

Gerald Mayr

The phylogenetic relationships of the early Tertiary Primoscenidae and Sylphornithidae and the sister taxon of crown group piciform birds

Received: 20 October 2003 / Revised: 1 December 2003 / Accepted: 1 December 2003 / Published online: 28 January 2004
© Dt. Ornithologen-Gesellschaft e.V. 2004

Abstract The phylogenetic relationships of the early Tertiary Primoscenidae and Sylphornithidae are, for the first time, evaluated in a cladistic context. Both taxa include small arboreal birds with a permanently (Primoscenidae) or facultatively (Sylphornithidae) retroverted fourth toe. Primoscenidae were hitherto considered to be most closely related to either woodpeckers and allies (Piciformes) or to songbirds (Passeriformes), whereas the Sylphornithidae were classified into the roller-kingfisher-hornbill assemblage (“Coraciiformes”). Analysis of 56 morphological characters supports monophyly of a clade including Sylphornithidae and crown group Piciformes and results in sister group relationship between Passeriformes and a clade including Primoscenidae and the early Miocene Zygodactylidae. However, an analysis in which the search was constrained to trees supporting piciform affinities of the Primoscenidae resulted in trees that were only five steps longer than those from the primary analysis. The character evidence for each hypothesis is discussed. The systematic position of the Primoscenidae appears to be connected to the identity of the sister taxon of crown group Piciformes, as the primary search indicated Upupiformes (hoopoes and wood-hoopoes) and Bucerotiformes (hornbills) as sister taxa of Piciformes, whereas the constrained search resulted in sister group relationship between Coliiformes (mousebirds) and Piciformes. Songbirds do not show the slightest indication of a zygodactyl foot but in these birds the hindtoe is greatly elongated, an alternative strategy to increase the grasping capabilities of the foot. If Passeriformes are indeed the sister group of the clade (Primoscenidae + Zygodactylidae), these birds would be an example that, in closely related taxa, selection

towards the same functional demands can result in entirely different morphological specializations.

Keywords Aves · Passeriformes · Phylogeny · Piciformes · Zygodactylidae

Introduction

The avian taxon Primoscenidae was established by Harrison and Walker (1977) for an incomplete carpo-metacarpus from the Lower Eocene London Clay of England. Referring to this specimen, Harrison and Walker (1977) and Harrison (1982) considered primoscenids to be songbirds (Passeriformes); this assignment was however questioned by Olson and Feduccia (1979).

Meanwhile, new specimens of the Primoscenidae are known from the London Clay (Daniels in Feduccia 1996:166ff., who listed primoscenids as “perching bird/coly mosaic”), and articulated skeletons of these birds were also identified in the Middle Eocene deposits of Messel in Germany, the early Eocene Green River Formation in North America, and the late Paleocene/early Eocene Fur Formation of Denmark (Mayr 1998; Kristoffersen 2002). Primoscenids are now known from a large number of complete skeletons, and from isolated three-dimensionally preserved bones, and were apparently among the most abundant small arboreal birds in the early Eocene. However, as will be shown below, despite their excellent fossil record, phylogenetic assignment of these birds is not straightforward.

All members of the Primoscenidae had zygodactyl feet, i.e. the fourth toe was permanently retroverted, a derived feature they share with piciform birds (woodpeckers and allies), cuckoos (Cuculiformes), and parrots (Psittaciformes). The distal end of the tarsometatarsus most closely resembles that of the early Miocene Zygodactylidae, which are known from isolated distal tarsometatarsi and tibiotarsi only (Ballmann 1969a,

Communicated by F. Bairlein

G. Mayr
Division of Ornithology, Forschungsinstitut Senckenberg,
Senckenberganlage 25, 60325 Frankfurt am Main,
Germany
E-mail: Gerald.Mayr@senckenberg.de

mulgidae: *Caprimulgus*, *Chordeiles*, *Hydropsalis*, *Nyctidromus*, *Phalaenoptilus*. Alcedinidae: *Alcedo*, *Ceryle*, *Dacelo*, *Halcyon*, *Ispidina*. Meropidae: *Merops*. Momotidae: *Momotus*. Coraciidae: *Coracias*, *Eurystomus*. Brachypteraciidae: *Uratelornis*. Upupidae: *Upupa*. Phoeniculidae: *Phoeniculus*. Bucerotidae: *Bucorvus*, *Bycanistes*, *Tockus*, *Penelopides*. Passeriformes: Eurylaimidae: *Cymbirhynchus*, *Psarisomus*; Furnariidae: *Furnarius*; Formicariidae: *Thammophilus*; Tyrannidae: *Tyrannus*, *Pitangus*; Cotingidae: *Rupicola*; Pittidae: *Pitta*; Alaudidae: *Alauda*; Grallinidae: *Grallina*; Artamidae: *Artamus*; Cracticidae: *Gymnorhina*; Corvidae: *Corvus*, *Garrulus*, *Pica*; Paradisaeidae: *Paradisaea*; Sturnidae: *Gracula*, *Lamprotornis*, *Sturnus*; Turdidae: *Erithacus*, *Turdus*; Fringillidae: *Carduelis*, *Fringilla*, *Loxia*. Piciformes: Pici: Ramphastidae: *Bailloni*, *Lybius*, *Megalaima*, *Pogoniolus*, *Psilopogon*, *Pteroglossus*, *Ramphastos*, *Selenidera*, *Trachyphonus*; Indicatoridae: *Indicator*; Picidae: *Campethera*, *Chrysocolaptes*, *Colaptes*, *Dendrocopos*, *Dendropicops*, *Jynx*, *Melanerpes*, *Picus*; Galbulae: Galbulidae: *Galbula*; Bucconidae: *Chelidoptera*, *Monasa*, *Notharchus*.

Fossil terminal taxa: Primoscenidae: *Primozygodactylus danielsi* Mayr 1998; Sandcoleidae: *Eoglaucidium pallas* Fischer 1987, *Anneavis annea* Houde and Olson 1992, *Sandcoleus copiosus* Houde and Olson 1992. Sylphornithidae: *Sylphornis bretouensis* Mourer-Chauviré 1988. The colliiform Sandcoleidae (Houde and Olson 1992; Mayr and Peters 1998) were included in this study because crown group Coliiformes show a highly apomorphic morphology concerning several osteological features included in the analysis.

Institutional abbreviations: SMF: Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; UCB: Université Claude Bernard, Lyon-1, France (collection Lamaud); USTL: Université des Sciences et Techniques du Languedoc, Montpellier, France; WN: collection M. Daniels, Clacton-on-Sea, England.

Anatomical terminology follows Baumel and Witmer (1993) and Vanden Berge and Zweers (1993), if not indicated otherwise.

Fifty-six characters for 17 taxa (see character matrix in Table 1) were coded for a phylogenetic analysis with PAUP 3.1 (Swofford 1993); part of the character matrix is from Mayr et al. (2003). Further included in the analysis are characters that were listed by Mayr (1998) as indicative of the phylogenetic affinities of the Primoscenidae. All non-osteological characters were taken from the literature. The most parsimonious tree was found with the branch-and-bound search option which guarantees to find the shortest tree. Characters were optimized under the delayed transformation (DELTRAN) mode. Two characters (22 and 42 in Appendix I) were coded as ordered. The consistency index (CI) and rescaled consistency index (RC) were calculated. As most of the characters included in this analysis are unknown

for the Zygodactylidae, a second analysis with the same settings was performed without this taxon. The robustness of the resulting trees was evaluated with a bootstrap analysis of 1,000 replicates.

