoglobin (intron II) genes follow protocols described in ERICSON et al. (2002) and IRESTEDT et al. (2002).

The multiple segments obtained by sequencing with different primers were assembled to complete sequences using SeqMan IITM (DNASTAR[®]). When nucleotides could not be unambiguously determined, the IUB coding system was used. The combined sequences were aligned by eye with MegAlignTM (DNASTAR[®]). The DNA segments from the two genes were analysed both separately and in combination. There were no indels observed in RAG-1, and the myoglobin sequences were easily aligned as well, due to a rather low number of indels.

Parsimony and maximum-likelihood analyses were performed using Paup* 4.0b10 (SWOFFORD 1998). Searches for most parsimonious trees were done under the heuristic search option, with random additions of taxa and tree bisection-reconnection (TBR) branch-swapping. Ten random additions were performed to reduce the risk of finding local optima only. Data were unweighted and coded as unordered. Gaps were treated as missing values. The strict consensus tree was based on all the most parsimonious trees obtained, and nodal supports were estimated with 1000 bootstrap replicates.

The GTR + G + I model of evolution of nucleotide substitutions was chosen for the maximum-likelihood analysis of the combined data set using Modeltest 3.06 (POSADA & CRANDALL 1998).

Results

Morphological, behavioral, and parasitological evidence supporting monophyly of the taxon (Mesitornithidae + Cuculidae)

Analysis of the 91 morphological characters of the character matrix in Appendix II resulted in 191 most

parsimonious trees (Length = 320, CI = 0.32, RI = 0.60, RC = 0.19), the strict consensus tree of which is shown in Fig. 1. The analysis supported monophyly of the taxon (Cuculidae + Mesitornithidae) which received a high bootstrap value of 88 %. Monophyly of the taxon (Mesitornithidae + Cuculidae) is supported by the fol-

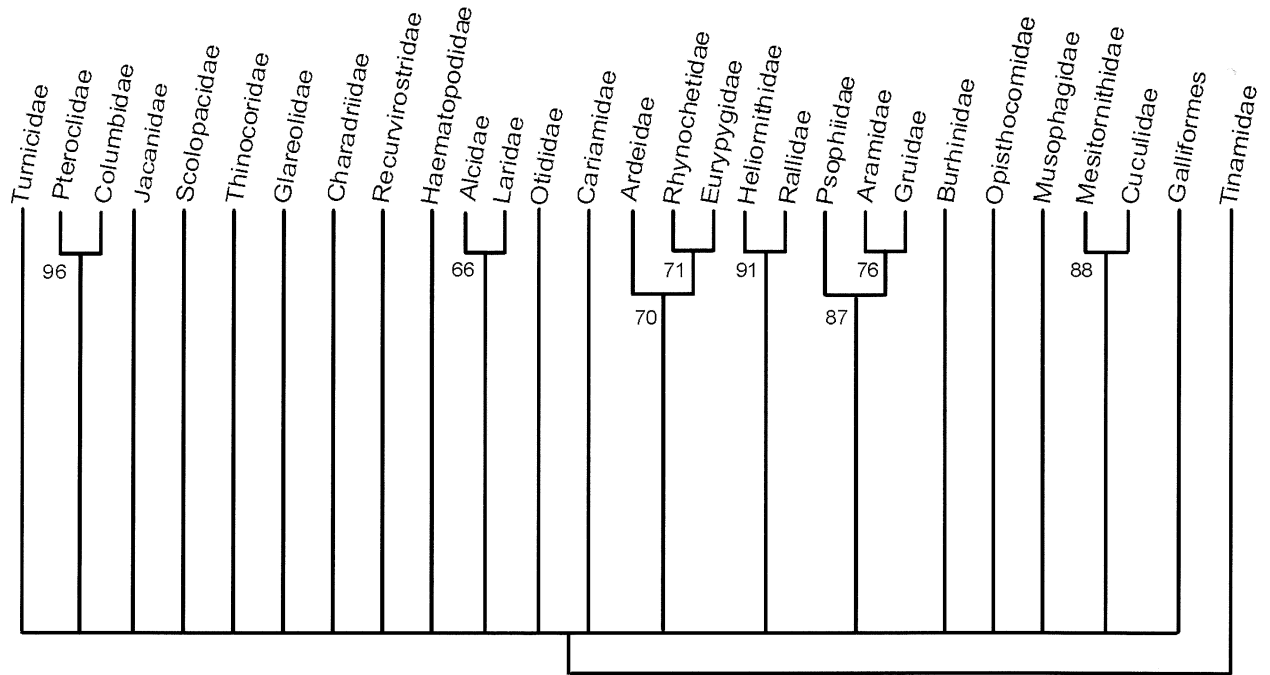


Fig. 1. Strict consensus tree of 191 most parsimonious trees (Length = 320, CI = 0.32, RI = 0.60, RC = 0.19) resulting from an analysis of the morphological data set. Bootstrap values of more than 50 % are indicated.

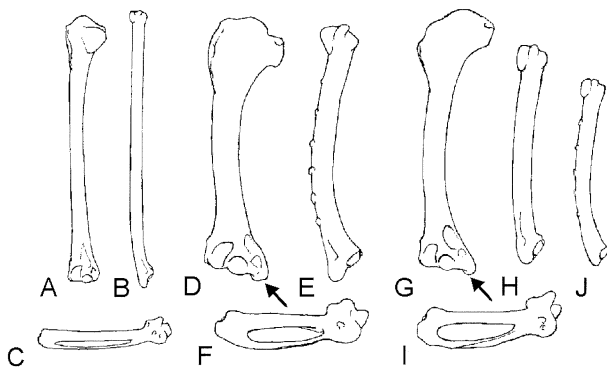


Fig. 2. Right humerus (A, D, G), ulna (B, E, H, J), and carpo-metacarpus (C, F, I) of Ardeidae, Mesitornithidae, and Cuculidae in comparison. A, B, C: *Ixobrychus minutus* (Ardeidae), D, E, F, *Monias benschi* (Mesitornithidae), G, H, I: *Guira guira* (Cuculidae); J, *Ceuthmochares aereus* (Cuculidae). Note the marked papillae remigales in E and J; the arrows indicate the processus flexorius of the humerus. A–C, D–F, and G–J are shown in the same magnification.

lowing derived characters (numbers in parentheses refer to the characters in Appendix I):

(6) Os ectethmoidale greatly expanded and more or less inflated, plate-like, with dorsal margin largely fused with os frontale (Figs. 6 B, E).

(16) Cranium, fossae temporales well developed, length reaching at least $\frac{1}{3}$ of the circumference of the dorsal half of the cranium.

(55) Humerus, processus flexorius strongly protruding in ventro-distal direction (Fig. 2). The distal end of the humerus of Mesitornithidae and Cuculidae is very similar and an equally strongly protruding processus flexorius occurs in only few other taxa, as the extinct Sylphornithidae (see MOURER-CHAUVIRÉ 1988), the Coliidae, and piciform birds. We consider the absence of this feature in the closely related (HUGHES 2000, JOHNSON et al. 2000, SORENSON & PAYNE 2002) genera *Cuculus* and *Chrysococcyx* to be autapomorphic, possibly due to the elongated wing of these taxa.

(61) Os carpi ulnare with crus longum abbreviated, shorter than crus breve (Fig. 3). The derived morphology of the os carpi ulnare was noted by HUGHES (2000) as evidence for a sister group relationship between Cuculidae and Musophagidae. However, the os carpi ulnare of mesites closely resembles the corresponding bone of turacos. The corresponding bone of the Cuculidae exhibits an even more derived morphology.

(64) Pelvis with prominent laterally protruding flange in midsection of crista dorsolateralis ilii; this character otherwise occurs in Opisthocomidae, Rallidae, and few Galliformes.

