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Monophyletic groups within ‘higher land birds’ – comparison of morphological and molecular data

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Abstract

The relationships within the ‘higher land birds’ and putatively related taxa are analysed in a study using 89 morphological characters and DNA sequences of three nuclear, protein-coding genes, *c-myc*, *RAG-1*, and myoglobin intron II. Separate analyses of the different data sets and a ‘total evidence’ analysis in which the data sets of the morphological and molecular analyses were combined are compared. All three analyses support the hitherto disputed sister group relationship between Pici (Rampastidae, Indicatoridae and Picidae) and Galbulae (Galbulidae and Bucconidae). Previously unrecognized osteological synapomorphies of this clade are presented. All analyses further resulted in monophyly of the taxon [Aegothelidae + (Apodidae/Hemiprocnidae + Trochilidae)]. Analysis of the morphological data and of the combined data set also supported monophyly of the taxon [Strigiformes + (Falconidae + Accipitridae)]. The morphological data further support monophyly of the taxon (Upupidae + Bucerotidae). Other placements in the three analyses received either no or only weak bootstrap support.

Key words: Phylogeny – higher land birds – morphology – *c-myc* – *RAG-1* – myoglobin intron II

Introduction

The current classification of birds (e.g. Wetmore 1960) is largely based on studies of nineteenth century ornithologists, and still only few higher avian taxa, which are composed of more than one ‘family’, have been convincingly shown to be monophyletic. One of the major divisions was introduced by Garrod (1874) who united several avian groups that lack the *musculus ambiens*, a small muscle of the hind limb, in a taxon, which he called the ‘Anomalogonatae’ (see Sibley and Ahlquist 1990 for a review of the history of classification of birds). According to Beddard (1898), this taxon includes the Strigiformes (owls – these were originally not included by Garrod 1874), Caprimulgiformes (nightjars and allies), Apodiformes (swifts and hummingbirds), Coliiformes (mousebirds), Trogoniformes (trogons), Coraciiformes (rollers and allies), Pici-formes (woodpeckers and allies) and Passeriformes (songbirds). Although usually not explicitly named, the ‘Anomalogonatae’, which are equivalent to the ‘higher land bird’ assemblage of Olson (1985), were kept together in many subsequent classifications (e.g. Mayr and Amadon 1951; Wetmore 1960).

The mere absence of a character is, however, a poor basis for phylogenetic conclusions as homology of missing characters in principal cannot be shown. The phylogenetic significance of the *musculus ambiens* is further diminished by the fact that it has also been lost in several taxa outside the ‘Anomalogonatae’ (see McKittrick 1991: pp. 22). Indeed, monophyly of the ‘Anomalogonatae’ has not been supported by any recent phylogenetic analysis based on molecular or morphological data (e.g. Sibley and Ahlquist 1990; Johansson et al. 2001; Livezey and Zusi 2001).

Most earlier authors (including Garrod 1874), for example, considered owls and diurnal birds of prey (Falconiformes) to be closely related, and it is mainly due to the work of Fürbringer (1888) and Gadow (1893) that the Strigiformes are currently separated from the Falconiformes and classified into the ‘higher land birds’.

The composition of many taxa within the ‘higher land birds’ also is controversial. Whereas monophyly of the Apodiformes received strong support in virtually all phylogenetic analyses (e.g. Sibley and Ahlquist 1990; Johansson et al. 2001; Livezey and Zusi 2001; Mayr 2002a), the ‘Caprimulgiformes’ have recently shown to be paraphyletic (Mayr 2002a). Within the Coraciiformes some well-defined clades can be recognized (see Mayr 1998, 2002b; Johansson et al. 2001), but monophyly of the whole taxon has not been convincingly established with derived characters. Inclusion of the Trogonidae into the Coraciiformes was proposed by several authors (e.g. Feduccia 1977; Maurer and Raikow 1981), but was not supported by other studies (e.g. Espinosa de los Monteros 2000). Monophyly of the Piciiformes, i.e. the taxon including Galbulae (Galbulidae, jacamars; and Bucconidae, puffbirds) and Pici (woodpeckers and allies), was also repeatedly questioned by recent authors who considered the Galbulae to be more closely related to some of the coraciiform birds (e.g. Olson 1983; Burton 1984; Lanyon and Zink 1987; Sibley and Ahlquist 1990).

While the basal divergences among birds gained increasing attention in recent years (e.g. Groth and Barrowclough 1999; van Tuinen et al. 2000; Cracraft and Clarke 2001; Ericson et al. 2001), there are only few phylogenetic analyses which address the relationships among the ‘higher land birds’. Among these, the DNA–DNA hybridization studies of Sibley and Ahlquist (1990), which cover most extant avian taxa, were repeatedly criticized for methodological reasons (e.g. Houde 1987; Lanyon 1992; Harshman 1994). Bleiweiss et al. (1994) undertook another analysis of DNA–DNA hybridization data but sampled only very few representatives of each higher taxon. Also only few ‘higher land birds’ were included in an analysis of hind limb musculature by McKittrick (1991). An analysis of skull and vertebra characters of all extant higher avian taxa by Livezey and Zusi (2001) was explicitly considered preliminary by the authors; moreover, no derived characters were listed which support the resulting phylogeny.

The only study which specifically addresses the relationships within the 'higher land birds' and included a comprehensive sample of taxa is the molecular analysis of Johansson et al. (2001), who analysed sequences of two nuclear, protein-coding genes.

In this study, the first phylogenetic analysis of 'higher land birds' which is based on morphological data and covers a wide range of osteological and myological characters, is presented. To evaluate monophyly of this clade a number of avian taxa which do not belong to the 'higher land birds', but are considered to be closely related to these birds by some authors were included. The results of the analysis are compared with analyses of molecular data and a combined data set.

Materials and methods

Analysis of morphological data

Skeletons of representatives of the following taxa were examined in the collections of Forschungsinstitut Senckenberg, Museum für Naturkunde Berlin, and Staatliches Museum für Naturkunde Stuttgart: 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*, *Syrnaticus*, *Tragopan*; Numidinae: *Acryllium*, *Numida*; Meleagrinae: *Meleagris*. Anatidae: *Aix*, *Anas*, *Anser*, *Aythya*, *Calonetta*, *Cygnus*, *Dendrocygna*, *Melanitta*, *Oxyura*, *Somateria*, *Tadorna*. Opisthocomidae: *Opisthocomus*. Falconidae: *Falco*, *Milvago*, *Polyborus*. Accipitridae: *Accipiter*, *Aquila*, *Butastur*, *Buteo*, *Circus*, *Elanus*, *Gypaetus*, *Gyps*, *Spizaetus*, *Harpagus*, *Hieraetus*, *Pandion*, *Pernis*, *Spilaeornis*. Strigiformes: Tytonidae: *Tyto*; Strigidae: *Aegolius*, *Asio*, *Athene*, *Bubo*, *Glucidium*, *Otus*, *Rhynopteryx*, *Strix*, *Surnia*. Psittacidae: *Agapornis*, *Amazona*, *Anodorhynchus*, *Ara*, *Aratinga*, *Brotogeris*, *Cacatua*, *Chamosyna*, *Coracopsis*, *Cyanoramphus*, *Eos*, *Loriculus*, *Melopsittacus*, *Myiopsitta*, *Neophema*, *Nestor*, *Nymphicus*, *Platycercus*, *Probosciger*, *Psittacus*, *Psittichas*, *Strigops*, *Trichoglossus*. Cuculidae: *Carpococcyx*, *Centropus*, *Ceuthmochares*, *Chrysococcyx*, *Clamator*, *Coccyzus*, *Coua*, *Crottophaga*, *Cuculus*, *Geococcyx*, *Guira*. Musophagidae: *Corythaixoides*, *Crinifer*, *Musophaga*, *Tauraco*. Coliidae: *Colius*, *Urocolius*. Leptosomidae: *Leptosomus*. Alcedinidae: *Alcedo*, *Ceryle*, *Dacelo*, *Haleyon*, *Ispidina*. Meropidae: *Merops*. Todidae: *Todus*. Momotidae: *Momotus*. Coraciidae: *Coracias*, *Eurystomus*. Brachypteraciidae: *Geobiastes*. Steatornithidae: *Steatornis*. Podargidae: *Batrachostomus*, *Podargus*. Caprimulgidae: *Caprimulgus*, *Chordeiles*, *Macrodipteryx*, *Phalaenoptilus*, *Semeiophorus*. Nyctibiidae: *Nyctibius*. Aegothelidae: *Aegotheles*. Apodiformes: Hemiprocnidae: *Hemiprocne*. Apodidae: *Apus*, *Chaetura*. Trochilidae: *Amazilia*, *Chrysolampis*, *Colibri*, *Phaetornis*. Upupidae: *Upupa*. Phoeniculidae: *Phoeniculus*. Bucerotidae: *Bucorvus*, *Bycanistes*, *Tockus*, *Penelopides*. Passeriformes: Eurylaimidae: *Cymbirhynchus*, *Psarisomus*. Furnariidae: *Furnarius*. Formicariidae: *Thamnophilus*. Tyrannidae: *Pitangus*. Cotingidae: *Rupicola*. Menuridae: *Menura*. Alaudidae: *Alauda*; Corvidae: *Corvus*. Pici: Ramphastidae: *Bailloniulus*, *Lybius*, *Megalaima*, *Pogoniolus*, *Psilopogon*, *Pteroglossus*, *Ramphastos*, *Selenidera*, *Trachyphonus*. Indicatoridae: *Indicator*. Piciidae: *Campethera*, *Chrysocolaptes*, *Colaptes*, *Dendrocopos*, *Dendropicops*, *Jynx*, *Melanerpes*, *Picus*. Galbulidae: Galbulidae: *Galbula*; Bucconidae: *Chelidoptera*, *Monasa*, *Notharchus*. Trogonidae: *Harpactes*, *Pharomachus*, *Trogon*.