In order to evaluate tree statistics and character distribution of a tree with piciform affinities of Primoscenidae and Zygodactylidae, another analysis was performed in which the search was constrained to trees supporting monophyly of the clade [Primoscenidae + Sylphornithidae + Galbulae + (Zygodactylidae + Pici)]. For this analysis, the constraint tree was constructed in MacClade 3.08a (Maddison and Maddison 1995) and then loaded into PAUP 3.1; all settings of the analysis were as above.

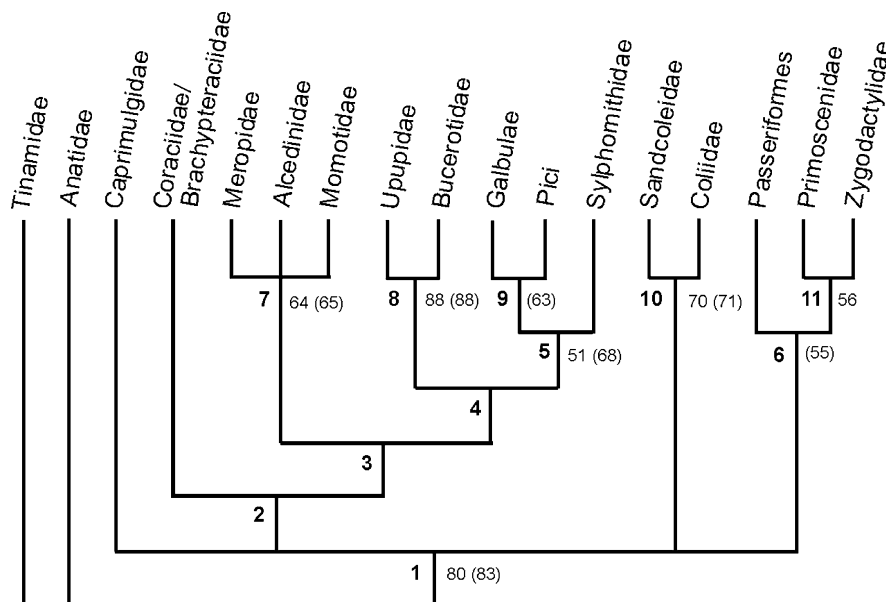
Outgroup comparisons were made with the palaeognathous Tinamidae (tinamous) which are the sister taxon of all neognathous birds and the Anatidae (ducks), one of the most basal lineages of neognathous birds (e.g., Sibley and Ahlquist 1990; Groth and Barrowclough 1999).

Results

Primary search

Analysis of the character matrix in Table 1 with two characters ordered resulted in five most parsimonious trees (length = 127, CI = 0.50, RC = 0.30), the consensus tree of which is shown in Fig. 1. (The consensus tree for the constrained search is shown in Fig. 2.) A second

Fig. 1 Strict consensus tree of five most parsimonious trees (MPTs) (length = 127, CI = 0.50, RC = 0.30) resulting from an analysis of the character matrix in 1. The nodes are characterized by the following synapomorphies that were found in all of the resulting trees (if not indicated otherwise, character transformation is 0 → 1): 1 8, 37, 50, 52; 2 1, 14, 36, 38; 3 24; 4 3, 7, 9 (0 → 1/0 → 2), 20, 25; 5 16, 22 (0 → 2), 42; 6 9 (0 → 2), 10 (0 → 2), 20, 38, 39; 7 6, 45, 48, 54; 8 - 13, 15, 29, 32, 38 (1 → 2), 49; 9 12, 26, 42 (1 → 2), 53, 55; 10 18, 30, 32, 42, 44, 47; 11 40 (1 → 0), 42 (0 → 3). Bootstrap values above 50% are indicated to the right of the internodes; values in parentheses indicate bootstrap support after exclusion of the Zygodactylidae from the analysis (which then also resulted in 5 MPTs with, for the remaining taxa, the same topology of the consensus tree)



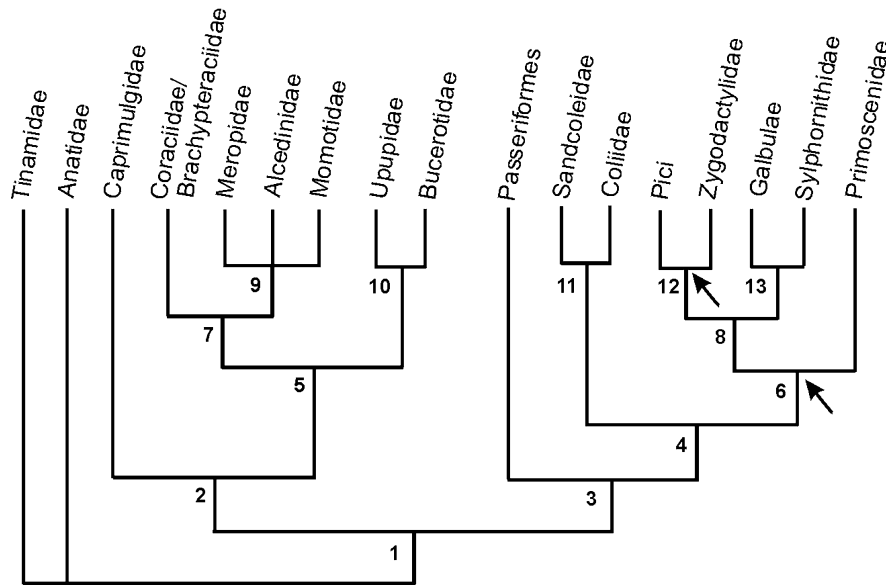


Fig. 2 Strict consensus tree of three most parsimonious trees (length = 132, CI=0.48, RC=0.27) resulting from an analysis of the character matrix in 1 with the search constrained to trees retaining the nodes that are indicated by an *arrow*, i.e. trees supporting monophyly of the taxon [Primoscenidae + Sylphornithidae + Galbulae + (Zygodactylidae + Pici)]. The nodes are characterized by the following synapomorphies that were found in all of the resulting trees (if not indicated otherwise, character transformation is 0 → 1): 1 8, 37, 38 (0 → 2), 41, 43, 50, 51, 52; 2 17; 3 9 (0 → 2), 22, 33; 4 3, 15 (1 → 0), 42; 5 1, 36; 6 20, 42 (1 → 2); 7 14, 15 (1 → 0), 38 (2 → 1); 8 7, 12, 16, 22 (1 → 2), 24, 25, 26, 38 (2 → 1), 53, 55; 9 6, 24, 45, 48, 54; 10 3, 7, 9, 13, 20, 25, 29, 31, 49; 11 18, 30, 32, 43 (1 → 0), 44, 47; 12 42 (2 → 4); 13 33 (1 → 0), 36

analysis, in which the Zygodactylidae were excluded, also resulted in five most parsimonious trees (length = 126, CI=0.50, RC=0.29) with, for the remaining taxa, an identical consensus tree topology but with a higher bootstrap support for several clades (Fig. 1).