(73) Tarsometatarsus, hypotarsus block-like, enclosing two canals which in the Cuculidae enclose the tendons of musculus flexor digitorum longus and m. flexor hallucis longus (BERGER 1960: 73); we assume that the same tendons also pass through the canals in the very similar hypotarsus of the Mesitornithidae (Figs. 4 B, E).

(76) Tarsometatarsus, proximal end, tuberositas musculi tibialis cranialis situated on medial side of shaft, fora-

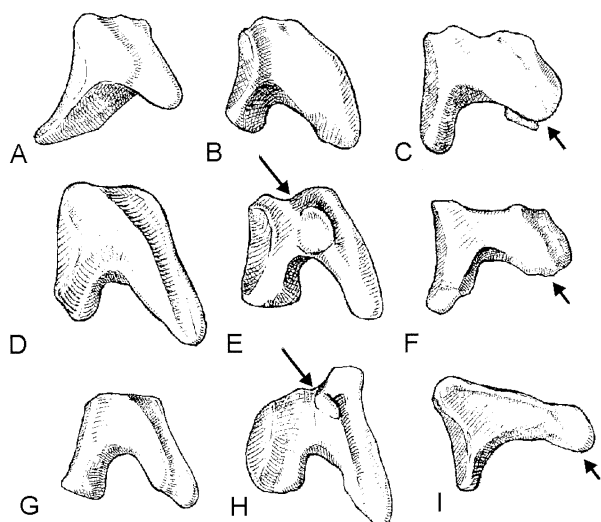


Fig. 3. Right os carpi ulnare in comparison. A: *Rhynchotus rufescens* (Tinamidae); B: *Psophia crepitans* (Psophiidae); C: *Monias benschi* (Mesitornithidae); D: *Aramus guarauna* (Aramidae); E: *Haematopus ostralegus* (Haematopodidae); F: *Corythaixoides concolor* (Musophagidae); G: *Aramides saracura* (Rallidae); H: *Glareola pratincola* (Glareolidae); I: *Guiraguira* (Cuculidae). The large arrows indicate the tuberculum at the area of insertion of ligamentum humerocarpaceum in charadriiform birds (character 60 in the matrix in Appendix II). The small arrows point to the short crus longum in Mesitornithidae, Musophagidae, and Cuculidae. Not to scale.

mina vascularia proximalia widely separated (Fig. 4). This character occurs in many taxa of the “higher land birds”, but is absent in “gruiform” birds.

(77) Tarsometatarsus, distal end, trochlea metatarsi II hardly turned in plantar direction, without plantarly or medially projecting wing-like flange, dorsal surface convex, essentially rounded, and without distinct sulcus (Figs. 4 A, D).

(90) Dorsal and ventral side of podotheca of tarsometatarsus scutellate, i.e. covered with large scales.

Characters (55), (61), and (76) also occur in the Musophagidae and were optimized as apomorphies of a more inclusive clade in the analysis with PAUP (see discussion).

In addition to the above listed characters, *Monias* (Mesitornithidae), most Musophagidae, and many Cuculidae share distinctly raised papillae remigales on the ulna (character 57, Figs. 2 E, J). *Monias* and most Cuculidae further share an osseous bridge from processus transversus to midsection of the corpus vertebrae of at least the 7th and 8th cervical vertebra (ch. 27, Figs. 6 C, F).

MASCHA (1904) further described an unusual derived structure on the hamuli of the distal barbulae of the wing feathers of Cuculidae and Musophagidae which in these taxa bear distinct “prong”-like projections (MASCHA 1904: pl. 30, figs. 16, 17). We could confirm the presence of these structures on the hamuli of the remiges of the

Mesitornithidae. Apart from their occurrence in the wing converts of some Columbidae (CHANDLER 1916: pl. 29, fig. 67 a), these “prongs” were not found in any other of the numerous taxa investigated by MASCHA (1904) and CHANDLER (1916).

Mesitornithidae and Cuculidae further share a primitive type of the dorsal horn of the spinal grey matter which is found in few other avian taxa (character 91 in Appendix I, see WOODBURY 1998).

Another derived similarity between Mesitornithidae, Musophagidae, and Cuculidae is that the young are gaping when being fed (APPERT 1968: 411) — a behavior which, according to APPERT (1968), is otherwise only known from the Coliidae (mousebirds), Upupiformes (hoopoes and wood-hoopoes), and from piciform and passeriform birds.

According to MEY (1993), the ischnoceran chewing lice of the Mesitornithidae most closely resemble those of the Cuculidae, Piciformes, Passeriformes, and Trogoniformes (all belong to the *Degeeriella*-complex).

Additional clades that were retained in the bootstrap analysis of the morphological data

A taxon including Psophiidae, Aramidae, and Gruidae received bootstrap support of 87 %; a non-homoplastic (i.e. CI = 1.0) apomorphy of this clade is: (72) tibiotarsus with prominent tubercle latero-distal to the pons supratendineus; this taxon further shares the following apomorphies: (43), facies visceralis of sternum with numerous pori pneumatici along midline and (44) lateral margins and margo caudalis without notches/fenestrae,

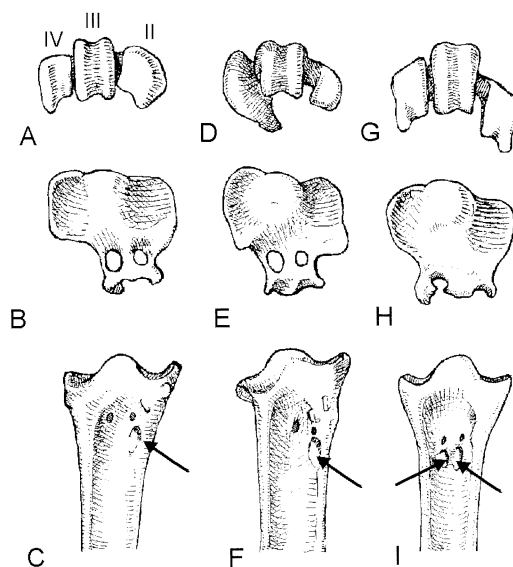


Fig. 4. Right tarsometatarsus in comparison. A, B, C: *Monias benschi* (Mesitornithidae); D, E, F: *Guiraguira* (Cuculidae); G, H, I: *Eurypyga helias* (Eurypygidae). A, D, G, distal end in distal view, B, E, H, proximal end in proximal view, C, F, I, proximal end in dorsal view. The trochleae metatarsorum are numbered (Roman numerals), the arrows indicate the tuberositas musculi tibialis cranialis. Not to scale.