All non-osteological characters were taken from the literature. Anatomical terminology follows Baumel and Witmer (1993) and Vanden Berge and Zweers (1993), if not indicated otherwise.

Eighty-nine characters of 29 taxa were coded for the phylogenetic analysis with PAUP* 4.0b10 (Swofford 1998) (see character matrix in Appendix 1). Owing the lack of well-corroborated phylogenies for many taxa included in the analysis, it was often impossible to determine the polarity of polymorphic characters; these have accordingly been coded as multistate ('polymorphisms'). Except for one, all characters were coded as 'unordered'. The most parsimonious

tree was found with the heuristic search option, and the analysis was run with the delayed transformation (DELTRAN) mode. 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. A few taxa of which monophyly is generally accepted were combined in the character matrix.

Outgroup comparisons were made with the palaeognathous Tinamidae, and with representatives of the Galliformes and Anseriformes, as these taxa were shown to be the most basal neornithine birds in recent phylogenetic analyses (e.g. Groth and Barrowclough 1999; Livezey and Zusi 2001).

Analysis of molecular data

Samples included for the molecular part of this study are listed in Table 1. These represent all terminal taxa included in the morphological analysis, except Upupidae. Although this taxon was initially included in the molecular study, it did not yield reliable sequence data for the myoglobin intron II and was thus excluded from the analysis.

The total aligned molecular matrix consists of 3254 basepairs (bp) and is compiled from sequences obtained from three nuclear genes, *c-myc*, RAG-1 and the myoglobin. The analysed part of the *c-myc* gene corresponds to the region between position 759 and 1235 of the exon 3 in the published *Gallus* sequence (Watson et al. 1983), whereas the analysed part of RAG-1 includes 1914 bp of the single exon of this gene (Carlson et al. 1991). The third gene fragment sequenced is the complete intron II of the myoglobin gene, including 13 and 10 bp of the flanking exons 2 and 3, respectively (Heslewood et al. 1998). All new sequences generated for this study have been deposited on GenBank and the accession numbers for all included DNA sequences are given in Table 1.

All three of these genes have previously been proven useful in resolving the earliest divergences in the avian phylogeny (Groth and Barrowclough 1999; Johansson et al. 2001; Barker et al. 2002; Ericson et al. 2002a; Irestedt et al. 2002), and the genes show low levels of homoplasy at this phylogenetic level (Groth and Barrowclough 1999; Irestedt et al. 2001; Johansson et al. 2001).

The laboratory procedures for amplifying and sequencing the different genes follow standard techniques, and primers and thermocycling conditions are described in Johansson and Ericson (in press) (see also Norman et al. 1998; Ericson et al. 2001, 2002b; Irestedt et al. 2001; Johansson et al. 2001). However, because of sequencing problems caused by the presence of a poly-A region in the myoglobin intron II sequence for *Aegotheles*, a modified protocol was needed for this taxon. The PCR product was initially sequenced with the external sequencing primers Myo2 and Myo3F (see Johansson and Ericson, in press). Yet, both primers failed to read across the poly-A stretch resulting in a single-stranded sequence with an uncertain number of A's. To obtain a double stranded reading of the gene, two internal primers (MyoEriF3 5'-TGT CGT ACA AAC ACA GGG GAT-3' and MyoEriR3 5'-TCT TGG TCT CCA AGG GAC TCT CCA-3') were designed to match a region downstream the poly-A stretch and as close to this region as possible. As both internal primers read away and not over this region, approximately 50 bp around this region is based on a single-stranded reading and the exact number of A's in the sequence is uncertain.

The sequences were aligned by eye in MEGALIGN™ (DNASTAR Inc., Madison, Wisconsin, USA). No length variation was observed in the protein-coding RAG-1 gene, whereas two indels were found in the *c-myc* gene. The first of these is a deletion of 6 bp in *Picumnus cirratus* (see Johansson et al. 2001). The second indel in the *c-myc* gene is a duplication of 12 bp, which has previously been observed in Apodidae, Hemiprocnidae and Trochilidae (Johansson et al. 2001). In *Aegotheles* a similar duplication was observed in all three species investigated. The exact location of this duplication is not certain, it can be inserted either at position 772, 784, or 796 relative to the published *Gallus* sequence (Watson et al. 1983). In this region, a duplication of 12 bp occurs in all investigated taxa, but in Apodidae, Hemiprocnidae, Trochilidae and Aegothelidae the insertion observed is the result of yet another duplication of this 12-bp-long sequence. A similar duplication has also

Table 1. Samples used in the study

Taxon	Species	Sample no.	Owner	GenBank (c-myc)	Ref.	GenBank (RAG-1)	Ref.	GenBank (myo)	Ref.
Anseriformes	<i>Chauna torquata</i>		T.J. Parsons	AY034413	5			AY165805	6
	<i>Chauna torquata</i>					AF143728	4		
Galliformes	<i>Alectura lathamii</i>	B20851	LSUMZ	AF296417	2	AF294687	2	AY165801	6
Opisthocomidae	<i>Opisthocomus hoazin</i>	B10753	LSUMZ	AY233351	1	AY233357	1	AY233363	1
Falconidae	<i>Polyborus plancus</i>	947200	NRM	AY233352	1	AY233358	1	AY233364	1
Accipitridae	<i>Heterospizias meridionalis</i>	947034	NRM	AY233353	1	AY233359	1	AY233365	1
Strigiformes	<i>Asio flammeus</i>		S. Dunham	AF295129	2	AF294657	2	AY233366	1
Psittacidae	<i>Pyrrhura frontalis</i>	966989	NRM	AY233354	1	AY233360	1	AY233367	1
Cuculidae	<i>Guira guira</i>	937391	NRM	AY165835	6	AY165799	6	AY165818	6
Musophagidae	<i>Corythaixoides leucogaster</i>	P509	ZMCU	AF295126	2	AF294654	2	AY233368	1
Coliidae	<i>Colius striatus</i>	P398	ZMCU	AF295141	2	AF294669	2	AY233369	1
Leptosomidae	<i>Leptosomus discolor</i>	uncatalogued	FMNH	AY233355	1	AY233361	1	AY233370	1
Alcedinidae	<i>Alcedo atthis</i>	968171	NRM	AF295143	2	AF294671	2	AY165800	6
Meropidae	<i>Merops viridis</i>	P935	ZMCU	AF295147	2	AF294675	2	AY165815	6
Momotidae	<i>Momotus momota</i>	947281	NRM	AF295170	3	AF295170	3	AY165816	6
Coraciidae	<i>Coracias caudata</i>	750	NMWM	AF295148	2			AY165807	6
	<i>Coracias caudata</i>					AF143737	4		
Steatornithidae	<i>Steatornis caripensis</i>	B7474	LSUMZ	AF295135	2	AF294663	2	AY233371	1
Podargidae	<i>Podargus strigoides</i>		S. Dunham	AF295134	2	AF294662	2	AY233372	1
Caprimulgidae	<i>Podager nacunda</i>	947016	NRM	AF295132	2	AF294660	2	AY233373	1
Nyctibiidae	<i>Nyctibius aethereus</i>	B11236	LSUMZ	AF295131	2	AF294659	2	AY233374	1
Aegothelidae	<i>Aegothales albertsii</i>	E044	MV	AY233356	1	AY233362	1	AY233375	1
Hemiprocnidae	<i>Hemiprocne longipennis</i>	1273	ANSP	AF295137	2	AF294665	2	AY233376	1
Trochilidae	<i>Hylocharis chrysura</i>	937161	NRM	AF295139	2	AF294667	2	AY233377	1
Bucerotidae	<i>Tockus erythrorhynchus</i>	P487	ZMCU	AF295152	2	AF294679	2	AY165823	6
Passeriformes	<i>Tyrannus savana</i>	976722	NRM	AF295182	3	AF295203	3	AY165826	6
Picidae	<i>Picumnus cirratus</i>	976666	NRM	AF295174	3	AF295195	3	AY165819	6
Galbulae	<i>Bucco capensis</i>		T.J. Parsons	AF295154	2	AF294681	2	AY165801	6
Trogonidae	<i>Trogon melanurus</i>	P494	ZMCU	AF295142	2	AF294670	2	AY165828	6

Abbreviations: ANSP – Academy of Natural Sciences of Philadelphia; FMNH – Field Museum of Natural History, Chicago; LSUMZ – Louisiana State University, Museum of Natural Science; MV – Museum Victoria, Melbourne; NMWM – National Museum of Namibia; NRM – Swedish Museum of Natural History, Department of Vertebrate Zoology; ZMCU – Zoological Museum, University of Copenhagen; References: 1. this study; 2. Johansson et al. 2001; 3. Irestedt et al. 2001; 4. Groth and Barrowclough 1999; 5. Ericson et al. 2001; 6. U.S. Johansson and P.G.P. Ericson, in press.

been observed in *Megalaima virens* (Capitonidae) (Johansson and Ericson, in press).

In the non-coding myoglobin intron, insertions and deletions are frequent, ranging in size from single bases in several species to an insertion of 43 bp in *Tockus erythrorhynchus* (Bucerotidae). Despite this, alignment was relatively straightforward and in most cases, the nucleotide positions could easily be homologized. The alignment has been deposited on GenBank.

The phylogenetic analyses of the molecular data sets were conducted with PAUP* 4.0b10 (Swofford 1998) under the parsimony criterion with all characters coded as unordered. Gaps were coded as missing data, and the few occurrences of superimposed peaks in the sequence-chromatograms were coded with the appropriate IUPAC code and treated as uncertainties. Searches for maximum parsimony trees were performed with 500 random taxon additions and tree-bisection-reconnection (TBR) branch swapping. Nodal support was estimated with 1000 bootstrap replicates, each with 10 random additions of taxa.