The analysis did not support piciform affinities of the Primoscenidae but resulted in sister group relationship between Passeriformes and a taxon including Primoscenidae and Zygodactylidae. This clade (Fig. 1, node 6) was not retained in the bootstrap analysis, but is supported by the following synapomorphies in all of the resulting most parsimonious trees (MPTs; numbers in parentheses refer to the character list in Appendix I): (9) furcula with processus acrocoracoideus and processus acromialis well-developed and wide, forming a plate-like extremitas omalis of roughly triangular shape; (10) furcula with well-developed, blade-like apophysis furculae; (20) carpometacarpus with ventral part of trochlea carpalis cranio-caudally narrow and proximo-distally elongate, slanting caudally towards the midline of the caudal side; fovea carpalis caudalis marked; (38) tarso-metatarsus, hypotarsus with bony canal for the tendon of musculus flexor hallucis longus (Fig. 3e); (39) tarso-metatarsus with well-developed crista plantaris lateralis. Character (20) was noted by Harrison (1982) as evidence for passeriform affinities of the Primoscenidae but also

occurs in Piciformes. However, none of these characters is unique to the above taxa and characters (9) and (10) are also present in some Piciformes (see character matrix in Table 1).

Sister group relationship between Primoscenidae and Passeriformes received bootstrap support of 55% after exclusion of the Zygodactylidae from the analysis.

Sister group relationship between Primoscenidae and Zygodactylidae (Fig. 1, node 11) is supported by a bootstrap value of 56% and in all MPTs by the following synapomorphies: (40) trochlea metatarsi II with well-developed, plantarly projecting process (Fig. 3d, e); (42) trochlea metatarsi IV with large trochlea accessoria which is separated by a furrow from the trochlea metatarsi IV (Fig. 3d, e). Character (40) unquestionably is primitive within neornithine birds as it is present in most basal avian lineages and its recognition as an apomorphy of this clade is questionable. Character (42) also occurs in piciform birds.

Monophyly of a clade including Galbulae, Sylphornithidae, and Pici (Fig. 1, node 5), to the exclusion of Primoscenidae, received bootstrap support of 51% if the Zygodactylidae were included in the analysis and was retained in 68% of the bootstrap replicates if they were excluded. The following synapomorphies were recovered for this clade in all MPTs: (16) humerus with far ventro-distally extending, large fossa musculi brachialis which is situated on the far medial side of the bone and has a weakly developed ventral margin (Fig. 4); (22) carpometacarpus with well-developed processus intermetacarpalis which is fused with the os metacarpale minus (Fig. 5); (42) trochlea metatarsi IV with plantarly projecting wing-like flange.

Sister group relationship between Galbulae and Pici (Fig. 1, node 9) received no bootstrap support if the Zygodactylidae were included in the analysis, but was retained in 63% of the bootstrap replicates after exclusion of this taxon. In all MPTs it is supported by

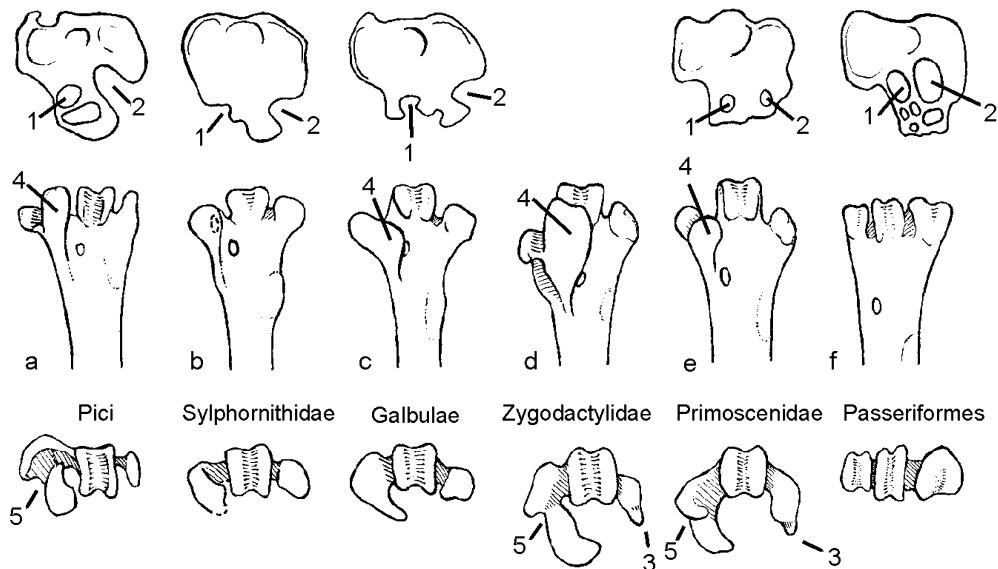


Fig. 3a–f Right tarsometatarsus in comparison; *upper row* proximal end in proximal view, *middle row* distal end in plantar view, *lower row* distal end in distal view. **a** Pici (*Eubucco bourcierii*, Ramphastidae), **b** Sylphornithidae (*Sylphornis bretouensis*, distal end after specimen USTL BRT 1025; proximal view after Mourer-Chauviré 1988: text-fig. 4; reversed to facilitate comparisons), **c** Galbulae (*Chelidoptera tenebrosa*, Bucconidae), **d** Zygodactylidae (*Zygodactylus grivensis*, holotype, after Mayr 1998: fig. 28B), **e** Primoscenidae (*Primozygodactylus* sp., specimen WN 88583A, after Mayr 1998: fig. 28A), **f** Passeriformes (*Menura novaehollandiae*, Menuridae). 1 canal for tendon of musculus flexor digitorum longus, 2 canal for tendon of musculus flexor hallucis longus, 3 plantarly projecting process on trochlea metatarsi II, 4 trochlea accessoria, 5 furrow between trochlea accessoria and trochlea metatarsi IV. Not to scale

the following synapomorphies: (12) extremitas sternalis of coracoid with notch on margo medialis (Mayr et al. 2003: fig. 4); (26) proximal end of phalanx proximalis digiti majoris with large, proximally directing process on ventral side (Fig. 5); (42) trochlea metatarsi IV with large trochlea accessoria; (53) origin of musculus flexor hallucis longus with three heads, iliofibularis tendon passes lateral to lateral head; (55) tendon of musculus flexor hallucis longus supplying digits I, II, and IV. These characters were already listed as apomorphies of crown group Piciformes by Mayr et al. (2003).

