

Combined phylogenetic analysis of a new North American fossil species confirms widespread Eocene distribution for stem rollers (Aves, Coracii)

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We report a nearly complete skeleton of a new species of stem roller (Aves, Coracii) from the early Eocene Green River Formation of North America. The new species is most closely related to two species-depauperate lineages, Coraciidae (rollers) and Brachypteraciidae (ground rollers), that form a monophyletic crown clade (Coracioidea) with an exclusively Old World extant distribution. Phylogenetic analysis utilizing a matrix of 133 morphological characters and sequence data from three genes (*RAG-1*, *c-myc*, and *ND2*) identifies the new species as a stem member of the Coracii more closely related to the crown clade than the only previously identified New World taxon, *Primobucco mcgrewi*. The phylogenetic placement of the new species and *Primobucco mcgrewi* indicates a widespread northern hemisphere distribution in the Eocene with subsequent restriction to Africa, Madagascar, Australia, and temperate to tropical parts of Europe and Asia. It provides evidence of further ecological diversity in early stem Coracii and convergence on crown morphologies. The new species contributes to mounting evidence that extant distributions for major avian subclades may be of comparatively recent origin. Further late Palaeogene sampling is needed to elucidate potential drivers for shifting avian distributions and disappearance of Coracii from North America.

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INTRODUCTION

Rollers (Coraciidae) and ground rollers (Brachypteraciidae) are medium-sized birds with colourful plumage, large heads, and recurved beaks. The common name roller is derived from the characteristic acrobatic display flights of ‘true’ rollers (Coraciidae), although the ground rollers do not exhibit this behaviour (Whitfield, 1988). The five species of predomi-

nantly terrestrial Brachypteraciidae are endemic to Madagascar, whereas the more arboreal ‘true’ rollers have an extant distribution that spans Europe, Africa, south Asia, and Australia (Fry, Fry & Harris, 1992; Langrand, 2001; Fig. 1). These two taxa formed the clade Coracioidea of Cracraft (1971, 1981). The Lep-tosomidae (cuckoo-rollers) are represented by a single predominately arboreal species from Madagascar and the Comoro Islands (Langrand, 2001) and have at times been considered closely related to the Coracioidea, largely following the early work of Sclater

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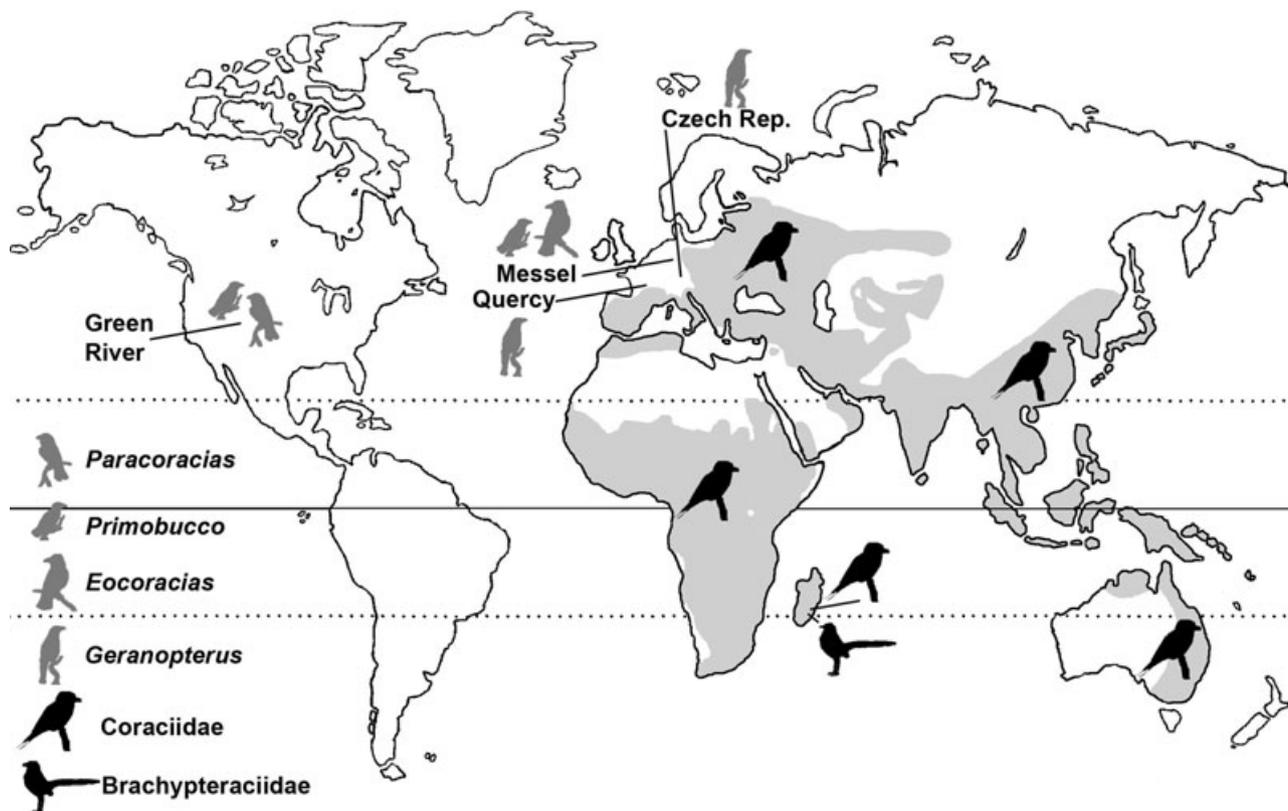


Figure 1. Map showing the distribution of extant and extinct Coracii.