In addition, a Bayesian phylogenetic analysis was performed with MRBAYES 2.01 (Huelsenbeck and Ronquist 2001). The Bayesian approach to phylogeny reconstruction, as it is implemented in MRBAYES 2.01, approximates the posterior probability for a phylogenetic tree by successively altering the model parameter values in a Markov chain Monte Carlo procedure (Huelsenbeck and Ronquist 2001). Initially, a random tree and parameter values are chosen as a starting point, and for each step in the chain a new combination of topology and parameter values is either accepted or rejected according to the Metropolis-Hastings-Green algorithm. At each step the log likelihood values are recorded and after these have reached a plateau and stabilized, the frequency by which a certain clade appears among the sampled trees is an approximation of its posterior probability. In order to more efficiently traverse the parameter space, several chains

with different 'temperatures' can be run simultaneously. A heated chain can more easily cross deep valleys and thus avoid that the chain is entrapped on local optima (see Yang and Rannala 1997; Larget and Simon 1999; Huelsenbeck and Ronquist 2001 for a more detailed description of Bayesian inference). The model for the Bayesian analysis was selected with the likelihood-ratio test implemented in MODELTEST 3.06 (Posada and Crandall 1998). This test chooses the simplest model of sequence evolution that cannot be rejected in favour of a more complex model. Based on the test of maximum likelihood models, the general-time reversal (GTR) model with an estimate of invariable sites (I) and a discrete (four rate categories) Γ -distribution model of among site rate heterogeneity was selected. Four different analyses were run, starting from random starting trees, and in each of the analyses four Markov chains (three heated and one cold, temperature = 0.2) were run for 500 000 generations with trees sampled every 10th generation. The log likelihood values stabilized after approximately 60 000 generations, and the posterior probabilities were calculated from the remaining 44 000 trees.

Analysis of combined morphological and molecular data

The two data sets were also combined into a single matrix and analysed with PAUP* 4.0b10 (Swofford 1998), with the individual settings from the separate analyses retained. Searches for maximum parsimony trees were performed with 500 random taxon additions and TBR branch swapping, and nodal support was estimated with 1000 bootstrap replicates, each with 10 random additions of taxa. Morphological and molecular characters were equally weighed. Owing to the incomplete sequence data (see above), the Upupidae were excluded from the combined analysis.

Results

Analysis of morphological data

Analysis of the 89 morphological characters in the character matrix in Appendix 2 resulted in 24 most parsimonious trees (length = 333, CI = 0.49, RI = 0.58, RC = 0.29), the consensus tree of which is shown in Fig. 1. In the following, only those clades which were retained in the bootstrap analysis are discussed.

Monophyly of a group including Strigiformes, Falconidae and Accipitridae received high bootstrap support of 96%. This clade is supported by the following unambiguous synapomorphies (i.e. those characters with CI = 1.0; the numbers refer to the character list in Appendix 1): (5) skull, presence of long, caudally projecting processus supraorbitales; (52) pelvis, crista dorsolateralis ilii strongly developed, overhanging a marked concavitas infracristalis and a marked sulcus antitrochantericus and convexly bowed if pelvis is viewed from its dorsal side, praeacetabular part much longer than postacetabular part, spina dorsolateralis ilii reduced; (60) fibula very long, extending over almost the entire length of the tibiotarsus, distal end fused to shaft; (62) hypotarsus without bony canals, crista lateralis separated from crista medialis by a wide sulcus; (72) claws with pair of foramina lateral and medial to tuberculum extensorium; (76) musculus flexor cruris lateralis, pars pelvica reduced. In addition, this node is supported by the following derived characters (i.e. those with CI < 1.0): (4) cere at base of narial openings; (70) second and third phalanx of fourth toe greatly abbreviated, measuring less than half the length of the fourth phalanx; (77) musculus flexor cruris lateralis, pars accessoria absent.

Monophyly of Accipitridae and Falconidae received bootstrap support of 89% but is not supported by unambiguous synapomorphies. A derived character which supports this node is: (56) femur with pneumatic foramen at cranio-lateral side of proximal end. This character also occurs in the Musophagidae, within the Cracidae/Phasianidae, and in the clade comprising Upupidae/Phoeniculidae and Bucerotidae.

The taxon (Caprimulgidae + Nyctibiidae) is supported by a bootstrap value of 81% and can be supported with the following unambiguous synapomorphies: (13) processus paroccipitales widely separated and strongly ventrally protruding; basis cranii concave; (14) cone-like bony protrusion at caudal margin of foramen nervi optici; (21) mandible with intraramal joint and caudal half of rami mandibulae greatly widened and dorso-ventrally flattened; (22) mandible, proximal end unusually small, with very short cotyla lateralis and stout processus medialis. This node is further supported by the following derived characters (see also Mayr 2002a): (10) ossa palatina with extremely cranio-laterally expanded pars lateralis; (41) proximal end of ulna with distinct elongate, ridge-like elevation along midline of shaft, distad of cotyla ventralis.

The clade including Aegothelidae, Hemiprocnidae/Apodidae, and Trochilidae received high bootstrap value of 87% and these taxa share the following unambiguous synapomorphy: (85) musculus splenius capitis with cruciform origin. This node is further supported by the following derived characters: (17) quadratum, processus oticus, dorsal margin of caudal surface with many small pneumatic foramina; (27) furcula, extremitas omalis with distinct, laterally protruding facies articularis acrocoracoidea; (55) pelvis, processus terminalis ischii very narrow and slender, touching pubis at an angle of 45–90°, fenestra ischiopubica very wide; (79) musculus fibularis longus absent. In addition, this clade is supported by the presence of two deep furrows (which are closed to canals in Apodidae and Trochilidae) for the tendons of musculus interosseus dorsalis and m. interosseus ventralis on the dorsal surface of the symphysis metacarpalis distalis of the carpometacarpus (this character was not included in the present analysis since its homology with similar structures occurring in few other taxa, e.g. some parrots, is questionable). See also Mayr (2002a), for additional characters that were not included in the present analysis.

Monophyly of Apodidae, Hemiprocnidae and Trochilidae is supported by a bootstrap value of 91%. This taxon is supported by the following unambiguous synapomorphies: (3) proximo-dorsal part of narial openings covered by a thin

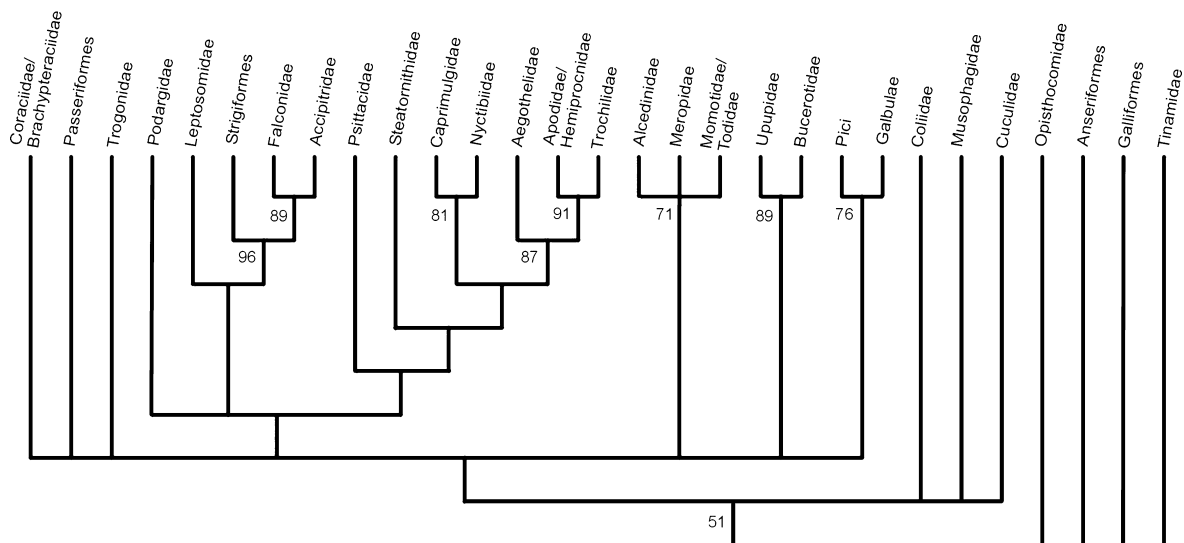


Fig. 1. Strict consensus tree of 24 most parsimonious trees resulting from an analysis of the morphological data set (Length = 333, CI = 0.49, RI = 0.58, RC = 0.29). Bootstrap values of more than 50% are indicated next to the internodes. Derived characters supporting the nodes are listed in the text

osseous sheet; (34) sternum, facies articularis coracoideus weakly saddle-shaped or convex; (35) sternum, caudal margin without notches or fenestrae; (39) humerus greatly abbreviated and stocky. In addition, this taxon is supported by the following derived characters: (65) tarsometatarsus with arcus extensorius (ossified retinaculum extensorium tarsometatarsi); (77) musculus flexor cruris lateralis, pars accessoria absent.

In all of the resulting trees, the following unambiguous synapomorphy supports monophyly of the taxon (Alcedinidae + Meropidae + Momotoidea) which received a bootstrap support of 71%: (83) tendon of musculus flexor hallucis longus not supplying hallux (Maurer and Raikow 1981). The following derived characters further support this node (see also Mayr 1998, 2002b): (18) columella with large, hollow, bulbous basal and footplate area exhibiting a large fenestra on one side; (31) scapula, acromion distinctly bifurcate, with an additional medial process; (69) proximal phalanx of hallux with proximal end greatly widened.