Sylphornithidae and crown group Piciformes were shown to be the sister group of the clade [Upupiformes (hoopoes and wood-hoopoes) + Bucerotiformes (hornbills)], and the analysis thus indicates paraphyly of the traditional (e.g., Wetmore 1960) “Coraciiformes”. Sister group relationship between the clades (Sylphornithidae + crown group Piciformes) and (Upupiformes + Bucerotiformes), to the exclusion of the Primoscenidae (Fig. 1, node 4), was not recovered in the bootstrap analysis, but is supported by: (3) os ectethmoidale, greatly expanded, plate-like, with dorsal margin largely fused with frontals; (7) pygostyle with large, shield-like discus pygostyli with sharply defined, ridge-like lateral

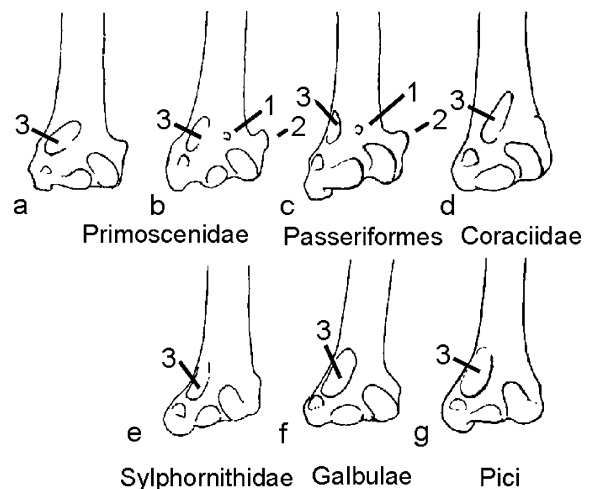


Fig. 4a–g Distal end of left humerus in comparison (cranial aspect). **a** Primoscenidae (*Primozygodactylus* sp., specimen WN 88583A, after Mayr 1998: fig. 25B, reversed to facilitate comparisons), **b** Primoscenidae (unnamed genus and species, specimen WN 92747, after Mayr 1998: fig. 25A; reversed to facilitate comparisons), **c** Passeriformes (*Turdus merula*, Turdidae), **d** Coraciidae (*Coracias garrulus*), **e** Sylphornithidae (*Sylphornis bretouensis*, after Mourer-Chauviré 1988: plate 3), **f** Galbulae (*Galbula ruficauda*, Galbulidae), **g** Pici (*Trachyphonus margaritatus*, Ramphastidae). 1 tubercle above condylus dorsalis, 2 processus supracondylaris dorsalis, 3 fossa musculi brachialis. Not to scale

margins; (9) furcula, extremitas omalis widened, with blunt or slightly convex end and short processus acrocoracoideus and processus acromialis; (20) carpometacarpus with ventral part of trochlea carpalis cranio-caudally narrow and proximo-distally elongate, slanting caudally towards the midline of the caudal side; fovea carpalis caudalis marked; (25) carpometacarpus, distal end of os metacarpale minus strap-like, dorso-ventrally wide, and more or less strongly tilted dorso-ventrally; articulation surface for digitus minor forming a marked knob (Fig. 5). Character (7) was listed as apomorphy of

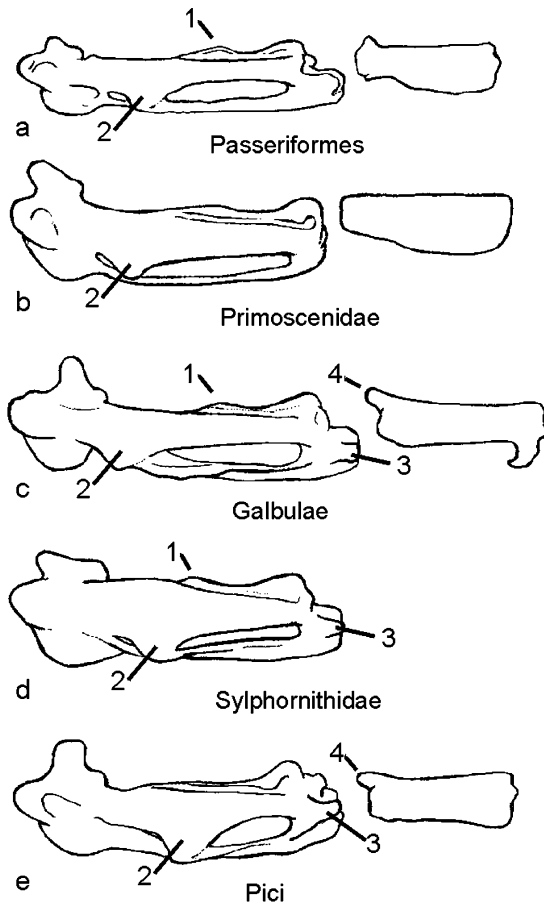


Fig. 5a–e Right carpometacarpus and proximal phalanx digiti majoris in comparison (dorsal aspect). **a** Passeriformes (*Turdus merula*, Turdidae), **b** Primoscenidae (*Primozygodactylus danielsi*, specimen SMF-ME 2522, after Mayr 1998: fig. 26A), **c** Galbulae (*Galbula ruficauda*, Galbulidae), **d** Sylphornithidae (*Sylphornis bretouensis*, after specimens UCB BRL 17 and UCB BRL 8), **e** Pici (*Trachyphonus margaritatus*, Ramphastidae). 1 processus dentiformis, 2 processus intermetacarpalis, 3 articulation surface for digitus minor on os metacarpale minus, 4 proximally directing process on proximal end of phalanx digiti majoris. Not to scale

the Piciformes by Mayr et al. (2003). Characters (3), (7), and (9) are unknown for the Sylphornithidae.

Constrained search

A search that was constrained to trees supporting monophyly of the clade [Primoscenidae + Sylphornithidae + Galbulae + (Zygodactylidae + Pici)] in order to evaluate character distribution in a tree supporting piciform affinities of the Primoscenidae resulted in three most parsimonious trees (length = 132, CI = 0.48, RC = 0.27), the consensus tree of which is shown in Fig. 2.

In this analysis, monophyly of a clade including Primoscenidae, Sylphornithidae, Zygodactylidae and crown group Piciformes (Fig. 2, node 6) is supported in all of the resulting MPTs by the following synapomorphies: (20) carpometacarpus with ventral part of trochlea carpalis cranio-caudally narrow and proximo-

distally elongate, slanting caudally towards the midline of the caudal side; fovea carpalis caudalis marked; (42) trochlea metatarsi IV with large trochlea accessoria which is separated by a furrow from the trochlea metatarsi IV. Character (42) was also listed by Mayr (1998) as evidence for piciform affinities of the Primoscenidae but is absent in the Bucconidae (Galbulae).

Monophyly of a clade including Galbulae, Sylphornithidae, Zygodactylidae, and Pici (Fig. 2, node 8) received no bootstrap support but the following synapomorphies were recovered in all MPTs, all of which are, however, unknown for the Zygodactylidae: (7) pygostyle with large, shield-like discus pygostyli with sharply defined, ridge-like lateral margins; (12) coracoid, extremitas sternalis with notch on margo medialis; (16) humerus with large fossa musculi brachialis which is situated on far medial side of bone, with weakly developed ventral margin, and extending far ventro-distally; (22) carpometacarpus with processus intermetacarpalis well-developed, fused with os metacarpale minus; (24) carpometacarpus with os metacarpale minus distally distinctly protruding beyond os metacarpale majus; (25) carpometacarpus with distal end of os metacarpale minus strap-like, dorso-ventrally wide, and more or less strongly tilted dorso-ventrally; articulation surface for digitus minor forming a marked knob; (26) phalanx proximalis digiti majoris, proximal end with large, proximally directing process on ventral side; (38) tarsometatarsus, hypotarsus, tendon of musculus flexor hallucis longus situated in a marked sulcus which is medially bordered by a prominent crista lateralis hypotarsi; (53) musculus flexor hallucis longus origin with three heads, iliofibularis tendon passes lateral to lateral head; (55) tendon of musculus flexor hallucis longus supplying digits I, II, and IV.