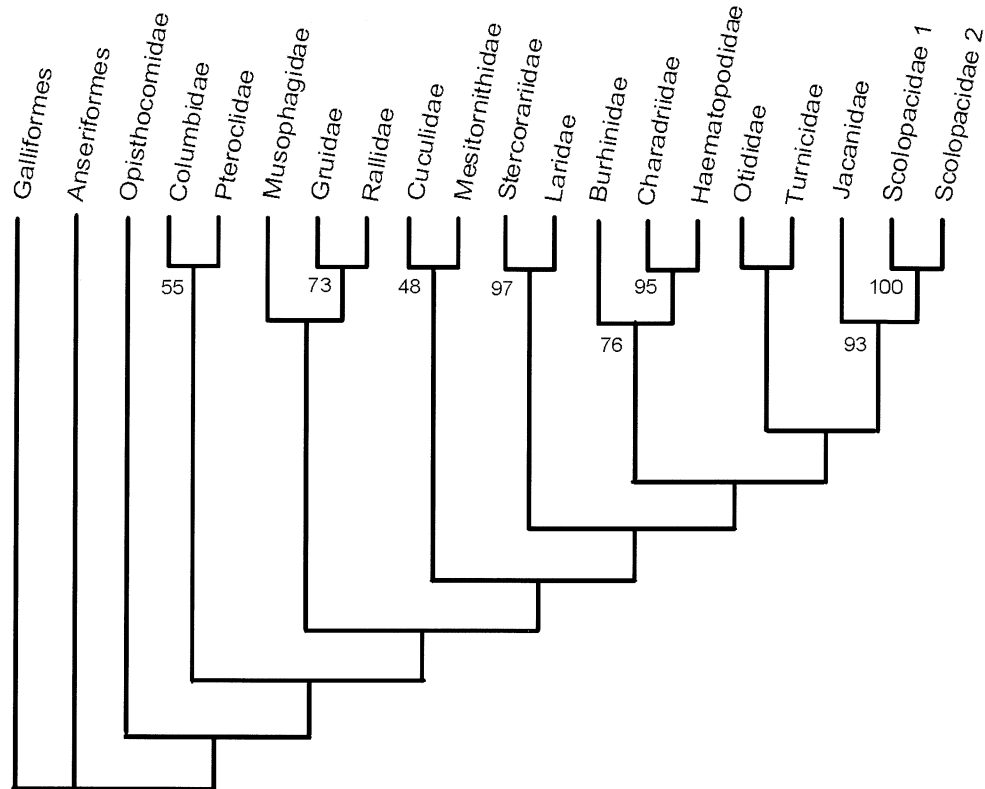


Fig. 5. Single most parsimonious tree resulting from an analysis of the molecular data set (Length = 1177, CI = 0.69, RI = 0.38, RC = 0.26). Bootstrap values (1000 replicates) are indicated.

(66) pelvis with cristae iliacae dorsales fused over entire length with crista spinosa of synsacrum, thus forming a completely closed canalis iliosynsacralis.

Monophyly of the taxon (Aramidae + Gruidae) was supported with a bootstrap value of 76%; apomorphies of this taxon are: (2) nostrils schizorhinal, (17) fenticuli occipitales present in cranium of adult birds, (31) several thoracic vertebrae fused to a notarium, (63) pelvis with praeacetabular part of ilium much longer than postacetabular part, alae ischii dorsoventrally narrow, and incisura caudalis deep.

Sister group relationship between Rallidae and Heliornithidae is supported with a bootstrap value of 91%; a previously unrecognized non-homoplastic apomorphy of this clade is: (75) hypotarsus with crista lateralis well developed but crista medialis strongly reduced to a proximodistally short osseous lamella; an additional apomorphy of this taxon is: (51) humerus without foramina pneumatica at bottom of fossa pneumotricipitalis.

Sister group relationship between Eurypygidae and Rhynochetidae has a bootstrap support of 71%. Apomorphies of this taxon are: (2) nostrils schizorhinal, (31) several thoracic vertebrae fused to a notarium, (69) pelvis with incisura marginis caudalis very deep, U-shaped, spina dorsolateralis long and narrow, (82) musculus

longus colli ventralis attaching on processus articulares caudales of section II of cervical vertebrae and transferring its attachment to ribs in section I.

The latter taxon was shown to be the sister taxon of the Ardeidae and this clade received a bootstrap support of 70%. This clade is supported by the following non-homoplastic apomorphy: (8) os palatinum, pars lateralis, caudal end truncate with distinct angulus caudolateralis which has about equal caudal extent to the processus pterygoideus; additional apomorphies of this taxon are: (16) cranium, fossae temporales well developed, length reaching at least 1/3 of the circumference of the dorsal half of the cranium, (21) quadratum, processus orbitalis greatly elongated and strongly mediadorsally deflected (reversed in Rhynochetidae).

Sister group relationship between Pteroclididae and Columbidae was supported with a high bootstrap value of 96%. This clade is supported by the following non-homoplastic apomorphies: (11) os pterygoideum inflated, (46) humerus short and stocky with crista deltopectoralis strongly protruding and triangular; additional apomorphies are: (12) vomer vestigial or absent, (31) several thoracic vertebrae fused to a notarium, (58) carpometacarpus, fovea carpalis cranialis very marked.

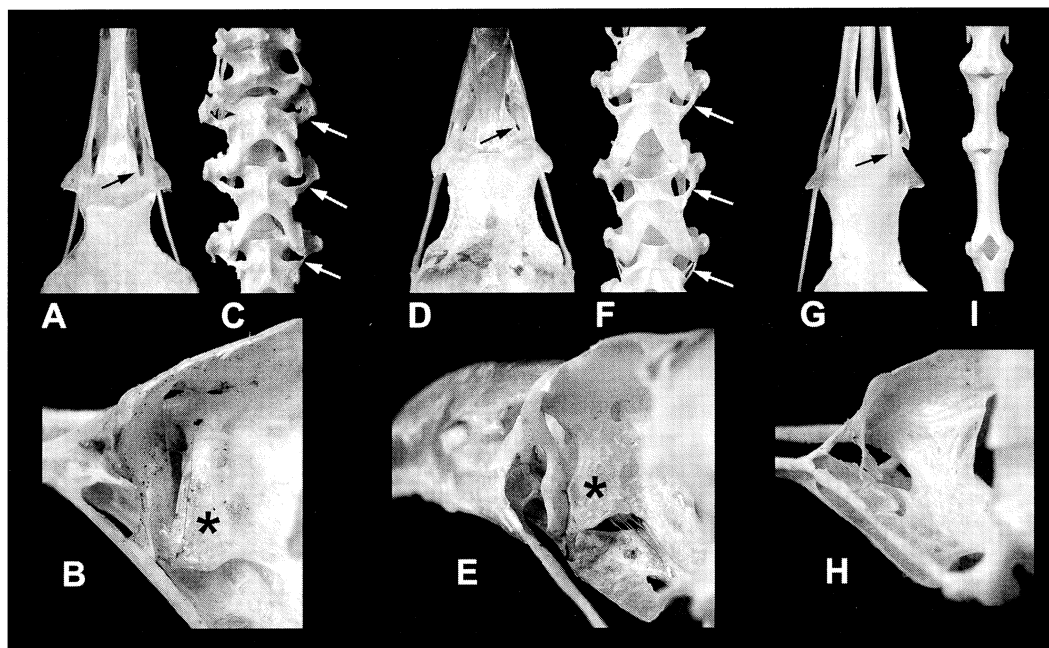


Fig. 6. Caudal end of nostrils (A, D, G), lacrimal-ectethmoid complex (B, E, H) and 4 th and 7 th cervical vertebrae (C, F, I) in comparison. A, B, C: *Monias benschi* (Mesitornithidae), D, E: *Guira guira* (Cuculidae), F: *Clamator levaillantii* (Cuculidae), G, H, I: *Eurypyga helias* (Eurypygidae). The black arrows mark the caudal end of the nostrils (note the caudally elongated nostrils in *Guira guira*), the white arrows point to the osseous bridge from the processus transversus to the midsection of the corpus vertebrae, the asterisks indicate the os ectethmoidale. Not to scale.

Analysis of the molecular data

Cuckoos and mesites are sister groups in the single, most parsimonious tree based on the DNA sequence data obtained from the two nuclear genes (Fig. 5). In this tree, monophyly of the ingroup (Neoaves) receives a 100 % bootstrap support, while most other strongly supported clades consist of charadriiform taxa. Only a few other clades in the tree were supported by values exceeding 50 %. A bootstrap support value of 73 % was obtained for the crane-rail clade, and a sistergroup relationship between the dove and the sandgrouse received

55 % support. The cuckoo-mesite clade received 48 % bootstrap support. This value is lower than 50 %, but it should be noted that no alternative systematic affinity suggested for these taxa received a higher bootstrap value. A maximum-likelihood analysis also recognized monophyly of the ingroup (not shown). Above this node, the best-fit tree is rather bush-like, with short internodes between taxa and long terminal branches. A cuckoo-mesite relationship is not recovered by this analysis. Instead, the cuckoo is left unresolved within Neoaves, and the mesite groups with the bustard (Otidae) (the branch leading to this latter clade is very short).