Bootstrap support for a sister group relationship between Upupidae/Phoeniculidae and Bucerotidae is 89%, and the following unambiguous synapomorphies support monophyly of this group: (20) mandible with rectangular cross-section in area of pars symphysialis; (67) tarsometatarsus with very short incisurae intertrochleares. In addition, the members of this node share the following derived characters (see also Mayr 1998, 2002b): (25) pygostyle with large, shield-like discus pygostyli with sharply defined, ridge-like lateral margins; (55) pelvis, processus terminalis ischii very narrow and slender, touching pubis at an angle of 45–90°, fenestra ischiopubica very wide; (56) femur with pneumatic foramen at cranio-lateral side of proximal end; (79) musculus fibularis longus absent. Further characters which support this node and were not included in the analysis are: musculus pterygoideus with 'retractor palatini' slip (Burton 1984); musculus extensor carpi ulnaris attached to os metacarpale minus (usually this muscle is either attached to the os metacarpale majus or to the tip of the processus intermetacarpalis, see Stegmann 1965); musculus pectoralis, pars propatagialis longus tendinous (Maurer and Raikow 1981).

Monophyly of the Piciformes (Galbulae + Pici) received bootstrap support of 76% and these birds share the following unambiguous synapomorphies: (49) phalanx proximalis digiti majoris, proximal end with large, proximally directing process on ventral side (Fig. 2); (82) musculus flexor hallucis longus, origin with three heads (Swierczewski and Raikow 1981; Raikow and Cracraft 1983); (84) tendon of musculus flexor hallucis longus supplies digits I, II, and VI (deep flexor tendons type VI). Other characters which support this node are: (25) pygostyle with large, shield-like discus pygostyli with sharply defined, ridge-like lateral margins (Fig. 3); (30) coracoid, extremitas sternalis with notch on margo medialis (Fig. 4); (68) trochlea metatarsi IV with large trochlea accessoria.

Analysis of molecular data

Analysis of the molecular data resulted in five most parsimonious trees (length = 3490, CI = 0.54, RI = 0.23, RC = 0.12), the consensus tree of which is shown in Fig. 5. Except for monophyly of the clade [Aegothelidae + (Apodidae/Hemiprocnidae + Trochilidae)] and sister group relationship between Pici and Galbulae, the tree topology is very different from that of the consensus tree resulting from the analysis of the morphological characters. However, only sister group relationship between Cuculidae and Passeriformes and

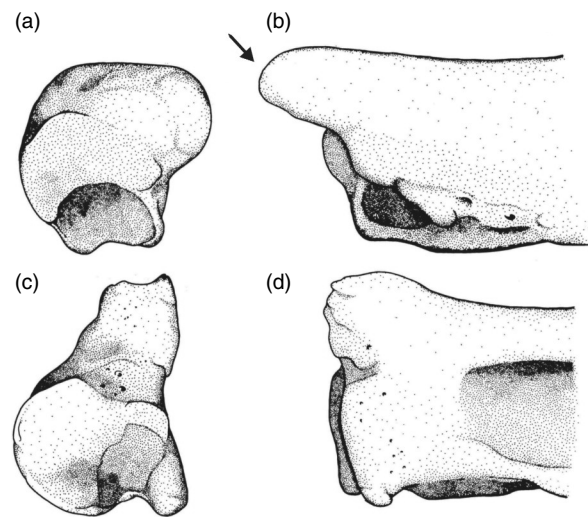


Fig. 2. Proximal part of left phalanx proximalis digiti majoris in proximal (a, c) and ventral view (b, d); (a, b) *Ramphastos vitellinus* (Ramphastidae; Pici); (c, d) *Corvus corax* (Passeriformes). In the Galbulae and Pici there is a large, proximally directing process on the ventral side, which is concave on its medial side and, in proximal view, continuous with the facies articularis metacarpalis. We consider this character to be synapomorphic for the Piciformes

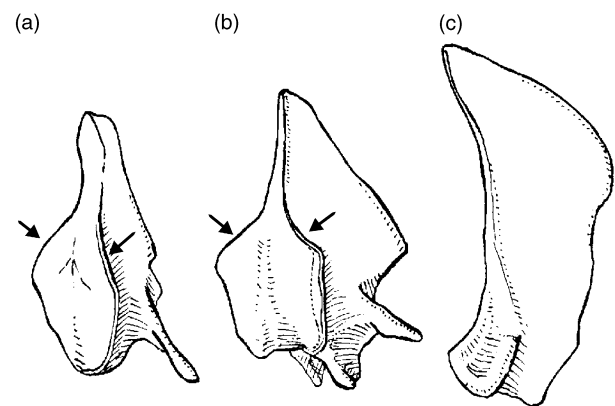


Fig. 3. Pygostyle in disto-lateral view; (a) *Trachyphonus margaritatus* (Ramphastidae, Pici); (b) *Monasa nigrifrons* (Bucconidae, Galbulae); (c) *Coracias garrulus* (Coraciidae, 'Coraciiformes'). The arrow indicates the large discus pygostyli in Galbulae and Pici which we consider to be a synapomorphy of these taxa. Not to scale

between Pici and Galbulae received bootstrap support of 55 and 76%, respectively. Bootstrap analysis further supported monophyly of the taxon (Aegothelidae + Hemiprocnidae), to the exclusion of the Trochilidae, with a low bootstrap value of 54%.

The taxa (Pici + Galbulae), [Aegothelidae + (Hemiprocnidae + Trochilidae)], (Alcedinidae + Meropidae), and a clade including the latter taxon and Meropidae and Coraciidae received a 100% posterior probability in a Bayesian phylogenetic analysis (Fig. 6).

Analysis of combined morphological and molecular data

Analysis of the combined morphological and molecular data sets resulted in two most parsimonious tree (length = 3846, CI = 0.53, RI = 0.26, RC = 0.14), the consensus tree of

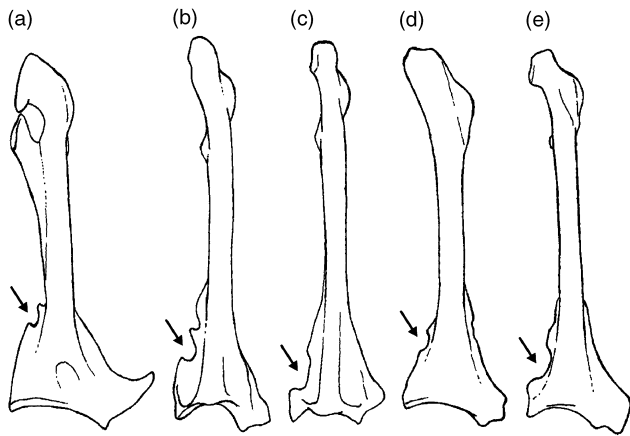


Fig. 4. Ventral surface of left coracoid in comparison; (a) *Monasa nigrifrons* (Bucconidae, Galbulae); (b) *Selenidera culik* (Ramphastidae, Pici); (c) *Trachyphonus margaritatus* (Ramphastidae, Pici); (d) *Indicator variegatus* (Indicatoridae, Pici); (e) *Jynx torquilla* (Picidae, Pici). The arrow indicates the notch on the margo medialis of the extremitas sternalis which is here considered to be a synapomorphy of Galbulae and Pici. Not to scale

which is shown in Fig. 7. Although the tree topology differs in many aspects from the consensus trees resulting from the separate analyses, some clades indicated by either the molecular or the morphological analyses also occur in the analysis of the combined data set.

As in the analysis of the morphological data, the combined data set supports monophyly of the taxon [Strigidae + (Accipitridae + Falconidae)] which received bootstrap support of 76%. Monophyly of the taxon (Falconidae + Accipitridae) is supported by a bootstrap value of 77%. Also in concordance with the analysis of the morphological data, monophyly of the taxon [Aegothelidae + (Apodidae/Hemiprocnidae + Trochilidae)] is corroborated by a bootstrap value of 81%; the taxon (Apodidae/Hemiprocnidae + Trochilidae) also received a bootstrap support of 81%. In concordance with the analyses of both, the morphological and molecular data, analysis of the combined data supported monophyly of the taxon (Pici + Galbulae), which received a high bootstrap value of 93%. The taxon (Cuculidae + Passeriformes), which was also supported in the analysis of the molecular data, received a bootstrap support of 62%. A taxon including Nyctibiidae,

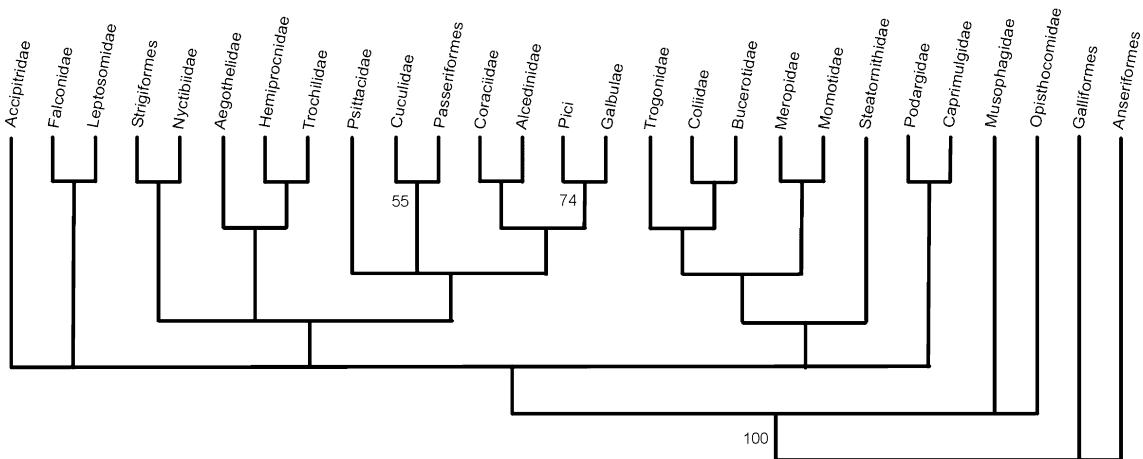


Fig. 5. Strict consensus tree of five most parsimonious trees resulting from an analysis of the molecular data set (length = 3490, CI = 0.54, RI = 0.23, RC = 0.12). Bootstrap values of more than 50% are indicated next to the internodes