Sister group relationship between Zygodactylidae and Pici (Fig. 2, node 12) is supported by a single synapomorphy: (42) trochlea metatarsi IV with large, distally elongated trochlea accessoria that is separated by a furrow from the trochlea metatarsi IV and reaches beyond the midst of the trochlea metatarsi III. This character was also listed by Simpson and Cracraft (1981) and Mayr (1998) as evidence for a closer relationship between Zygodactylidae and Pici.

Sister group relationship between Galbulae and Sylphornithidae (Fig. 2, node 13) is supported by the following two synapomorphies in all MPTs: (33) proximal end of tibiotarsus without ridge opposite crista fibularis; (36) tarsometatarsus, hypotarsus passing into a well-developed crista medianoplantaris; fossa parahypotarsalis medialis very marked and proximal part of margo medialis forming a sharp ridge. The first of these characters represents a reversal into the primitive condition.

Monophyly of a clade including, Coliiformes, Sylphornithidae, Primoscenidae, Zygodactylidae and crown group Piciformes (Fig. 2, node 4) is supported by the following synapomorphies: (3) os ectethmoidale, greatly expanded, plate-like, with dorsal margin largely fused with frontals; (15) caudal margin of sternum with four

notches; (42) trochlea metatarsi IV with plantarly projecting wing-like flange.

Discussion

In all of the resulting trees, the Sylphornithidae were shown to be most closely related to crown group Piciformes, i.e. the clade (Galbulae + Pici), although their exact position varied depending on the kind of search that was performed: they were optimized as sister group of crown group Piciformes in the primary search and as sister group of Galbulae in the constrained search (Figs. 1 and 2). Compared to the Primoscenidae, the Sylphornithidae exhibit a less derived morphology of the trochlea accessoria (tarsometatarsus) for the reversed fourth toe, but share derived features of the carpometacarpus with crown group Piciformes (Fig. 1, node 5; Figs. 4, 5). Mourer-Chauviré (1988) noted similarities between Sylphornithidae and the piciform Buccinidae but classified sylphornithids into the “Coraciiformes” without specifying a possible sister taxon. However, at the time of the original description of these birds the carpometacarpus was unknown and it is especially this skeletal element that supports piciform affinities of the Sylphornithidae (Fig. 5). Whether the enigmatic *Eutreptodactylus* from the Paleocene of South America (Baird and Vickers-Rich 1997) also belongs to the Sylphornithidae is uncertain (cf. Mourer-Chauviré 1999; Mayr 2001). This taxon has not been included in the present analysis because it is known from a single bone only, which has been lost before its description was published (Baird and Vickers-Rich 1997).

The Primoscenidae were shown in all analyses to be outside a clade including Sylphornithidae and crown group Piciformes (contra Mayr 1998), and especially the carpometacarpus and the proximal phalanx of the major digit of primoscenids lack apomorphies of crown group Piciformes (i.e., the os metacarpale minus is distally not protruding beyond the os metacarpale majus, the processus intermetacarpalis is not fused with the os metacarpale minus, and the proximal end of the phalanx proximalis digiti majoris lacks the proximally directing process).

Analysis of the character matrix in Table 1 does not support piciform affinities of the Primoscenidae but resulted in sister group relationship between Passeriformes and the clade (Primoscenidae + Zygodactylidae) (Fig. 1), although not all of the characters listed by Harrison (1982:78) as evidence for songbird affinities of the primoscenid *Primoscens* were included [some are difficult to code into discrete states, e.g., presence of a “short and stout alular metacarpal” (= processus extensorius), position of the “rounded hollow for the ligament of the palmar end of the cuneiform bone” (= Facies ligamentalis interna of Ballmann 1969a)].

Very indicative of passeriform affinities of the Primoscenidae is the presence of a striking derived

character complex, which is otherwise only known from passeriform birds, at the distal humerus of an as yet unnamed primoscenid taxon from the London Clay (Fig. 3b, c; Mayr 1998: plate 7). In this species, which exhibits a zygodactyl foot as other primoscenid birds, there is a distinct tubercle in the center of the cranial surface of the distal end, above the condylus dorsalis, and a large, proximally directing processus supracondylaris dorsalis (the known fossil specimens of this species are housed in a private collection and were thus not included in the present analysis). This character complex, that is absent in the primoscenid *Primozygodactylus*, may be an underlying synapomorphy (e.g., Saether 1979) of the clade [Passeriformes + (Primoscenidae + Zygodactylidae)]. Paraphyly of the Primoscenidae with respect to Passeriformes is unlikely as it would imply an origin of songbirds from a zygodactyl ancestor.

Songbirds do not show the slightest indication of a zygodactyl foot but in these birds the hindtoe is greatly elongated, an alternative strategy to increase the grasping capabilities of the foot. There are other cases of divergent evolution in closely related taxa, e.g. the very different morphology of the feeding apparatus of the sister taxa Phoenicopteridae (flamingos) and Podicipedidae (grebes) (van Tuinen et al. 2001; Mayr 2004). However, in the latter case the differences result from specialization towards different feeding strategies whereas the zygodactyl foot of primoscenids almost certainly evolved for the same reason as the elongated hindtoe of songbirds, the formation of a perching foot. If Passeriformes indeed are the sister group of the clade (Primoscenidae + Zygodactylidae), these birds would exemplify that in closely related taxa selection towards the same functional demands can result in entirely different morphological specializations (see also Bock 1974:239).

Owing to the high degree of homoplasy in the data set, the clade including Passeriformes, Primoscenidae, and Zygodactylidae received no significant bootstrap support. Moreover, several of the characters identified as synapomorphies of this clade are also present in piciform birds, and the trees resulting from the analysis that was constrained to trees supporting monophyly of the clade [Primoscenidae + Sylphornithidae + Galbulae + (Zygodactylidae + Pici)] (Fig. 2) are only five steps longer than the trees resulting from the primary search. However, the present study offers a framework for future research in which the competing hypotheses can be tested:

Figures 1 and 2 indicate that the position of the Primoscenidae is connected to the identity of the sister taxon of crown group Piciformes (Galbulae + Pici). Whereas the clade (Upupiformes + Bucerotiformes) was identified as sister taxon of crown group Piciformes in the primary search (Fig. 1), colliiform birds were shown to be the sister taxon in the constrained search (Fig. 2). Molecular analyses of nuclear gene sequences yielded some support for sister group relationship

between Piciformes and the clade (Upupiformes + Bucerotiformes) (Johansson et al. 2001; Mayr et al. 2003). From a study of the feeding apparatus, a close relationship between piciform, upupiform, and bucerotiform birds was also assumed by Burton (1984). However, this was not supported in the molecular studies of Sibley and Ahlquist (1990; DNA-DNA hybridization data), Espinosa de los Monteros (2000; mitochondrial DNA sequences), and Johansson and Ericson (2003; nuclear gene sequences of a smaller taxon sample than in the studies of Johansson et al. 2001 and Mayr et al. 2003). Although an analysis of a combined morphological and molecular data set resulted in sister group relationship between Piciformes and Coliiformes (Mayr et al. 2003), there is as yet little morphological evidence for such a grouping. Also, if the Zygodactylidae were the sister taxon of the Pici (Mayr 1998 and Fig. 2), it is to be expected that they would exhibit the apomorphies of crown group Piciformes. Additional skeletal elements of these very incompletely known birds may thus further support or refute the phylogeny in Fig. 2.