Discussion

In concordance with several other studies (e.g., HOUDE et al. 1997, LIVEZEY & ZUSI 2001), the present analysis indicates that the Gruiformes sensu WETMORE (1960) is a polyphyletic assemblage. The analysis of the morphological data supports previous hypotheses concerning monophyly of the taxa (Psophiidae + (Aramidae + Gruidae)), (Rallidae + Heliornithidae), and (Eurypygidae + Rhynochetidae) (e.g., CRACRAFT 1982, HESSE 1990, HOUDE 1994, HOUDE et al. 1997, LIVEZEY 1998 — contra SIBLEY & AHLQUIST 1990, MAYR 2002).

A closer relationship between Mesitornithidae and Cuculidae, however, has not been proposed before and radically differs from current classifications. Cuckoos are, among other features, characterized by a zygodactyl foot in which the fourth toe is permanently retroverted and the absence of even the faintest indication of a zygodactyl foot in the Mesitornithidae might have prevented earlier authors from comparing mesites and cuculiform birds (although the zygodactyl piciform birds, for example, are considered by many authors to be most closely

related to passeriform or coraciiform birds which likewise completely lack zygodactyl feet).

Apart from presumably autapomorphic specializations (e.g., the unique shape of the sternum of the Mesitornithidae and the zygodactyl foot of the Cuculidae), mesites and putatively more basal (see HUGHES 1996, 2000, JOHNSON et al. 2000, SORENSON & PAYNE 2002) members of the Cuculidae as, for example, *Carpococcyx*, *Coua*, *Guira*, or *Geococcyx* are fairly similar in overall morphology of most parts of the skeleton. There is also some overall similarity in external appearance between the Mesitornithidae and some Cuculidae, e.g. if one compares *Monias benschi* with *Dromococcyx phasianellus*. In *Mesitornis variegata*, the facial skin behind the eye is naked and blue (APPERT 1985: fig. 3), as is that of many (especially the more basal, see above) members of the Cuculidae (and various other birds).

Unfortunately very little is known on the biology of the Mesitornithidae (APPERT 1985, EVANS et al. 1996). Young mesites apparently are covered with dark down (APPERT 1985: fig. 11), whereas the young of most Cuculidae are naked at hatching (in some taxa, e.g. *Centropus*, they are covered with hair-like feathers, so-called "trichoptiles", see STRESEMANN 1927–34: fig. 322, PAYNE 1997: 528). Contrary to the altricial young of Musophagidae and Cuculidae, the young of the Mesitornithidae are, however, praecocial.

Many authors considered Cuculidae and Musophagidae to be sister taxa (e.g., FÜRBRINGER 1888, GADWD 1893, STRESEMANN 1927–34, CRACRAFT 1981) but so far no derived characters have been presented which convincingly support this assumption. Although turacos have a semi-zygodactyl foot, the morphology of the distal end of the tarsometatarsus otherwise is very different in Musophagidae and Cuculidae. As noted above, the derived morphology of the os carpi ulnare shared by turacos and cuckoos (HUGHES 2000) is also found in the Mesitornithidae (Fig. 3), and the same is true for the derived structure of the hamuli of the wing feathers which was noted by MASCHA (1904). Monophyly of the taxon (Cuculidae + Musophagidae) is not supported by recent phylogenetic studies (e.g. SIBLEY & AHLQUIST 1990, MINDELL et al. 1997, HUGHES & BAKER 1999, HUGHES 2000, JOHANSSON et al. 2001, LIVEZEY & ZUSI 2001). Molecular studies support monophyly of Musophagidae and Opisthocomidae (MINDELL et al. 1997: fig. 8.5 A, HUGHES & BAKER 1999, MAYR et al. 2003: fig. 6) which was also suggested by earlier anatomists (e.g. VERHEYEN 1956).

Apart from the Musophagidae, no other taxon has been seriously considered as sister taxon of the Cuculidae.

The assumption of a closer relationship between Mesitornithidae, Eurypygidae, Rhynochetidae, and Ardeidae (see introduction) appears to have been largely based on the presence of powder down patches in these four taxa. However, mesites have five pairs of powder down patches, whereas in the Ardeidae the number of these patches varies from two pairs in bitterns (*Botaurus*) to four in,

e.g., the Boat-billed Heron *Cochlearius* (OLSON 1979). The powder downs of mesites and herons are restricted to well defined patches, whereas those of the Eurypygidae and Rhynochetidae are more diffusely distributed. FORBES (1882: 269) noted that in their exact distribution the powder down patches of the Mesitornithidae "differ materially" from those of any other birds (including Ardeidae, Eurypygidae, and Rhynochetidae). Powder down patches occur in a number of other unrelated birds, as Podargidae (frogmouths), Leptosomidae (cuckoo-rollers), and some Accipitridae (e.g. CHANDLER 1916: 258) and it is well possible that these structures are autapomorphic for mesites. Although the Mesitornithidae have pseudo-holorhinal nostrils which somewhat resemble the schizorhinal nostrils of Eurypygidae and Rhynochetidae, a rhynochokinetic bill evolved in many unrelated avian taxa (ZUSI 1984). The nostrils of the Cuculidae are holorhinal but in some taxa they are elongated and approach the naso-frontal hinge (Fig. 6). Although differences as such do not prove non-relationship of taxa, given the similar terrestrial way of living of Mesitornithidae, Eurypygidae, and Rhynochetidae, the quite dissimilar osteology of the hindlimb does not make a close relationship between mesites and the sunbittern and kagu very likely.

The cuckoo-mesite clade was also recovered in the parsimony analysis of the molecular data but not in the maximum-likelihood analysis, which employs a codon site-specific model for nucleotide substitutions. In the best-fit likelihood tree, the cuckoo was instead left unresolved within Neoaves, while the mesite grouped with the bustard (Otididae). The likelihood tree is characterised by basal, terminal branches that are very long (true for those leading to the cuckoo and the mesite, respectively) and separated by short internodes. Such a tree topology indicates that the groups underwent a rapid cladogenesis long ago. This, in turn, causes serious difficulties to reconstruct the true evolutionary branching pattern between taxa with molecular data. The observed differences between the trees obtained with the parsimony and maximum-likelihood methods, respectively, could thus to some extent be due to stochastic factors caused by the rather low number phylogenetically informative sites acquired during the short time periods between the branching events. Although not all analyses of the DNA sequence data unambiguously support a close relationship between the cuckoos and mesites, the observation that this clade is recovered by the parsimony analysis does lend support to the morphological analysis presented herein.

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Appendix

Character descriptions and character matrix. The character matrix contains 91 morphological characters for the 29 taxa included in this study. Polymorphic characters are coded as such, unknown character states are indicated by “?”.