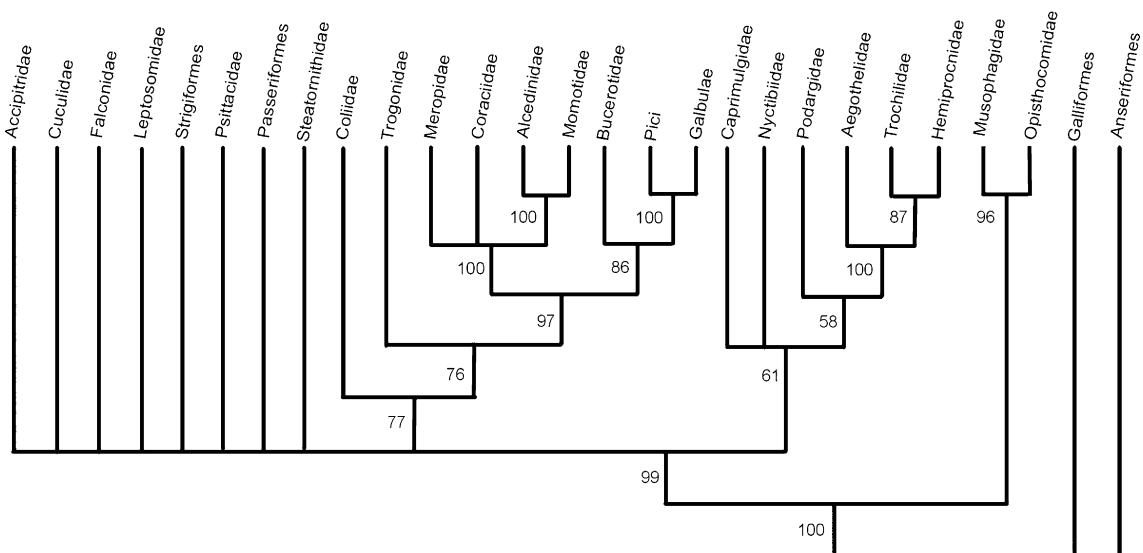


Fig. 6. Fifty per cent majority rule consensus tree obtained from the Bayesian phylogenetic analysis of the molecular data set. Posterior probability values are indicated next to the internodes. The results of the three other analyses only slightly differed in the posterior probability values

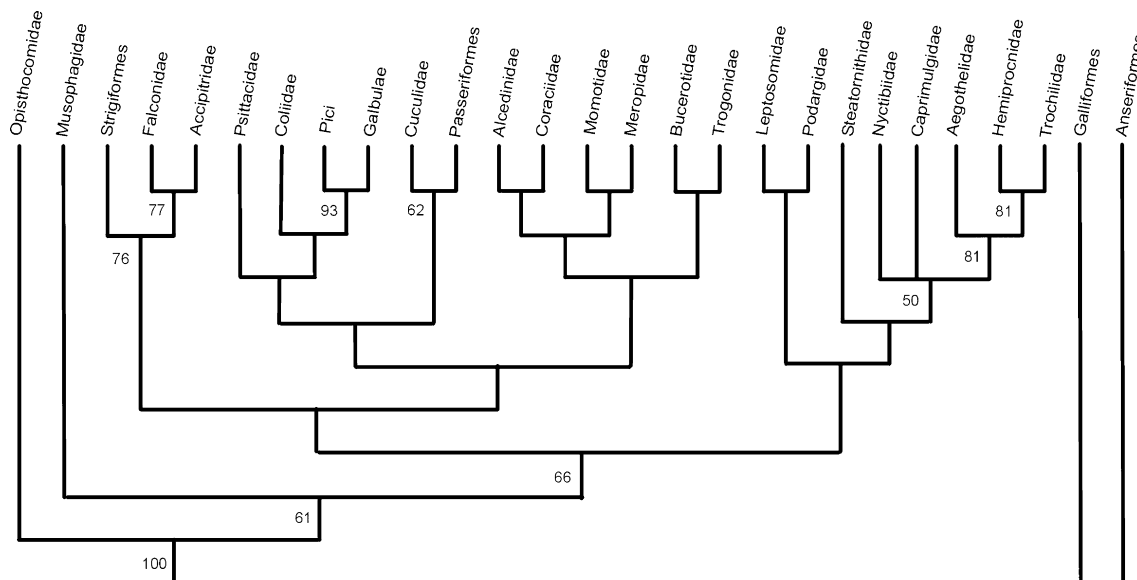


Fig. 7. Strict consensus tree of two most parsimonious tree resulting from an analysis of the combined morphological and molecular data sets (Length = 3846, CI = 0.53, RI = 0.26, RC = 0.14). Bootstrap values of more than 50% are indicated next to the internodes

Caprimulgidae, Aegothelidae, and the apodiform birds was weakly supported with a bootstrap value of 50%.

Discussion

Comparison of the three data sets

In concordance with most other recent phylogenetic analyses (see Introduction), analyses of all three data sets did not support monophyly of the 'higher land birds'. Otherwise, however, there is considerable incongruency between the consensus trees which resulted from analysis of the morphological and molecular data sets, and only two clades, i.e. sister group relationship between Galbulae and Pici and monophyly of a taxon including Aegothelidae and apodiform birds, were supported in all three analyses.

Most nodes of the consensus tree of the analysis of the molecular data did not get any bootstrap support, and in the analysis of the combined data set the few morphological characters outweighed the molecular data in many cases. Possibly, the weak support of the trees resulting from the molecular data is due to the fact that most internodes are very short compared with the terminal branches which means that, between the branching events, not enough mutations (i.e. phylogenetically informative characters) were accumulated in the conservative genes to support a robust phylogeny.

In the following, only those nodes which received bootstrap support of more than 60% in any of the analyses are discussed.

Strigiformes, Accipitridae and Falconidae

Both, analysis of the morphological data and analysis of the combined data set supported monophyly of Strigiformes, Falconidae and Accipitridae.

Although there were some earlier authors who doubted the Fürbringer and Gadow classification (e.g. Barnikol 1951; Starck and Barnikol 1954; Starck 1959), the idea of a closer relationship between owls and some of the diurnal birds of prey was revived by Cracraft (1981, 1988). Monophyly of owls, falcons and hawks further resulted from an analysis of

hindlimb musculature by McKittrick (1991). The few other analyses of morphological data which included these taxa did not corroborate a closer relationship but were either restricted to a single morphological character complex (Griffiths 1994), or the characters supporting the resulting phylogenies were not listed (Kemp and Crowe 1990; Livezey and Zusi 2001).

In a study of avian egg white proteins, Sibley and Ahlquist (1972: pp. 105) found high similarity between falcons and owls, but from their DNA-DNA hybridization studies (1990) they concluded that owls and caprimulgiform birds are monophyletic, although in several of the melting curves underlying their analysis owls are next to the Falconidae (their Figs 89, 98, 139, 142). Also in a DNA-DNA hybridization study, Bleiweiss et al. (1994) reported high bootstrap support for a clade including Strigiformes and Caprimulgidae; falconiform birds were, however, not included. Analysis of the 12S mitochondrial rDNA by Mindell et al. (1997: Fig. 8.9) resulted in monophyly of Falconidae and Tytonidae, but combination of the 12S rDNA data with that from mitochondrial cytochrome *c* oxidase sequences supported monophyly of Sagittariidae (secretary bird), Falconidae and Accipitridae (the New World Vultures, Cathartidae, were not included).

A closer relationship between owls and diurnal birds of prey was mainly questioned because of a number of differences between these taxa (e.g. Gadow 1893: p. 75; Beddard 1898: p. 252). However, differences in general cannot be used to show non-relationship of taxa and concerning owls, no alternative phylogenetic hypotheses have been convincingly established. The Falconiformes sensu Wetmore (1960), i.e. a clade including Cathartidae, Sagittariidae, Falconidae and Accipitridae, is a very ill-defined taxon, and many authors raised doubt on the falconiform affinities of the Cathartidae and Sagittariidae (e.g. Hudson 1948; Ligon 1967; Jollie 1977b; König 1982; Jacob 1983; Rea 1983; Sibley and Ahlquist 1990; Avise et al. 1994; Wink 1995).

'Caprimulgiformes' and Apodiformes

The 'Caprimulgiformes' as currently recognized (e.g. del Hoyo et al. 1999) include the Steatornithidae, Podargidae,

Nyctibiidae, Caprimulgidae and Aegothelidae, whereas the Apodiformes comprise Hemiprocnidae, Apodidae and Trochilidae.

Concerning Nyctibiidae, Caprimulgidae, Aegothelidae and the Apodiformes, analysis of the morphological data yielded the same tree topology as the study by Mayr (2002a). The molecular support for sister-group relationship between Aegothelidae and apodiform birds (Fig. 6) is here reported for the first time. Analysis of the combined data set also supported monophyly of a taxon including Aegothelidae and apodiform birds, as well as monophyly of a clade including the latter taxa and Caprimulgidae and Nyctibiidae.

Except for the study by Sibley and Ahlquist (1990), there are hardly any other comprehensive analyses which include both 'Caprimulgiformes' and 'Apodiformes'. Monophyly of Nyctibiidae, Caprimulgidae, Aegothelidae and the Apodiformes also resulted from an analysis of Livezey and Zusi (2001), although these authors regarded their study preliminary and did not list any characters supporting the resulting phylogeny. The analysis of Johansson et al. (2001), in which the Aegothelidae were not included, did not resolve the relationships between the 'caprimulgiform' taxa.

For further discussion of the phylogenetic implications resulting from the phylogeny of 'caprimulgiform' and apodiform birds in Fig. 1, see Mayr and Manegold (2002); Mayr (2002a); Mayr (2003).