Acknowledgements I thank C. Mourer-Chauviré for making available for study specimens of the Sylphornithidae, M. Daniels for enabling me to study his collection, and P. Houde and S. Olson for allowing me to investigate specimens of the Sandcoleidae during an earlier visit to the Smithsonian Institution. I further thank A. Helbig and S. Peters for reviewing the manuscript. I also thank A. Manegold for drawing my attention to the proximally directing process on the proximal phalanx of the major digit in Pici and Galbulae.

Appendix I

Character descriptions.

1. Skull, completely ossified septum nasale: absent (0), present (1). The ossified nasal septum of few passerines (e.g., *Rupicola* sp., Cotingidae) which are deeply nested within Passeriformes (e.g., Barker et al. 2002) is here considered to be an autapomorphy of these taxa.

2. Os lacrimale, descending process greatly enlarged and medially expanded: no (0), yes (1).

3. Os ectethmoidale, greatly expanded, plate-like, with dorsal margin largely fused with frontals: no (0), yes (1).

4. Processus postorbitales strongly elongated, touching (or nearly touching) the jugals: no (0), yes (1).

5. Os palatinum and os pterygoideum fused: yes (0), no (1). Separated palatines and pterygoids are an apomorphy of neognathous birds.

6. 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 (see Mayr et al. 2003).

7. Pygostyle with large, shield-like discus pygostyli with sharply defined, ridge-like lateral margins (Mayr et al. 2003: fig. 3): no (0), yes (1).

8. Number of praesacral vertebrae (all vertebrae cranial to synsacrum): more than 19 (0), 19 (1).

9. Furcula, extremitas omalis: not as follows (0), widened, with blunt or slightly convex end and short processus acrocoracoideus and processus acromialis (1), with processus acrocoracoideus and processus acromialis well-developed and wide, forming a plate-like extremitas omalis of roughly triangular shape (2). The extremitas omalis of the furcula is very similar in Upupiformes, Bucerotiformes, and Galbulae (see Höfling and Alvarenga 2001).

10. Furcula, apophysis furculae: absent (0), present, rod-like (1), well-developed, blade-like (2). Within Galbulae, a blade-like apophysis furculae is present in the Bucconidae but absent in the Galbulidae. The absence of an apophysis furculae in *Eurystomus* (Coraciidae) is here considered autapomorphic for that taxon, because an apophysis furculae is present in other Coraciidae and in the Brachypteraciidae.

11. Coracoid, processus procoracoideus well-developed, strap-like: no (0), yes (1). There are two types of coracoid as candidates for the coracoid of *Sylphornis* (Mourer-Chauviré 1988; Mayr 1998) but in both the processus procoracoideus is greatly reduced.

12. Coracoid, extremitas sternalis with notch on margo medialis (Mayr et al. 2003: fig. 4): no (0), yes (1). Mayr et al. (2003) listed the presence of this notch as an apomorphy of the taxon (Galbulae + Pici).

13. Coracoid, facies articularis sternalis dorso-ventraly very wide: no (0), yes (1).

14. Scapula, acromion distinctly bifurcate, i.e. with an additional ventro-medial process (Mayr 1998: fig. 16; Höfling and Alvarenga 2001: fig. 8): no (0), yes (1).

15. Caudal margin of sternum: with four notches (0), with two notches (1). Within Passeriformes, a four-notched sternum occurs in some species of Rhinocryptidae and Formicariidae (e.g., Feduccia and Olson 1982). As these taxa are deeply nested within Suboscines (e.g., Ericson et al. 2003), it is assumed that this condition is derived within Passeriformes and that the stem species of Passeriformes had a two-notched sternum.

16. Humerus, far ventro-distally extending, large fossa musculi brachialis which is situated on the far medial side of the bone and has a weakly developed ventral margin (Fig. 4): no (0), yes (1). Within Galbulae, this character is present in the Galbulidae but absent in the Bucconidae.

17. Ulna distinctly exceeding humerus in length: no (0), yes (1).

18. Ulna, cotyla ventralis greatly enlarged: no (0), yes (1).

19. Ulna, proximal end, olecranon very long, narrow, and pointed (Mayr 1998: fig. 10H): no (0), yes (1).

20. Carpometacarpus, ventral part of trochlea carpalis cranio-caudally narrow and proximo-distally elongate, slanting caudally towards the midline of the caudal side; fovea carpalis caudalis marked: no (0), yes (1).

21. Carpometacarpus, processus dentiformis (Fig. 5): absent (0), present (1). The presence of a well-developed

processus dentiformis in *Uratelornis* (Brachypteraciidae) is here considered autapomorphic for the Brachypteraciidae because a processus dentiformis is absent in Coraciidae and fossil stem group rollers (Mayr and Mourer-Chauviré 2000). Within Galbulae, a processus dentiformis is well-developed in *Galbula ruficauda* and *Monasa nigrifrons* but absent in *Chelidoptera tenebrosa* and *Notharchus macrorhynchus*.

22. Carpometacarpus, processus intermetacarpalis (Fig. 5): absent or small (0), well-developed, reaching os metacarpale minus (1), well-developed, fused with os metacarpale minus (2). The fusion of the processus intermetacarpalis with the os metacarpale minus in the Brachypteraciidae is here considered to be autapomorphic for that taxon because this feature is absent in the Coraciidae and fossil stem group rollers (Mayr and Mourer-Chauviré 2000). This character was coded as ordered.

23. Carpometacarpus, proximal end of os metacarpale minus with distinct, ventrally protruding tubercle (Mayr and Mourer-Chauviré 2000: fig. 10): no (0), yes (1).

24. Carpometacarpus, os metacarpale minus distally protruding distinctly beyond os metacarpale majus (Fig. 5): no (0), yes (1).

25. Carpometacarpus, distal end of os metacarpale minus strap-like, dorso-ventrally wide, and more or less strongly tilted dorso-ventrally; articulation surface for digitus minor forming a marked knob (Fig. 5): no (0), yes (1).

26. Phalanx proximalis digiti majoris, proximal end with large, proximally directing process on ventral side (Fig. 5): no (0), yes (1).

27. Pelvis, foramen ilioischadicum caudally closed: no (0), yes (1). A caudally closed foramen ilioischadicum is an apomorphy of neognathous birds.

28. Pelvis, mid-section of cristae iliacae dorsales greatly reduced: no (0), yes (1).

29. Pelvis, processus terminalis ischii very narrow and slender, touching pubis at an angle of 45°-90°, fenestra ischiopubica very wide: no (0), yes (1).

30. Femur, distal end thickened, tuberculum musculi gastrocnemialis lateralis large: no (0), yes (1).

31. Femur, pneumatic foramen at cranio-lateral side of proximal end: absent (0), present (1).

32. Tibiotarsus, both cristae cnemiales and crista patellaris forming a ridge which circumscribes a groove on the cranial side of the bone: no (0), yes (1). The occurrence of state 1 in the Dendrocolaptidae (Passeriformes) is here considered to be an autapomorphy of this taxon which is deeply nested within Passeriformes (e.g., Ericson et al. 2003).