1. Largely/completely ossified septum nasale: absent (0), present (1). In the Rhynochetidae, Pteroclididae, and Thinochoridae only a small part of the nasal septum is ossified and this character has been coded as absent.
2. Nostrils: holorhinal, i.e. caudal margin rounded and situated well before naso-frontal hinge; cranial kinesis amphiprokinetic (0), schizorhinal, i.e. caudal margin slit-like and extending caudally to naso-frontal hinge; cranial kinesis rhynchokinetic (1), pseudo-holorhinal (“atypical holorhinal”), i.e. caudal margin rounded and reaching the naso-frontal hinge; cranial kinesis rhynchokinetic (2); see ZUSI (1984) for a discussion of the various types of kinesis in birds.
3. Os lacrimale, caudally projecting processus supraorbitales: absent (0), present (1). In Laridae (*Larus*), Haematopodidae and Recurvirostridae the lacrimale forms a caudolaterally protruding projection which we do not consider homologous to true supraorbital processes. All of these taxa possess large supraorbital saltglands and the formation of the supraorbital projection apparently is due to erosion of the os frontale.
4. Os lacrimale with well developed descending process which touches or nearly touches the jugal bar: yes (0), no (1). This character was coded as unknown in the Turnicidae in which the lacrimale is reduced. In the Cariamidae it is the processus uncinatus and not the descending process of the lacrimale itself which touches the jugal bar (see CRACRAFT 1968: 339), accordingly this character has been coded as absent.
5. Os lacrimale, descending process: not as follows (0), fused with os ectethmoidale, both bones forming a large fenestra (1) (see also STRAUCH 1978: figs. 5, 7 C). This character was coded as unknown in the Turnicidae in which the lacrimale is reduced.
6. Os ectethmoidale, greatly expanded and more or less inflated, plate-like, with dorsal margin largely fused with the os frontale: no (0), yes (1).
7. Os maxillare, processus maxillopalatinus: not as follows (0), slender and strut-like osseous bar (1).
8. Os palatinum, pars lateralis, caudal end truncate with distinct angulus caudolateralis which has about equal caudal extent to the processus pterygoideus (LIVEZEY 1998: character 35): no (0), yes (1). Since the palate is damaged in the specimen of *Rhynochetos* available to us, concerning this species, the character was coded after the information provided by BEDDARD (1898: 378) and LIVEZEY (1998).
9. Os palatinum, pars lateralis: absent or very small (0), present and well developed (1).
10. Os pterygoideum, rostral part greatly mediolaterally widened: no (0), yes (1). Within the Rallidae investigated, this character is absent in *Rallus limicola*.
11. Os pterygoideum inflated: no (0), yes (1).
12. Vomer: present variably developed (0), vestigial or absent (1). Within the Galliformes, the vomer is present in the Cracidae but absent in the Phasianidae; we consider its absence to be derived. Although a vomer is generally considered to be absent in the Musophagidae (e.g. STRESEMANN 1927–34: 817), we found it to be well developed in *Corythaixoides concolor* and *Crinifer zonurus*; accordingly we coded the character as present in turacos.
13. Vomer, rostral end: pointed (0), truncate, often divided into two tips (see BEDDARD 1898: fig. 169) (1). This character was coded as unknown in taxa in which the vomer is reduced.
14. Vomer, caudal end deeply cleft: no (0), yes (1). This character was noted as a apomorphy of the Gruiformes by CRACRAFT (1988) and ROTTHOWE & STARCK (1998). It was coded as unknown in taxa in which the vomer is reduced.
15. Well-developed processus basipterygoidei that articulate with the ossa pterygoidea: present (0), absent (1). Contrary to HUXLEY (1867: 430), we could not confirm the presence of processus basipterygoidei in *Grus antigone* (Gruidae). The rudimentary, non-functional basipterygoid processes in *Goura* (Columbidae) are here considered to be autapomorphic for the genus.
16. Cranium, fossae temporales well developed, length reaching at least 1/3 of the circumference of the dorsal half of the cranium: no (0), yes (1).
17. Cranium, fonticuli occipitales in adult birds (see ERICSON 1997: character 1, STRAUCH 1978): absent (0), present (1).
18. Os opisthoticum/prooticum, pila otica pedestal-like and with one or more large fenestrae circumscribing numerous pneumatic openings (see LOWE 1925, 1926, ROTTHOWE & STARCK 1998): no (0), yes (1). This character was first noted by LOWE (1925, 1926) and corresponds to the “large fenestra/foramen [...] immediately posterior to the facet for the medial head of the quadrate” of CRACRAFT (1988: 351) and the “window in prooticum” of ROTTHOWE & STARCK (1998). It was listed as a apomorphy of gruiform birds by the latter authors.
19. Os basioccipitale, condylus occipitalis: with distinct incisura mediana condyli (0), without distinct incisura mediana condyli, essentially rounded (1).

	Characters																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Tinamidae	0	2	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1
Cracidae/Phasianidae	0	0	0	1	0	0	01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	01	0
Opisthocomidae	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0
Cariamidae	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	1	01	0	0
Psophiidae	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	1
Aramidae	0	1	1	0	0	0	0	0	1	1	0	0	0	1	1	0	1	1	1	2	0	0	0	?	0
Gruidae	0	1	1	01	0	0	0	0	1	1	0	0	0	1	1	0	1	1	0	2	0	01	0	0	1
Rallidae	0	0	1	1	0	0	0	0	1	01	0	0	0	1	1	0	0	1	1	2	0	0	0	1	01
Heliornithidae	0	0	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	1	2	0	0	0	1	01
Otididae	0	0	0	0	0	0	01	0	1	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	01
Eurypygidae	0	1	0	1	0	0	0	1	1	0	0	0	0	1	1	1	0	1	0	2	1	0	0	0	1
Rhynchoetidae	0	1	1	1	0	0	0	1	1	0	0	0	0	1	1	1	0	1	0	1	0	1	0	0	0
Turnicidae	0	2	?	?	?	1	1	0	1	0	0	0	01	1	0	0	0	1	1	0	0	0	1	1	0
Jacaniidae	0	1	0	1	1	0	0	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	0
Thinocoridae	0	2	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0
Burhinidae	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	1	2	0	0	0	0	0
Alcidae	0	1	0	1	1	0	0	0	1	0	0	0	1	1	1	1	01	0	1	0	0	0	0	1	0
Laridae	0	1	0	1	1	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	0	01	1	0
Glareolidae	0	02	0	1	1	1	0	0	1	0	0	0	1	1	1	01	01	0	1	0	0	1	1	1	0
Recurvirostridae	0	1	0	1	1	0	0	0	1	0	0	0	1	1	0	0	1	0	1	0	0	0	1	1	0
Haematopodidae	0	1	0	1	1	0	0	0	1	0	0	0	1	1	0	1	01	0	1	2	0	0	1	1	0
Scolopacidae	0	1	0	1	1	0	0	0	1	0	0	0	01	1	0	0	01	1	1	01	0	0	1	1	0
Charadriidae	0	1	0	1	1	0	0	0	1	0	0	0	01	1	0	0	1	0	1	2	0	1	1	1	0
Pteroclididae	0	2	0	1	0	1	1	0	0	0	1	1	?	?	0	0	0	0	0	0	0	1	0	1	0
Columbidae	0	1	0	0	0	1	0	0	1	0	1	1	?	?	0	0	0	0	0	0	0	1	0	1	1
Ardeidae	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	0	0	0	1	1	1	0	0	1
Mesitornithidae	0	2	0	0	0	1	0	0	1	0	0	0	0	1	1	1	0	1	1	1	0	0	0	0	0
Cuculidae	1	0	0	0	0	1	0	01	1	0	0	1	?	?	1	1	0	01	1	0	0	1	1	01	0
Musophagidae	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	01	1	0	0	1	0	01	0