'Coraciiformes'

The 'Coraciiformes' as currently recognized (e.g. del Hoyo et al. 2001) include the Leptosomidae, Coraciidae, Brachypteraciidae, Upupidae, Phoeniculidae, Bucerotidae, Alcedinidae, Meropidae, Todidae and Momotidae. This taxon was not shown to be monophyletic by any of the more comprehensive recent phylogenetic analysis (e.g. Espinosa de los Monteros 2000; Johansson et al. 2001; Livezey and Zusi 2001), and this study is no exception therein.

Monophyly of the taxon (Upupidae/Phoeniculidae + Bucerotidae), which is strongly supported by analysis of the morphological data, is in line with most other phylogenetic analyses of different data sets (e.g. Burton 1984; Sibley and Ahlquist 1990; Mayr 1998; Espinosa de los Monteros 2000; Johansson et al. 2001; however contrary to Maurer and Raikow 1981).

Monophyly of a taxon including Alcedinidae, Meropidae, Momotidae and Todidae is also supported by other analyses of morphological characters (e.g. Feduccia 1977; Maurer and Raikow 1981; Burton 1984) and by the molecular studies of Sibley and Ahlquist (1990). The molecular analyses of Espinosa de los Monteros (2000) and Johansson et al. (2001) did not support inclusion of the Meropidae into this clade, but did not suggest a convincing alternative position of the taxon.

Both data sets did not conclusively resolve the position of the cuckoo-roller (Leptosomidae), although it is interesting to note that the Leptosomidae were optimized as the sister taxon of the Podargidae in the analysis of the combined data set. Sister group relationship between these two taxa was already suggested by Mayr (1998: p. 10) and the occurrence of this clade in the analysis of the combined data set is so much the more surprising as it did not result from the separate analyses of the morphological and molecular data, and since several derived characters shared by Leptosomidae and Podargidae were not included in the analysis (e.g. the presence of powder downs on the back of the rump).

Piciformes

So far, monophyly of the Piciformes was mainly based on derived features related to the zygodactyl foot of these taxa, which include a unique arrangement of the deep plantar tendons (character 84 in Appendix 1, see also Simpson and Cracraft 1981; Swierczewski and Raikow 1981). Here three additional synapomorphies (characters 25, 30 and 49 in Appendix 1), which are not related to this toe arrangement, are reported. As the taxon (Pici + Galbulae) also received strong support in the Bayesian analysis of the molecular data and a high bootstrap value in the analysis of the combined data set, the traditional Piciformes is considered monophyletic.

The only alternative classification of the Galbulae which is supported by derived morphological characters is a sister-group relationship to rollers and cuckoo-rollers. In an analysis of the feeding apparatus of coraciiform birds, Burton (1984: p. 436) listed the following characters in order to support this hypothesis: elongated processus postorbitalis (character 16 in Appendix 1), quadratum with deep condylus medialis (not included in the analysis because this character cannot be coded in discrete characters), a modification of musculus serpihyoideus, and, in all but the Leptosomidae, loss of musculus stylohyoideus (the latter two characters were not included in the present analysis because their distribution among most other taxa is unknown). Even among the comparatively few taxa studied by Burton (1984), the m. stylohyoideus is, however, also absent in the Bucerotidae, some Todidae, and some Picidae. Burton (1984: p. 389) further noted that the modification of m. serpihyoideus is absent in *Eurystomus* (Coraciidae).

Olson (1983) listed few additional characters which are shared by Galbulae and rollers, including a similar shape of the coracoid which here is considered to be plesiomorphic (a similar type of coracoid occurs in several other avian taxa as, for example, Cuculidae and Meropidae). Olson (1983: p. 130) also pointed out that the skull and mandible of the Galbulae show a 'remarkable similarity to those of *Coracias* (Coraciidae) in almost every aspect', but did not specify whether this similarity is primitive or derived (see Raikow and Cracraft 1983 for a critique of Olson's study).

Only few molecular studies addressed the question of piciform monophyly. It was not supported by the DNA-DNA hybridization studies of Sibley and Ahlquist (1990) and by an analysis based on starch-gel electrophoresis by Lanyon and Zink (1987). The study of Johansson et al. (2001) did not conclusively resolve the position of the Galbulae.

Passeriformes and Cuculidae

Analysis of the molecular and of the combined data set resulted in monophyly of Cuculidae and Passeriformes. This clade, which has not been suggested before, is not supported by current morphological evidence and received only weak bootstrap support.

Most recent authors who studied morphological features considered the Passeriformes to be most closely related to the Pici (e.g. Olson 1983; Höfling and Alvarenga 2001; Livezey and Zusi 2001). Despite a great overall resemblance in many osteological features, there are, however, only few derived characters, which are shared by Pici and Passeriformes to the exclusion of the Galbulae (e.g. the modification of the proximal end of the ulna, character 42 in Appendix 1). Olson (1983: p. 131) mentioned the greatly reduced processus procoracoideus as a

possible synapomorphy of these taxa, but this process is fairly well developed in some suboscine Passeriformes (e.g. the tyrant flycatcher *Pitangus sulphuratus*, see Höfling and Alvarenga 2001: Fig. 5d). Höfling and Alvarenga (2001: p. 207) further listed a 'triangular-shaped extremitas omalis' of the furcula in order to support monophyly of Passeriformes and Pici, which is also absent in some suboscine Passeriformes (e.g. *Pitangus sulphuratus*, see Höfling and Alvarenga 2001: Fig. 1c).

The zygodactyl Cuculidae were considered by most earlier authors to be the sister taxon of the semi-zygodactyl Musophagidae (e.g. Fürbringer 1888; Gadow 1893; Stresemann 1927–34; Cracraft 1981) which is, however, not supported by most recent phylogenetic analyses (e.g. Sibley and Ahlquist 1990; Mindell et al. 1997; Johansson et al. 2001; Livezey and Zusi 2001; see also Hughes 2000: p. 288). Hughes (2000) and Hughes and Baker (1999) considered the Cuculidae to be the sister group of the taxon (Opisthocomidae + Musophagidae). The study of Hughes and Baker (1999) did, however, only include these three taxa and is thus insufficiently comprehensive. Hughes (2000: p. 288) listed three characters of the os carpi ulnare in order to support her phylogeny, the presence of which could not be verified for the Opisthocomidae (in the hoatzin, the angle of juncture of crus breve and crus longum of os carpi ulnare is not approximately 90°, and the crus longum is not nearly straight).

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Zusammenfassung

Monophyletische Gruppen innerhalb der 'höheren Landvögel' – Vergleich morphologischer und molekularer Daten

Die Verwandtschaftsbeziehungen zwischen den 'höheren Landvögeln' und möglicherweise verwandter Taxa werden anhand von 89 morphologischen Merkmalen und DNA-Sequenzen von drei protein-kodierenden Kerngenen – *c-myc*, RAG-1 und dem Myoglobin-Intron II – untersucht. Getrennte Analysen der verschiedenen Datensätze und eine Analyse, in welcher die Datensätze der morphologischen und molekularen Analysen kombiniert wurden, werden verglichen. Alle drei Analysen stützen die bisher umstrittene Schwestergruppenbeziehung zwischen Pici (Ramphastidae, Indicatoridae, und Picidae) und Galbulae (Galbulidae und Bucconidae), und neue osteologische Synapomorphien dieses Taxons werden beschrieben. Ebenfalls gestützt durch alle drei Analysen ist Monophylie des Taxons [Aegothelidae + Apodidae/Hemiprocnidae + Trochilidae]. Analyse des morphologischen Datensatzes und des kombinierten Datensatzes resultierte in Monophylie des Taxons [Strigiformes + (Falconidae + Accipitridae)], und Analyse der morphologischen Daten stützte Monophylie des Taxons (Upupidae + Bucerotidae). Andere Gruppierungen in den drei Analysen erhielten entweder gar keine oder nur sehr geringe Bootstrap-Werte.

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Appendix 1

Character descriptions

1. Skull, largely/completely ossified septum nasale: absent (0), present (1). Although present in most taxa included in this study, an ossified nasal septum is rarely found outside the 'higher landbirds' (see Ericson 1997). The nasal septum is also ossified in few passeriforms (e.g. *Rupicola* sp.), which is here considered to be an autapomorphy of these taxa.
2. Beak short and very wide at its base, with narial openings large and reaching far into its tip: no (0), yes (1).
3. Proximo-dorsal part of narial openings covered by a thin osseous sheet: no (0), yes (1). The osseous lamella subdividing the nostrils of the Upupidae/Phoeniculidae and the Leptosomidae is considered to be not homologous to the structure found in Hemiprocnidae/Apodidae and Trochilidae.
4. Cere at base of narial openings: absent (0), present (1). A cere is also present in few other taxa, which were not included in this analysis (e.g. Sagittariidae, Columbigormes).
5. Well-developed, caudally projecting processus supraorbitales: absent (0), present (1). Although these processes are small in few Accipitridae (e.g. *Gypaetus*, *Neophron*, *Pandion*, *Pernis*, *Polyboroides*; see Jollie 1977a: Fig. 93), they are well developed in presumably basal (Griffiths 1994; Holdaway 1994) accipitrid taxa, as *Elanus*. It is thus most parsimonious to assume that enlarged, caudally projecting processus supraorbitales were present in the last common ancestor (stem species) of the Accipitridae. Pycraft (1903) incorrectly stated that all owls lack enlarged processus supraorbitales: within the Strigiformes, the development of these processes is variable. They are, for example, well developed in *Aegolius funereus*, *Athene noctua* and *Surnia ulula* but vestigial in *Strix aluco*, *Tyto alba* and some larger species. Well-developed processus supraorbitales are present in juveniles of *Strix aluco* (May 1962: p. 197), and it is thus most likely that these processes were also present in the last common ancestor of the Strigiformes and are secondarily reduced in some taxa.
6. Os lacrimale (os praefrontale) vestigial or completely reduced: no (0), yes (1), (Cracraft 1968 and personal observation). In the Pici and Bucerotidae the os lacrimale appears to be fused to the frontale (concerning the condition in the Pici see also Simpson and Cracraft