33. Tibiotarsus, proximal end with ridge opposite crista fibularis: no (0), yes (1).

34. Tarsometatarsus greatly elongated and slender, apart from tibiotarsus longest limb element, exceeding humerus in length: no (0), yes (1). The greatly elongated tarsometatarsus of most Brachypteraciidae is here considered to be derived within rollers because it is absent in

Coraciidae and fossil stem group rollers (Mayr and Mourer-Chauviré 2000). No complete humerus of the Sylphornithidae is known, but the preserved remains indicate that it was shorter than the tarsometatarsus.

35. Tarsometatarsus, arcus extensorius (ossified retinaculum extensorium tarsometatarsi): absent (0), present (1).

36. 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).

37. Tarsometatarsus, hypotarsus, ossified canal for tendon of musculus flexor digitorum longus: absent (0), present (1), present, cristae medialis et lateralis delimiting marked sulcus plantar to this canal (2). Within Galbulidae, this canal is open in *Galbula ruficauda* but closed in *G. cyanesceus* (Simpson and Cracraft 1981: fig. 6B); within Bucconidae, it is open in *Chelidoptera tenebrosa* and *Notharchus macrorhynchus* but closed in *Monasa nigrifrons*.

38. Tarsometatarsus, hypotarsus, tendon of musculus flexor hallucis longus: not as follows (0), situated in a marked sulcus which is medially bordered by a prominent crista lateralis hypotarsi (Fig. 3) (1), enclosed in a bony canal (2). Homology of a hypotarsal canal in the Caprimulgidae is uncertain.

39. Tarsometatarsus, well-developed crista plantaris lateralis: absent (0), present (1).

40. Trochlea metatarsi II, well-developed, plantarly projecting process (Fig. 3): present (0), absent (1).

41. Trochlea metatarsi II much shorter than trochlea metatarsi III: yes (0), no (1).

42. Trochlea metatarsi IV (Fig. 3): not as follows (0), with plantarly projecting wing-like flange (typical of semi-zygodactyl feet) (1), with large trochlea accessoria (typical for fully zygodactyl feet) which is not separated by a furrow from the trochlea metatarsi IV and does not reach beyond the midst of the trochlea metatarsi III (2), with large trochlea accessoria which is separated by a furrow from the trochlea metatarsi IV but does not reach beyond the midst of the trochlea metatarsi III (3), with large, distally elongated trochlea accessoria which is separated by a furrow from the trochlea metatarsi IV and reaches beyond the midst of the trochlea metatarsi III (4). In all known specimens of the Sylphornithidae the trochlea metatarsi IV is damaged but the preserved part indicates that it merely bore a plantarly projecting wing-like flange. Within the Galbulae a furrow between the trochlea accessoria and the trochlea metatarsi IV is present in Galbulidae but absent in Bucconidae. Presence of a furrow between the trochlea accessoria and the trochlea metatarsi IV was listed by Mayr (1998:53 ff.) as synapomorphy of a taxon including Primoscenidae, Zygodactylidae, and Pici; a distally elongated trochlea accessoria was considered to be a synapomorphy of a taxon including Zygodactylidae, and Pici. This character was coded as ordered.

43. Tarsometatarsus, canalis interosseus distalis: present (0), absent (1).

44. Tarsometatarsus facies articularis metatarsalis situated on medial margin of shaft (characteristic of pamprodactyl feet in which the hind toe can be turned forwards): no (0), yes (1).

45. Hallux, proximal phalanx with proximal end greatly widened (Mayr 1998: fig. 20F): no (0), yes (1).

46. Hallux greatly elongated, proximal phalanx about two times longer than proximal phalanx of third toe: no (0), yes (1).

47. Second and third phalanx of fourth toe greatly abbreviated, measuring less than half the length of the fourth phalanx: no (0), yes (1).

48. Third and fourth toe coalescent at least over length of basal phalanx of third toe: no (0), yes (1). Within 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 few Passeriformes (e.g. *Rupicola*, Cotinidae), however, unquestionably is a derived condition.

49. Tendon of musculus extensor carpi ulnaris inserting on os metacarpale minus (see Stegmann 1965 - usually this tendon inserts on the os metacarpale majus): no (0), yes (1).

50. Musculus ambiens: present (0), absent (1); (after McKittrick 1991). The musculus ambiens is present in most taxa outside those included in this study.

51. Musculus iliofemoralis externus ("D" muscle in the formula of George and Berger 1966: Tab. IX.1): present (0), absent (1); (after Steinbacher 1937; George and Berger 1966; Maurer and Raikow 1981; Berman and Raikow 1982; McKittrick 1991).

52. Musculus caudofemoralis, pars pelvica ("B" muscle in the formula of George and Berger 1966: Tab. IX.1): present (0), absent (1); (after McKittrick 1991).

53. Musculus flexor hallucis longus: not as follows (0); origin with three heads, iliofibularis tendon passes lateral to lateral head (1) (Swierczewski and Raikow 1981; Raikow and Cracraft 1983). According to Swierczewski and Raikow (1981:473) three heads 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."

54. Musculus flexor hallucis longus: tendon supplying hallux (0), tendon not supplying hallux (1); (after George and Berger 1966; Maurer and Raikow 1981).

55. Tendon of musculus flexor hallucis longus supplies digits I, II, and IV (deep flexor tendons type VI, see George and Berger 1966:448; Simpson and Cracraft 1981): no (0), yes (1).

56. Villi at the bases of the basalmost downy barbules of the breast feathers: absent (0), present (1); (after Brom 1990).