20. Quadratum, condylus medialis, rostrally projecting, concave articular surface: absent (0), indistinct (1), marked (2) (STRAUCH 1978: character 11; see also BOCK 1960). This character was coded as "ordered".
21. Quadratum, processus orbitalis greatly elongated and strongly mediodorsally deflected (LIVEZEY 1998: character 50): no (0), yes (1).
22. Mandible, fenestra caudalis present and well developed: yes (0), no (1). This fenestra is present in the Mesozoic Confuciusornithidae (CHIAPPE et al. 1999: fig. 13) and, despite its absence in the outgroup taxa, probably is primitive within neornithine birds.
23. Atlas, incisura fossae: widely open (0), largely or completely closed (1).
24. Axis, foramina transversaria: present (0), absent (1).
25. Third cervical vertebra, osseous bridge from processus transversus to processus articularis caudalis: present (0), absent (1).
26. Fourth cervical vertebra, osseous bridge from processus transversus to processus articularis caudalis: present (0), absent (1).
27. At least 7 th and 8 th cervical vertebra, osseous bridge from processus transversus to midsection of corpus vertebrae: absent (0), present (1). Within the Cuculidae, this character is present in *Ceuthmochares*, *Chrysococcyx*, *Coua*, *Guira*, *Clamator*, *Carpococcyx*, *Centropus*, *Saurothera*, but absent in *Geococcyx*, *Eudynamis*, and *Cuculus*. Within the Mesitornithidae, it is present in *Monias* but absent in *Mesitornis*.
28. 5 th to 8 th cervical vertebrae short, width across processus transversus as much as cranio-caudal length of corpus vertebrae: no (0), yes (1).
29. 6 th–13 th cervical vertebrae without processus costales: no (0), yes (1).
30. Thoracic vertebra medio-laterally compressed and with marked ovate depression on each side of corpus vertebrae (ERICSON 1997: fig. 10): absent (0), present (1).
31. Several thoracic vertebrae fused to a notarium: no (0), yes (1). Although this character is present in two outgroup taxa, it is certainly derived with neornithine birds. Contrary to the statement in STEGMANN (1969: 37), a notarium is absent in Cariamidae and Turnicidae.
32. Cranialmost thoracic and/or caudalmost cervical vertebrae with distinctly raised cristae obliquo-transversae which cranially fuse with the processus spinosus and form a marked, caudally facing concavity: no (0), yes (1).
33. Number of praesacral vertebrae (all vertebrae cranial to synsacrum): 18–19 (0), 20–22 (1), 23–24 (2). This character was coded as "ordered".
34. Number of free caudal vertebrae: 5–6 (0), 7–9 (1). In none of the specimens of Tinamidae available to us, the

	Characters																													
	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50					
Tinamidae	1	0	0	0	0	1	0	1	?	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0					
Cracidae/Phasianidae	0	0	0	0	0	1	0	1	0	0	0	2	0	0	1	0	0	0	0	0	0	1	0	0	0					
Opisthocomidae	0	1	0	0	0	1	0	1	0	0	1	0	0	0	1	?	?	1	01	0	0	0	0	0	0					
Cariamidae	1	1	0	0	0	0	0	0	01	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0					
Psophiidae	1	0	0	0	0	1	1	2	0	0	0	0	0	1	1	0	0	1	2	2	0	0	0	0	0					
Aramidae	0	1	0	0	0	1	1	2	0	0	0	0	0	1	0	0	0	1	2	1	0	0	0	0	0					
Gruidae	1	0	0	0	0	1	1	2	0	0	0	0	0	1	1	0	0	1	2	2	0	0	0	0	0					
Rallidae	01	0	0	0	0	0	0	12	1	0	0	0	0	1	01	0	0	0	1	1	0	0	0	0	0					
Heliornithidae	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0					
Otididae	01	01	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0					
Eurypyidae	1	0	0	1	0	1	1	2	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0					
Rhynochetidae	0	0	1	1	0	1	1	1	?	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0					
Turnicidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1					
Jacaniidae	0	0	0	0	1	1	0	1	0	1	0	0	1	0	0	1	0	0	1	1	0	0	1	0	1					
Thinocoridae	0	0	0	0	1	0	0	1	1	1	0	0	1	0	0	1	0	0	1	1	0	1	1	1	0					
Burhinidae	0	01	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0					
Alcidae	0	0	0	0	1	0	0	12	1	1	0	0	1	01	0	01	1	0	01	12	0	0	1	1	1					
Laridae	0	0	0	0	1	0	0	1	1	1	0	0	1	1	0	1	0	0	0	1	0	0	1	1	0					
Glareolidae	0	0	0	0	1	0	0	01	01	1	0	0	1	01	0	1	0	0	0	1	0	0	1	1	0					
Recurvirostridae	0	0	0	0	1	0	0	1	1	1	0	0	1	1	0	1	0	0	0	1	0	0	1	1	0					
Haematopodidae	0	0	1	0	1	0	0	1	01	1	0	0	1	1	0	0	0	0	0	1	0	0	1	1	0					
Scolopacidae	0	0	0	0	1	0	0	1	1	1	0	0	1	0	0	1	0	0	01	1	0	1	1	1	0					
Charadriidae	0	0	0	0	1	0	0	1	1	1	0	0	1	1	0	1	0	0	0	1	0	0	1	1	0					
Pteroclididae	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1					
Columbidae	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	01	0	01	0	1	1	1	0	1					
Ardeidae	1	0	0	01	0	0	1	2	01	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0					
Mesitornithidae	0	01	1	0	0	1	0	1	0	?	?	1	0	0	0	0	1	0	1	1	0	1	0	0	0					
Cuculidae	01	01	1	0	0	0	0	0	0	0	0	1	0	0	0	0	01	0	01	0	0	0	0	0	0					
Musophagidae	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0					

exact number of caudal vertebrae could be verified and thus this character was coded as unknown.

35. Furcula, processus acromialis long and slender: no (0), yes (1). Contrary to the opposite statement in SIBLEY & AHLQUIST (1972: 169), a furcula is present in the Musophagidae, although the scapi claviculares are not fused at the extremitas sternalis.
36. Furcula, extremitas omalis with strongly developed, laterally protruding facies articularis acroracoidea which articulates with the facies articularis clavicularis of the coracoid: no (0), yes (1). Although the extremitas omalis of the furcula is fused with the coracoid in the Opisthocomidae, a strongly laterally protruding facies articularis acroracoidea can be discerned.
37. Coracoid, facies articularis scapularis: more or less deeply excavated, cup-like (0), shallow (Tinamidae, Mesitornithidae, Columbidae, Cuculidae, Musophagidae) (1), shallow (Galliformes) (2). Although the facies articularis scapularis of all extant Galliformes is shallow, it is cup-like in early Tertiary stem group representatives of this taxon (MOURER-CHAUVIRÉ 1992, MAYR 2000). We consider a cup-like facies articularis to be plesiomorphic in Galliformes and accordingly coded this character as non-homologous in Cracidae and Phasianidae.
38. Coracoid, facies articularis clavicularis dorso-ventrally wide and roofing the sulcus supracoracoideus, tuberculum brachi-

ale well-developed and strongly ventromedially protruding: no (0), yes (1).

39. Coracoid, foramen nervi supracoracoidei: absent (0), present (1). In the Tinamidae, Opisthocomidae, and in *Coua cristata* (Cuculidae) there is a pneumatic opening situated directly below the facies articularis scapularis which does, however, not penetrate the shaft; its homology with the foramen nervi supracoracoidei is uncertain.
40. Coracoid, impressio musculi sternocoracoidei on dorsal surface of extremitas sternalis with large pneumatic opening: no (0), yes (1). Within the Rallidae, the character is present in *Himantornis* (OLSON 1973: fig. 2). We do not consider the small pneumatic foramina at the extremitas sternalis of the Columbidae to be homologous to this character.
41. Sternum, spina externa with a widened tip, forming a wall between the medial margins of the sulci coracoidei (STRAUCH 1978: character 38); sulci coracoidei very shallow: absent (0), present (1). In the Turnicidae the spina externa is much longer than in "typical charadriiform" birds but otherwise exhibits a similar morphology.
42. Sternum, labrum externum and ventral part of facies articularis sternalis of coracoid very wide: no (0), yes (1). Within the Cuculidae this character is present in *Geococcyx*, *Guira*, *Centropus*, *Crotophaga ani* but absent in *Carpococcyx*, *Cuculus*, *Chrysococcyx*, *Clamator*, *Ramphococcyx*, *Eudynamis*, *Coua*, *Crotophaga major*, *Saurothera*.