- 1981: p. 487) and its relative development is thus difficult to assess in the adult skull. In the Podargidae and Trochilidae it is uncertain whether it is reduced or fused to the frontal or nasal bones. We consider the great reduction of the os lacrimale in many Passeriformes to be derived within that taxon, as they are well developed in several taxa with that group (e.g. Corvidae).
7. Os lacrimale, descending process greatly expanded medially: no (0), yes (1). This character was listed by Cracraft (1981: p. 702) as a synapomorphy of a taxon including Coraciidae, Brachyteraciidae, and the alcediniform birds, but is absent in Meropidae and Momotidae.
 8. Os ectethmoidale, greatly expanded, plate-like, with dorsal margin largely fused with frontals: no (0), yes (1), (Cracraft 1968 and personal observation).
 9. Vomer: not as follows (0), with truncate rostral and bifurcate caudal end (typical of the 'aegithognathous' palate) (1). We have coded this character as unknown in taxa in which the vomer is vestigial or reduced.
 10. Os palatinum, pars lateralis extremely cranio-laterally expanded: no (0), yes (1) (see Mayr 2002a: Fig. 3C,D).
 11. Processus postorbitales strongly elongated, touching (or nearly touching) the jugals: no (0), yes (1). The presence of this character in few Strigiformes and Psittacidae, as well as in *Podargus* (Podargidae) is here considered autapomorphic for these taxa.
 12. Well-developed processus basiptygoidei that articulate with the ossa pterygoidea: yes (0), no (1).
 13. Processus paroccipitales widely separated and strongly ventrally protruding; basis cranii concave: no (0), yes (1).
 14. Cone-like bony protrusion at caudal margin of foramen nervi optici (Mayr 2002a: Fig. 5): absent (0), present (1).
 15. Quadratum, processus orbitalis: not greatly reduced (0), greatly reduced (1).
 16. Quadratum, condylus caudalis completely reduced, condylus lateralis separated from elongate condylus medialis by a deep but narrow furrow: no (0), yes (1).
 17. Quadratum, processus oticus, dorsal margin of caudal surface with many small pneumatic foramina (Mayr 2002a: Fig. 4): no (0), yes (1).
 18. Columella with large, hollow, bulbous basal and footplate area which exhibits a large fenestra on one side (Feduccia 1977): no (0), yes (1). The presence of this character in some suboscine Passeriformes (Feduccia 1974) is here considered autapomorphic for these birds since the columella of the Acanthisittidae, the putative sister taxon of all other Passeriformes (e.g. Ericson et al. 2002a), and that of oscine Passeriformes has a flat footplate and a slender bony shaft (Feduccia 1975a,b) as that of many non-passeriform birds. Therefore, this character is coded as absent for Passeriformes.
 19. Mandible, distal part of rami mandibulae very narrow, pars symphysialis very short: no (0), yes (1).
 20. Mandible, area of pars symphysialis with rectangular cross-section: absent (0), present (1).
 21. Mandible with intraramal joint and caudal half of rami mandibulae greatly widened and dorso-ventrally flattened: no (0), yes (1).
 22. Mandible, proximal end unusually small, with very short cotyla lateralis and stout processus medialis: no (0), yes (1).
 23. Atlas, incisura fossae: open (0), closed (1).
 24. Axis, foramina transversaria: present (0), absent (1).
 25. Pygostyle with large, shield-like discus pygostyli with sharply defined, ridge-like lateral margins (Fig. 3): no (0), yes (1). Few other taxa included in this study also possess a large discus pygostyli (e.g. Meropidae), which lacks, however, sharply defined, ridge-like lateral margins.
 26. Number of praesacral vertebrae (all vertebrae cranial to synsacrum) more than 19: yes (0), no (1). Virtually all taxa of the 'higher land birds' have 19 praesacral vertebrae. A smaller number is only found in the Cuculidae (18), but more than 19 praesacral vertebrae are found in all outgroup taxa and several other taxa included in the analysis.
 27. Furcula, extremitas omalis with distinct, laterally protruding facies articularis acroracoidea: no (0), yes (1). Within the Strigiformes, this character is absent in *Tyto*.
 28. Coracoid, facies articularis scapularis excavated and cup-like: yes (0), no (1).
 29. Coracoid, foramen nervi supracoracoidei: present (0), absent (1). In some Accipitridae and Falconidae the foramen nervi supracoracoidei is open which is here considered to be a derived condition of these taxa (see Becker 1987; Olson 1987).
 30. Coracoid, extremitas sternalis with notch on margo medialis (Fig. 4): no (0), yes (1). Within the Pici, this notch is well developed in *Indicator* (Indicatoridae), many Ramphastidae (e.g. *Ramphastos ambiguus*, *Selenidera maculirostris*, *Bailloni bailloni*, *Pteroglossus aracari*), and in *Jynx* (Picidae); in some Ramphastidae it is wide and shallow but indicated by a hook above the angulus medialis, in most Picidae it is very indistinct (see also Höfling and Alvarenga 2001: Fig. 5). The notch is also present in at least some Primoscenidae, early Eocene stem group members of the Pici (see Mayr 1998: 7) and we assume that this character was present in the stem species of the Pici.
 31. Scapula, acromion distinctly bifurcate, i.e. with an additional medial process (see Mayr 1998: Fig. 16; Höfling and Alvarenga 2001: Fig. 8): no (0), yes (1).
 32. Sternum, well-developed spina externa rostri: absent (0), present (1).
 33. Sternum, spina interna rostri: absent (0), present (1).
 34. Sternum, facies articularis coracoidea weakly saddle-shaped or convex: no (0), yes (1).
 35. Caudal margin of sternum: with four notches/fenestrae (0), with two notches/fenestrae (1) or without notches/fenestrae (2). In some Accipitridae (e.g. *Buteo jamaicensis*, see Jollie 1977a: p. 165), Falconidae (e.g. *Microhierax caerulescens*, see Jollie 1977b: p. 201), and Caprimulgidae (e.g. *Semeiophorus vexillarius*) the notches are completely reduced which we here consider autapomorphic for these taxa.
 36. Humerus, proximal end, sulcus transversus very deep, long, and rectangular-shaped: no (0), yes (1).
 37. Humerus, distal end, fossa musculi brachialis deep and sharply delimited: no (0), yes (1). Within the Pici, this character is present in *Indicator*, which is here considered an autapomorphy of this taxon.
 38. Humerus, processus flexorius strongly protruding in ventro-distal direction: no (0), yes (1).
 39. Humerus, greatly abbreviated and stocky: no (0), yes (1).
 40. Ulna distinctly exceeding humerus in length: no (0), yes (1).