References

- Baird RF, Vickers-Rich P (1997) *Eutrepodactylus itaboraiensis* gen. et. sp. nov., an early cuckoo (Aves: Cuculiformes) from the Late Paleocene of Brazil. *Alcheringa* 21:123–127
- Ballmann P (1969a) Die Vögel aus der altburdigalen Spaltenfüllung von Wintershof (West) bei Eichstätt in Bayern. *Zitteliana* 1:5–60
- Ballmann P (1969b) Les oiseaux miocènes de La Grive-Saint-Alban (Isère). *Geobios* 2:157–204
- Barker FK, Barrowclough GF, Groth JG (2002) A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence. *Proc R Soc Lond B* 269:295–308
- Baumel JJ, Witmer LM (1993) Osteologia. In: Baumel JJ, King AS, Breazile JE, Evans, HE, Vanden Berge JC (eds) *Handbook of avian anatomy: Nomina Anatomica Avium*. Publ Nuttall Ornithol Club 23:45–132
- Berman SL, Raikow RJ (1982) The hindlimb musculature of the mousebirds (Coliiformes). *Auk* 99:41–57
- Bock WJ (1974) The avian skeletomuscular system. In: Farner DS, King JR, Parkes KC (eds) *Avian biology*, vol 4. Academic Press, New York, pp 119–257
- Brom TG (1990) Villi and the phyly of Wetmore's order Piciformes (Aves). *Zool J Linn Soc* 98:63–72
- Burton PJK (1984) Anatomy and evolution of the feeding apparatus in the avian orders Coraciiformes and Piciformes. *Bull Brit Mus Nat Hist Zool* 47:331–443
- Ericson PGP, Irestedt M, Johansson U (2003) Evolution, biogeography, and patterns of diversification in passerine birds. *J Avian Biol* 34:3–15
- Espinosa de los Monteros A (2000) Higher-level phylogeny of Trogoniformes. *Mol Phylogen Evol* 14:20–34
- Feduccia A (1974) Morphology of the bony stapes in New and Old World suboscines: new evidence for common ancestry. *Auk* 91:427–429
- Feduccia A (1977) A model for the evolution of perching birds. *Syst Zool* 26:19–31
- Feduccia A (1996) *The origin and evolution of birds*. Yale University Press, New Haven
- Feduccia A, Olson SL (1982) Morphological similarities between the Menurae and the Rhinocryptidae, relict passerine birds of the southern hemisphere. *Smithson. Contrib Zool* 366:1–22
- Fischer KH (1987) Eulenreste (*Eoglaucidium pallas* nov.gen., nov.sp., Strigiformes, Aves) aus der mitteleozänen Braunkohle des Geiseltals bei Halle (DDR). *Mitt Zool Mus Berlin* 63:137–142
- George JC, Berger AJ (1966) *Avian myology*. Academic Press, New York
- Groth JG, Barrowclough GF (1999) Basal Divergences in Birds and the Phylogenetic Utility of the Nuclear RAG-1 Gene. *Mol Phylogen Evol* 12:115–123
- Harrison CJO (1982) Cuculiform, piciform and passeriform birds in the Lower Eocene of England. *Tert Res* 4:71–81
- Harrison CJO, Walker CA (1977) Birds of the British Lower Eocene. *Tert Res Spec Pap* 3:1–52
- Höfling E, Alvarenga HMF (2001) Osteology of the shoulder girdle in the Piciformes, Passeriformes and related groups of birds. *Zool Anz* 240:196–208
- Houde P, Olson SL (1992) A radiation of coly-like birds from the early Eocene of North America (Aves: Sandcoleiformes new order). In: Campbell KE (ed) *Papers in avian paleontology honoring Pierce Brodkorb*. Nat Hist Mus Los Angeles Cty Contrib Sci 36:137–160
- Johansson US, Ericson PGP (2003) Molecular support for a sister group relationship between Pici and Galbulae (Piciformes *sensu* Wetmore 1960). *J Avian Biol* 34:185–197
- Johansson US, Parsons TJ, Irestedt M, Ericson PGP (2001) Clades within the 'higher land birds', evaluated by nuclear DNA sequences. *J Zool Syst Evol Res* 39:37–51
- Kristoffersen AV (2002) The avian diversity in the latest Paleocene—earliest Eocene Fur Formation, Denmark. A synopsis. PhD thesis, University of Copenhagen
- Lanyon SM, Zink RM (1987) Genetic variation in piciform birds: monophyly and generic and familial relationships. *Auk* 104:724–732
- Livezey BC, Zusi RL (2001) Higher-order phylogenetics of modern Aves based on comparative anatomy. *Neth J Zool* 51:179–205

- Maddison WP, Maddison DR (1995) MacClade: Analysis of phylogeny and character evolution, version 3.08a: Sinauer, Sunderland, Mass.
- Maurer D, Raikow RJ (1981) Appendicular myology, phylogeny, and classification of the avian order Coraciiformes (including Trogoniformes). *Ann Carnegie Mus Nat Hist* 50:417–434
- Mayr G (1998) “Coraciiforme” und “piciforme” Kleinvögel aus dem Mittel-Eozän der Grube Messel (Hessen, Deutschland). *Cour Forsch Inst Senckenberg* 205:1–101
- Mayr G (2001) A new specimen of the tiny Middle Eocene bird *Gracilitarsus mirabilis* (new family: Gracilitarsidae). *Condor* 103:78–84
- Mayr G (2004) Morphological evidence for sister group relationship between flamingos (Aves: Phoenicopteridae) and grebes (Podicipedidae). *Zool J Linn Soc* (in press)
- Mayr G, Mourer-Chauviré C (2000) Rollers (Aves: Coraciiformes s.s.) from the Middle Eocene of Messel (Germany) and the Upper Eocene of the Quercy (France). *J Vert Palaeontol* 20:533–546
- Mayr G, Peters DS (1998) The mousebirds (Aves: Coliiformes) from the Middle Eocene of Grube Messel (Hessen, Germany). *Senckenbergiana Lethaea* 78:179–197
- Mayr G, Smith R (2002) Avian remains from the lowermost Oligocene of Hoogbutsel (Belgium). *Bull Inst R Sci Nat Belg* 72:139–150
- Mayr G, Manegold A, Johansson U (2003) Monophyletic groups within “higher land birds” - comparison of morphological and molecular data. *J Zool Syst Evol Res* 41:233–248
- McKittrick MC (1991) Phylogenetic Analysis of Avian Hindlimb Musculature. *Univ Michigan Mus Zool Misc Publ* 179:1–85
- Mourer-Chauviré C (1988) Le gisement du Bretou (Phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertébrés de l’Eocène supérieur. II Oiseaux. *Palaeontographica (A)* 205:29–50
- Mourer-Chauviré C (1999) Les relations entre les avifaunas du Tertiaire inférieur d’Europe et d’Amérique du Sud. *Bull Soc Geol Fr* 170:85–90
- Olson SL (1983) Evidence for a polyphyletic origin of the Piciformes. *Auk* 100:126–133
- Olson SL, Feduccia A (1979) An Old-World occurrence of the Eocene avian family Primobucconidae. *Proc Biol Soc Wash* 92:494–497
- Raikow RJ, Cracraft J (1983) Monophyly of the Piciformes: a reply to Olson. *Auk* 100:134–138
- Saether OA (1979) Underlying synapomorphies and anagenetic analysis. *Zool Scr* 8:305–312
- Sibley CG, Ahlquist JE (1990) Phylogeny and classification of birds: a study in molecular evolution. Yale University Press, New Haven.
- Simpson SF, Cracraft J (1981) The phylogenetic relationships of the Piciformes (Class Aves). *Auk* 98:481–494
- Stegmann B (1965) Funktionell bedingte Eigenheiten am Metacarpus des Vogelflügels. *J Ornithol* 106:179–189
- Steinbacher J (1937) Anatomische Untersuchungen über die systematische Stellung der Galbulidae und Bucconidae. *Arch Naturgesch B* 6:417–515
- Swierczewski EV, Raikow RJ (1981) Hindlimb morphology, phylogeny and classification of the Piciformes. *Auk* 98:466–480
- Swofford DL (1993) PAUP: Phylogenetic analysis using parsimony, version 3.1. Illinois Natural History Survey, Champaign
- Tuinen M van, Butvill DB, Kirsch JAW, Hedges SB (2001) Convergence and divergence in the evolution of aquatic birds. *Proc R Soc Lond B* 268:1345–1350
- Vanden Berge JC, Zweers GA (1993) Myologia. In: Baumel JJ, King AS, Breazile JE, Evans HE, Vanden Berge JC (eds) Handbook of avian anatomy: Nomina Anatomica Avium. *Publ Nuttall Ornithol Club* 23:189–247
- Wetmore A (1960) A classification for the birds of the world. *Smithson Misc Collect* 139(11):1–37