	Characters																								
	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
Tinamidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	0	0	0	0	0
Cracidae/Phasianidae	0	01	2	0	0	0	0	0	1	0	0	0	0	02	0	0	01	0	0	0	0	0	0	1	0
Opisthocomidae	0	0	0	0	0	0	0	0	1	0	0	0	1	2	1	1	2	0	0	0	0	0	0	1	0
Cariamidae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0
Psophiidae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0
Aramidae	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	1	2	0	0	0	0	1	0	1	0
Gruidae	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	2	0	0	0	0	1	0	1	0
Rallidae	1	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	1	0	0	0	0	01	0	01	1
Heliornithidae	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	1	1
Otididae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	1	0
Eurypygidae	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	2	0	0	0	0	0	0
Rhynchotidae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	2	0	0	0	0	0	0
Turnicidae	1	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	2	0	0	1	1	0	0	1	0
Jacaniidae	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	2	0	0	0	0	0	0	1	0
Thinocoridae	1	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	2	0	1	1	1	0	0	1	0
Burhinidae	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	2	01	1	1	0	0	0	01	0
Alcidae	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	2	01	1	1	1	0	0	01	0
Laridae	1	1	0	1	0	01	0	0	0	1	0	1	0	0	0	0	2	1	0	1	1	0	0	01	0
Glareolidae	1	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	2	1	12	1	1	0	0	1	0
Recurvirostridae	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	2	01	1	1	1	0	0	0	0
Haematopodidae	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	2	1	1	1	1	0	0	0	0
Scolopacidae	1	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	2	1	1	1	1	0	0	01	0
Charadriidae	1	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	2	1	1	1	1	0	0	1	0
Pteroclididae	0	0	1	0	0	1	0	1	1	0	0	1	0	1	0	0	2	0	0	1	0	0	0	1	0
Columbidae	0	0	1	0	0	1	0	1	1	1	0	1	0	0	0	0	2	0	1	1	1	0	0	1	0
Ardeidae	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	01	1	0
Mesitomithidae	0	0	0	0	1	0	01	0	1	0	1	0	0	2	1	0	1	0	0	0	0	0	1	1	0
Cuculidae	0	0	0	0	1	0	01	01	1	0	1	0	0	2	01	0	01	0	0	0	0	0	1	1	0
Musophagidae	0	0	0	0	1	0	01	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0

43. Sternum, facies visceralis with numerous pori pneumatici along midline and lateral margins: no (0), yes (1).
44. Sternum, margo caudalis: with four notches/fenestrae (0), with two notches/fenestrae (1) or without notches/fenestrae (2). Most Columbidae have a four-notched sternum but there are a few Australasian taxa in which only two notches occur (see BOLES 1999); we consider a two-notched sternum to be derived within the Columbidae.
45. Sternum, number of processus costales: 3–4 (0), 5–6 (1), 7–8 (2). This character was coded as “ordered”.
46. Humerus short and stocky with crista deltopectoralis strongly protruding and triangular: no (0), yes (1); see STEGMANN (1969) for considerations on the functional significance of the humeral morphology of Columbidae and Pteroclididae.
47. Humerus, tuberculum dorsale greatly elongated: no (0), yes (1).
48. Humerus, sulcus transversus very deep, long, and rectangular-shaped: no (0), yes (1).
49. Humerus, impressio coracobrachialis very distinct: no (0), yes (1).
50. Humerus, fossa pneumotricipitalis very large, forming a deep excavation in the humeral head: no (0), yes (1).
51. Humerus, foramina pneumatica at bottom of fossa pneumotricipitalis (LIVEZEY 1998: character 201): present (0), absent (1). Contrary to LIVEZEY (1998), we consider the presence of foramina pneumatica to be plesiomorphic.
52. Humerus, well-developed second fossa pneumotricipitalis: absent (0), present (1).
53. Humerus, marked crista incisurae capitis (“medial knob of humerus” of BOCK & McEVEY 1969: fig. 19): absent (0), present (Turnicidae, Pteroclididae, Columbidae) (1), present (Cracidae/Phasianidae) (2). Although this character is present in all extant Galliformes, it is absent in stem group representatives of this taxon (MOURER-CHAUVIRÉ 1992, MAYR 2000) and accordingly has been coded as non-homologous in Cracidae/Phasianidae and Turnicidae, Pteroclididae, and Columbidae.
54. Humerus, processus supracondylaris dorsalis greatly enlarged: no (0), yes (1).
55. Humerus, processus flexorius strongly protruding in ventro-distal direction (much farther distally than condylus dorsalis) (Fig. 2): no (0), yes (1). This feature is present in most Cuculidae investigated (*Saurothera*, *Geococcyx*, *Rhamphococcyx*, *Guira*, *Carpococcyx*, *Coua*). Based on the phylogenies of HUGHES (1996, 2000), JOHNSON et al. (2000), and SORENSON & PAYNE (2002), we consider the absence of this character in *Cuculus* and *Chrysococcyx* to be derived within the Cuculidae.
56. Ulna: shorter than or about subequal to humerus (0), distinctly exceeding humerus in length (1).
57. Ulna with strongly marked papillae remigales (Fig. 2): no (0), yes (1). Within the Musophagidae the papillae remigales

	Characters															
	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91
Tinamidae	0	0	0	1	0	0	0	01	0	0	0	1	01	1	0	0
Cracidae/Phasianidae	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Opisthocomidae	1	0	0	0	0	0	0	01	0	0	0	1	0	0	0	1
Cariamidae	0	0	0	1	0	0	0	1	1	01	1	1	0	0	01	?
Psophiidae	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0
Aramidae	0	0	0	0	0	0	0	?	1	0	0	0	0	0	0	?
Gruidae	0	0	0	01	0	0	0	0	01	01	0	0	0	0	0	0
Rallidae	0	0	0	0	0	0	0	0	0	0	01	01	0	0	0	0
Heliornithidae	0	0	0	0	0	0	0	?	0	0	0	1	0	1	01	0
Otididae	0	0	0	1	1	0	0	0	1	0	?	0	0	0	0	1
Eurypygidae	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1
Rhynochetidae	0	0	0	1	0	0	1	?	0	1	1	1	1	0	1	?
Tumicidae	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0
Jacanidae	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1
Thinocoridae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Burhinidae	0	0	0	1	1	0	0	0	01	0	0	0	0	0	0	1
Alcidae	0	0	0	1	1	1	0	0	0	01	0	0	0	0	0	?
Laridae	0	0	0	1	1	1	0	0	0	01	0	0	0	0	0	1
Glareolidae	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1
Recurvirostridae	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	?
Haematopodidae	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	?
Scolopacidae	0	0	0	1	1	0	0	0	0	1	0	0	0	0	01	1
Charadriidae	0	0	0	1	1	0	0	0	0	1	0	0	0	0	01	1
Pteroclididae	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	1
Columbidae	0	0	0	0	0	0	0	0	0	01	1	01	0	1	0	0
Ardeidae	01	0	0	0	1	0	0	?	0	1	01	0	2	0	0	1
Mesitornithidae	1	1	0	0	0	0	0	?	0	0	?	1	2	1	1	0
Cuculidae	1	1	1	0	1	0	0	0	0	1	1	1	0	1	1	0
Musophagidae	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1

are strongly marked in all taxa investigated except for *Crinifer zonurus*. Within the Cuculidae, they are marked in *Carpococcyx*, *Geococcyx*, *Ceuthmochares*, *Saurothera*, *Eudynamis*, and *Rhamphococcyx* but weakly developed in *Cuculus*, *Clamator*, *Centropus*, *Ceuthmochares*, *Guira*, and *Crotophaga*. Within the Mesitornithidae, this character is present in *Monias* but absent in *Mesitornis*.