41. Ulna, proximal end, distinct elongate, ridge-like elevation along midline of shaft, distad of cotyla ventralis: absent (0), present (1).
42. Ulna, proximal end, olecranon very long, narrow and pointed; tuberculum ligamenti collateralis ventralis strongly protruding (see Mayr 1998: Fig. 10H): no (0), yes (1).
43. Carpometacarpus, os metacarpale minus distinctly bowed, spatium intermetacarpale very wide: no (0); yes (1).
44. Carpometacarpus, processus intermetacarpalis: absent or small (0), well-developed, reaching the os metacarpale minus (1). In extant Upupidae/Phoeniculidae and Bucerotidae there is no trace of a processus intermetacarpalis but the tendon of musculus extensor carpi ulnaris inserts on the os metacarpale minus as it does in taxa with a processus intermetacarpalis (usually this tendon inserts on the os metacarpale majus). Stegmann (1965) suggested that the processus intermetacarpalis was completely reduced in the stem lineage of these taxa and we accordingly coded it with (1). The character is also present in most Phasianidae (exceptions are the Numidinae and Meleagrinae) which is here considered to be derived within this taxon since it is absent in the more basal (e.g. Mayr 2000) galliform taxa Megapodiidae and Cracidae. In the Numididae, the tendon of musculus extensor carpi ulnaris also inserts on the os metacarpale minus, and Stegmann (1978) assumed that in these birds the processus intermetacarpalis is secondarily reduced (see above). A fairly well-developed processus intermetacarpalis also occurs in extant Coliidae but is absent in early Tertiary stem group representatives of the Coliiformes (see Mayr and Peters 1998; Mayr 2001).
45. Os carpi ulnare with crus longum being much longer than crus breve: no (0), yes (1).
46. Os carpi ulnare with crus longum greatly abbreviated: no (0), yes (1).
47. Fossa dorsalis of phalanx proximalis digiti majoris divided into two depressions by a distinctly raised oblique bulge: no (0), yes (1).
48. Phalanx proximalis digiti majoris, well-developed processus internus indicis (terminology after Stegmann 1963): absent (0), present (1).
49. Phalanx proximalis digiti majoris, proximal end with large, proximally directing process on ventral side (Fig. 2): no (0), yes (1). This process is concave on its medial side and, in proximal view, continuous with facies articularis metacarpalis.
50. Pelvis wide in mediolateral direction, width across antitrochanters as much or more than length of synsacrum: no (0), yes (1).
51. Pelvis, mid-section of cristae iliacae dorsales greatly reduced: no (0), yes (1).
52. Pelvis, crista dorsolateralis ilii strongly developed, overhanging a marked concavitas infracristalis and a marked sulcus antitrochantericus and convexly bowed if pelvis is viewed from its dorsal side, praeacetabular part much longer than postacetabular part, spina dorsolateralis ilii reduced: no (0), yes (1). These characters might be part of a single character complex and were thus coded as a single character.
53. Pelvis, well-developed tubercula praeacetabularia: present (0), absent (1). Within Cracidae/Phasianidae, the tubercula praeacetabularia are vestigial in the Tetraoninae (Phasianidae) which we consider to be a derived feature of this taxon.
54. Pelvis, cranio-lateral edge of alae praeacetabulares ilii pointed and protruding: no (0), yes (1).
55. Pelvis, processus terminalis ischii very narrow and slender, touching pubis at an angle of 45–90°, fenestra ischiopubica very wide: no (0), yes (1).
56. Femur, pneumatic foramen at cranio-lateral side of proximal end: absent (0), present (1). Within the Cuculidae, this pneumatic foramen only occurs in *Morococcyx*, *Neomorphyx* (Hughes 2000), and *Geococcyx* (personal observation). These three taxa form a monophyletic group (Hughes 2000) and it is more parsimonious to assume that the fossa poplitea was absent in the stem species of the Cuculidae than to assume repeated loss of this character within the taxon.
57. Tibiotarsus, both cristae cnemiales and crista patellaris forming a ridge which circumscribes a groove on the cranial side of the bone, crista cnemialis cranialis continuous with a very marked ridge opposite to the crista fibularis: no (0), yes (1).
58. Tibiotarsus, distal end, pons supratendineus: ossified (0), tendinous (1). Although there is no ossified pons supratendineus in many extant Psittacidae, this character is present in fossil stem group representatives of the Psittaciformes (Mayr and Daniels 1998) and has accordingly been coded.
59. Tibiotarsus, distal end with proximo-distally short and widely spaced condyles, width of distal end two times or more than height of condylus lateralis: no (0), yes (1).
60. Fibula very long, extending over almost the entire length of the tibiotarsus, distal end fused to shaft: no (0), yes (1). This character occurs in only few other taxa, for example, cormorants (Phalacrocoracidae) and loons (Gaviidae). The fibula measures only about two-third of the length of the tibiotarsus in some Accipitridae (e.g. *Accipiter nisus*, *Circus* spp., *Necrosyrtes monachus*, *Spizaetus ornatus*). Although it is very long presumably basal (Griffiths 1994; Holdaway 1994) accipitrid taxa as *Elanus*, the polarity of the character in this taxon is uncertain and it was accordingly coded '01'.
61. Tarsometatarsus, hypotarsus passing into a well-developed crista medianoplantaris; fossa parahypotarsalis medialis very marked and proximal part of margo medialis forming a sharp ridge: no (0), yes (1).
62. Tarsometatarsus, hypotarsus without bony canals, crista lateralis separated from crista medialis by a wide sulcus: no (0), yes (1). Within the Accipitridae, the cristae hypotarsi are bridged by bone in *Pandion* and some of the perine kites (see Jollie 1977a: Fig. 137), which is here considered to be an autapomorphic feature of these taxa. The feature is absent in Sagittariidae and Cathartidae which are currently also included in the Falconiformes.
63. Tarsometatarsus, hypotarsus, tendon of musculus flexor hallucis longus enclosed in bony canal: no (0), yes (1). Contrary to the statement in George and Berger (1966: p. 433), the tendon of m. flexor hallucis longus is enclosed by a bony canal in the Upupidae and Phoeniculidae.
64. Tarsometatarsus, hypotarsus, tendon of musculus flexor digitorum longus enclosed in bony canal: no (0), yes (1).
65. Tarsometatarsus, arcus extensorius (ossified retinaculum extensorium tarsometatarsi): absent (0), present (1). The

- presence of this character in *Pandion* (Accipitridae) is here considered to be an autapomorphy of this taxon.
66. Tarsometatarsus, canalis interosseus distalis: present (0), absent (1). This canal opens into the incisura intertrochlearis lateralis and is not to be confused with the foramen vasculare distale.
 67. Tarsometatarsus, incisurae intertrochleares very short: no (0), yes (1).
 68. Trochlea metatarsi IV: not as follows (0), with plantarly projecting wing-like flange (typical of semi-zygodactyl feet) (1), with large trochlea accessoria (typical of fully zygodactyl feet) (2). In extant Coliidae the wing-like flange is rather poorly developed. However, as it is fairly large in fossil Coliiformes (Mayr and Peters 1998; Mayr 2001), it was coded as present in the Coliidae. This character was coded as 'ordered'.
 69. Hallux, proximal phalanx with proximal end greatly widened (Mayr 1998: Fig. 20F): no (0), yes (1).
 70. Second and third phalanx of fourth toe greatly abbreviated, measuring less than half the length of the fourth phalanx: no (0), yes (1).
 71. Third and fourth toe coalescent at least over length of basal phalanx of third toe: no (0), yes (1). Within the Bucerotidae this character is absent in *Bucorvus* but it cannot be conclusively shown *a priori* whether this absence is plesiomorphic or apomorphic. The presence of this character in several Passeriformes (e.g. *Rupicola*, Cotingidae; see also Raikow 1985), however, unquestionably is a derived condition.
 72. Claws, pair of canals lateral and medial to tuberculum extensorium: absent (0), present (1). This character is absent in the Sagittariidae (secretary bird) which have similar claws to those of owls, falcons and hawks.
 73. Musculus splenius capitis: without cruciform origin (0), with cruciform origin (1); (after Burton 1971). This character is accompanied by a modified shape of the axis (Burton 1971: p. 21) which among the taxa included in this study is only present in Aegothelidae, Hemiprocidae, Apodidae and Trochilidae.
 74. Musculus ambiens: present (0), absent (1); (after Gadow 1893; McKittrick 1991). The musculus ambiens is present in most taxa outside those included in this study (see George and Berger 1966: p. 421). Within the Psittacidae, there are some taxa which have the ambiens and others that lack it (Beddard 1898: p. 268).
 75. Musculus iliofemoralis externus ('D' muscle in the formula of George and Berger 1966: Tab. IX.1): present (0), absent (1); (after Steinbacher 1937; Hudson 1948; George and Berger 1966; Hoff 1966; Hudson et al. 1972; Maurer and Raikow 1981; Berman and Raikow 1982; McKittrick 1991). Hoff (1966) explained the absence of this muscle in some of the taxa he studied by its fusion with m. iliotrochantericus caudalis. This muscle is completely reduced in few other avian taxa (e.g. Podicipedidae and Columbidae; see George and Berger 1966: Tab. IX.2).
 76. Musculus flexor cruris lateralis, pars pelvica ('X' muscle in the formula of George and Berger 1966: Tab. IX.1): present (0), absent (1); (after Gadow 1893; Hudson 1948; Hoff 1966; McKittrick 1991; Baumel and Witmer 1993: p. 219). Concerning the condition of this character in swifts and hummingbirds, we followed McKittrick (1991: p. 13).
 77. Musculus flexor cruris lateralis, pars accessoria ('Y' muscle in the formula of George and Berger 1966: Tab. IX.1): present (0), absent (1); (after Gadow 1893; Hudson 1948; Baumel and Witmer 1993: p. 219). The pars accessoria is lost in a few taxa within the Galbulae (*Jacamerops*, Galbulidae) and Pici (*Sphyrapicus*, *Dendrocopos*, *Picoides*, Picidae) (Swierczewski and Raikow 1981), which in agreement with Swierczewski and Raikow (1981) is here considered to be an autapomorphic character of these taxa; accordingly it has been coded as present in the Galbulae and Pici.
 78. Musculus caudofemoralis, pars pelvica ('B' muscle in the formula of George and Berger 1966: Tab. IX.1): present (0), absent (1); (after Gadow 1893; Hudson 1948; George and Berger 1966; McKittrick 1991).
 79. Musculus fibularis longus: present (0), absent (1); (after Steinbacher 1937; Maurer and Raikow 1981; McKittrick 1991).
 80. Musculus popliteus ('G' muscle in the formula of George and Berger 1966: Tab. IX.1): present (0), absent (1); (after George and Berger 1966; Hudson et al. 1972; Maurer and Raikow 1981; Swierczewski and Raikow 1981; Berman and Raikow 1982; McKittrick 1991). The m. popliteus is present in most avian taxa which are not included in this study (see George and Berger 1966: Tab. IX.2).
 81. Vinculum between tendons of musculus flexor perforans et perforatus digiti III and m. perforatus digiti III: present (0), absent (1); (after George and Berger 1966; Hudson et al. 1972; McKittrick 1991).
 82. Musculus flexor hallucis longus, origin with three heads, iliofibularis tendon passes lateral to lateral head: no (0), yes (1) (Swierczewski and Raikow 1981; Raikow and Cracraft 1983: Fig. 1). According to Swierczewski and Raikow (1981: p. 473) three heads also occur in 'most Passerines, but in that case the iliofibularis tendon passes medial to the lateral head, while in Piciformes it passes lateral to the lateral head. The condition in the two orders is therefore probably not homologous'. The character is thus coded as absent in Passeriformes.
 83. Musculus flexor hallucis longus: tendon supplying hallux (0) tendon not supplying hallux (1); (after Gadow 1893; George and Berger 1966; Maurer and Raikow 1981).
 84. Tendon of musculus flexor hallucis longus supplies digits I, II, and VI; (deep flexor tendons type VI, see George and Berger 1966: 448; Simpson and Cracraft 1981: p. 483): no (0), yes (1); (after Gadow 1893; George and Berger 1966; Raikow 1985).
 85. Tendon of musculus extensor digitorum longus sending branch to hallux: no (0), yes (1); (after Berman and Raikow 1982; Berman 1984).
 86. Musculus abductor digiti II: present (0), absent (1); (after Hudson 1948; George and Berger 1966; Hudson et al. 1972; Maurer and Raikow 1981; Raikow 1982; McKittrick 1991).
 87. Oil gland: tufted (0) or minutely tufted (only vestigial feather remains present)/naked (1); (after Johnston 1988).
 88. Wing: diastataxic (0), eutaxic (1); (after Stephan 1970; Sibley and Ahlquist 1990: p. 217f.).
 89. Villi at the bases of the basalmost downy barbules of breast feathers: absent (0), present (1); (after Brom 1990).