58. Carpometacarpus, fovea carpalis cranialis very marked: no (0), yes (1). We could not confirm the presence of a marked fovea carpalis cranialis in the Rhynochetidae (contra LIVEZEY 1998: table 2, character 240 b).
59. Carpometacarpus, os metacarpale minus distinctly bowed and spatium intermetacarpale wide: no (0), yes (1).
60. Os carpi ulnare, tuberculum at area of insertion of ligamentum humerocarpale (character 63 of ERICSON 1997): no (0), yes (1); contrary to ERICSON (1997), we found this character in *Actophilornis* (Jacanidae) but not in *Heliornis* (Heliornithidae).
61. Os carpi ulnare with crus longum abbreviated, shorter than crus breve (Fig. 3): no (0), yes (1).
62. Phalanx proximalis digiti majoris, processus internus indicis (terminology after STEGMANN 1963): absent (0), present, variably developed (1).
63. Pelvis, praeacetabular part of ilium much longer than postacetabular part, alae ischii dorsoventrally narrow, deep semilunate incisura caudalis: no (0), yes (1). Since these

features describe the general form of the pelvis and might be functionally correlated, they have been coded as a single character.

64. Pelvis: not as follows (0), tubercle caudodorsal of foramen ilioischadicum ("process of iliac crest" of BOCK & McEVEY 1969: fig. 22 A) (1), prominent laterally protruding flange in midsection of crista dorsolateralis ilii (2).
65. Pelvis, caudal part of alae ischii dorsoventrally high, distance from spina dorsolateralis ilii to processus terminalis ischii about as much as craniocaudal length of alae ischii: no (0), yes (1).
66. Pelvis, cristae iliacae dorsales fused over entire length with crista spinosa of synsacrum, thus forming a completely closed canalis iliosynsacralis: no (0), yes (1). In the Galliformes, Rallidae, and Musophagidae only a part of the cristae iliacae dorsales is fused to the crista spinosa, accordingly the character was coded as absent in these taxa. The presence of this character in some Ardeidae (PAYNE & RISLEY 1976: fig. 19) is here considered to be an autapomorphy of these taxa.
67. Pelvis, tubercula praeacetabularia: large (0), small (1), absent (2). Within Cracidae/Phasianidae, the tubercula praeacetabularia are vestigial in the Tetraoninae (Phasianidae) which we consider to be a derived feature of this taxon. This character was coded as "ordered". We consider its absence in *Cuculus* and *Chrysococcyx* (Cuculidae) autapomorphic for these genera.

68. Pelvis with two rows of well-developed foramina intertransversaria along each side of synsacrum: no (0), yes (1).
69. Pelvis, incisura marginis caudalis: absent or shallow (0), moderately deep, V-shaped (1), very deep, U-shaped, spina dorsolateralis long and narrow (2). Owing to the fact that the foramen ilioischadicum is caudally open, the condition in the Tinamidae is not comparable to that in neognathous birds.
70. Pelvis, well developed recessus caudalis fossae (see LOWE 1925: 138): present (0), absent (1).
71. Pelvis, processus terminalis ischii very long, slender, and tapering, reaching much farther caudally than the spina dorsolateralis ilii: no (0), yes (1).
72. Tibiotarsus, prominent tubercle latero-distal to the pons supratendineus (LIVEZEY 1998: character 321; considered to be the tuberositas distalis retinaculi musculorum extensorum by LIVEZEY 1998 which is, however, located proximad of this tubercle): absent (0), present (1). Within the Rallidae this character is present in, e.g., *Aramides saracura*.
73. Tarsometatarsus, hypotarsus, tendon of musculus flexor hallucis longus enclosed in bony canal: no (0), yes (1).
74. Tarsometatarsus, hypotarsus, tendon of musculus flexor digitorum longus enclosed in bony canal: no (0), yes (1).
75. Tarsometatarsus, hypotarsus, crista lateralis well developed but crista medialis reduced to a proximo-distally short osseous lamella: no (0), yes (1). This character is unique to Rallidae and Heliornithidae.
76. Tarsometatarsus, proximal end, tuberositas musculi tibialis cranialis situated on medial side of shaft, foramina vascularia proximalia widely separated: no (0), yes (1). In most birds included in this study, the tuberositas musculi tibialis cranialis is situated in the midpart of the shaft.
77. Tarsometatarsus, distal end, trochlea metatarsi II hardly turned in plantar direction, without plantarly or medially projecting wing-like flange, dorsal surface convex, essentially rounded, and without distinct sulcus: no (0), yes (1).
78. Tarsometatarsus, distal end, trochlea metatarsi IV: not as follows (0), with plantarly projecting wing-like flange (forming a large trochlea accessoria in Cuculidae) (1). This character is functionally correlated with the (semi-) zygodactyl foot of Musophagidae and Cuculidae.
79. Hallux: not as follows (0), greatly reduced (proximal phalanx very short, measuring less than half of the length of the proximal phalanx of third toe) or completely absent (1).
80. Fourth toe, fourth (distal) phalanx: longer than third phalanx (0), as long as or shorter than third phalanx (1). This character was listed by HESSE (1990) as a putative apomorphy of charadriiform birds but is absent in *Thinocorus orbignyianus*.
81. Three anterior toes connected by web over their entire length: no (0), yes (1).
82. Musculus longus colli ventralis attaching on processus articulares caudales of section II of cervical vertebrae and transferring its attachment to ribs in section I: no (0), yes (1) (after ZUSI & STORER 1969: 48; these authors found a similar condition to that in Eurypygidae and Rhynchotidae only in Rheidae and Podicipedidae).
83. Musculus flexor alulae: present (0), absent (1); (after STEGMANN 1978). STEGMANN (1978) investigated five specimens of *Opisthocomus* and found this muscle to be absent in four of these and vestigial in one.
84. Musculus caudofemoralis, pars caudalis ("A" muscle in the formula of GEORGE & BERGER 1966: Tab. IX.1): present (0), absent (1); (after GADOW 1893, BEDDARD 1898, MITCHELL 1915, GEORGE & BERGER 1966, MCKITRICK 1991). The absence of this muscle in *Eudromia* (Tinamidae) and *Meleagris* (Phasianidae) is here considered autapomorphic.
85. Musculus caudofemoralis, pars pelvica ("B" muscle in the formula of GEORGE & BERGER 1966: Tab. IX.1): present (0), absent (1); (after GADOW 1893, BEDDARD 1898, MITCHELL 1915, GEORGE & BERGER 1966, MCKITRICK 1991).
86. Oil gland: tufted (0), minutely tufted (only vestigial feather remains present)/naked (1) (after JOHNSTON 1988). An oil gland is absent in Mesitornithidae and Otididae, and the character was coded as unknown for these taxa.
87. Wing: diastataxic (0), eutaxic (1); (after MITCHELL 1901, STEPHAN 1970, SIBLEY & AHLQUIST 1990: 217 f.).
88. Powder downs: absent (0), present, diffusely distributed (1), present, confined to at least one pair of distinct patches (2); (after FORBES 1882, BEDDARD 1898, LOWE 1924, OLSON 1979).
89. Aftershaft: present (0), rudimentary or absent (1); (after GADOW 1893, BEDDARD 1898, CHANDLER 1916, LOWE 1924).
90. Podotheca on dorsal and ventral side of tarsometatarsus scutellate (i.e. covered with large scales): no (0), yes (1). In most taxa included in this study the podotheca of the tarsometatarsus is granulate (covered with small tubercles) or reticulate (covered with polygonal scales) on either both sides (e.g., Opisthocomidae, Otididae, Burhinidae) or on the ventral side (e.g., Musophagidae). In galliform birds the conformation of the podotheca of the tarsometatarsus is highly variable, but it is not scutellate on its ventral side in putatively basal (e.g., MAYR 2000) taxa, as the Megapodiidae.
91. Medulla spinalis, cornu dorsale of substantia grisea (dorsal horn of spinal grey matter): "leiocerate", i.e. smooth and rounded (0), "schizocerate", i.e. markedly inflected, "split-horned" (1); (after WOODBURY 1998). The "leiocerate" type is found in other amniotes and thus probably is primitive within birds (WOODBURY 1998).

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