(1865). However, this relationship has been debated (e.g. Mayr & Amadon, 1951; Wetmore, 1960; Maurer & Raikow, 1981; Mayr, 1998; Cracraft *et al.*, 2004) and is unsupported in most recent analyses (e.g. Sibley & Ahlquist, 1990; Mayr & Clarke, 2003; Mayr, Manegold & Johansson, 2003; Mayr, Mourer-Chauviré & Weidig, 2004; Ericson *et al.*, 2006; Hackett *et al.*, 2008; although see Livezey & Zusi, 2006, 2007 and response by Mayr, 2008).

The taxon name 'Coraciiformes' was used by Fürbringer (1888) for Coraciidae, Leptosomidae, Caprimulgiformes, and Strigiformes, and in subsequent classifications, it has been applied to distinct sets of 'higher landbird' taxa. The proposed component taxa have varied significantly, and which taxa might comprise a monophyletic core with the Coraciidae and Brachypteraciidae remains debated (Mayr & Clarke, 2003; Mayr *et al.*, 2003; Ericson *et al.*, 2006; Livezey & Zusi, 2007; Hackett *et al.*, 2008). Proposed parts of this clade have included hornbills (Bucerotiformes), hoopoes (Upupiformes), trogons (Trogonidae), motmots (Momotidae), todies (Todidae), bee-eaters (Meropidae), and kingfishers (Alcedinidae) (e.g. Gadow, 1892; Stresemann, 1959; Wetmore, 1960; Cracraft, 1981; Maurer & Raikow, 1981; Sibley & Ahlquist, 1990; Mayr *et al.*, 2004; Ericson *et al.*,

2006; Livezey & Zusi, 2007; Hackett *et al.*, 2008). More recently, the clade including only extinct stem taxa more closely related to Coracioidea than to any other extant lineage was referred to as 'Coracii-formes *sensu stricto*' by Mayr (1998). Given that the taxon Coraciiformes has consistently included an array of other 'higher land birds' as well as rollers over the past 100 years (e.g. Forbes, 1884; Fürbringer, 1888; Stresemann, 1959; Sibley, Ahlquist & Monroe, 1988; Sibley & Ahlquist, 1990) and is currently so used by most contemporary references (e.g. Höfling & Alvarenga, 2001; Johansson & Ericson, 2003; Cracraft *et al.*, 2004; Livezey & Zusi, 2007; Hackett *et al.*, 2008), it seems best to reserve this taxon name for this more inclusive clade in keeping with its prior use. We instead recommend the available taxon name 'Coracii', which has been consistently used at the 'subordinal' level (e.g. Wetmore & Miller, 1926; Stresemann, 1959; Wetmore, 1960; Cracraft, 1971; Maurer & Raikow, 1981; Burton, 1984; Sibley *et al.*, 1988; Sibley & Ahlquist, 1990; Johansson & Ericson, 2003), to be phylogenetically defined for the stem clade including all taxa more closely related to Coracioidea than to its nearest outgroup [equivalent contents to 'Coraciiformes *sensu stricto*' of Mayr (1998); with external specifiers

amongst the other major lineages of traditional coraciiform and piciform birds].

Wetmore & Miller (1926) were apparently the first to use 'Coracii' instead of 'Coraciae' while standardizing subordinal endings across Aves and recognizing restricted contents relative to Fürbringer (1888) and other prior authors. 'Coracii' of Wetmore & Miller (1926), unlike prior usages of the taxon name 'Coraciae', included rollers but no other 'higher landbird' taxa. The name 'Coraciae' was later resurrected for a 'parvclass' including Coraciiformes (e.g. Sibley *et al.*, 1988; Sibley & Ahlquist, 1990), although this taxon name does not appear to be in broad use.

We use 'Coracioidea' consistent with its originally recognized contents, including Coraciidae and Brachypteraciidae and excluding Leptosomidae (Cracraft, 1971), but recommend redefining the term phylogenetically as the most recent common ancestor of Coraciidae and Brachypteraciidae and all of its descendants. The monophyly of this crown clade has been supported by morphological (Mayr *et al.*, 2003, 2004) and molecular sequence data (e.g. Kirchman *et al.*, 2001; Cracraft *et al.*, 2004; Ericson *et al.*, 2006; Hackett *et al.*, 2008). Following the usage recommended here, whether Coracioidea includes the fossil taxon Geranopteridae hinges on whether it is recovered to be part of the crown clade (see Discussion). This usage is distinct from that of Mayr & Mourer-Chauviré (2000) who applied this taxon name to a more inclusive clade (crown clade + Geranopteridae).

An array of fossil taxa from Europe and North America has been identified as part of 'Coraciiformes' and, more specifically, allied with extant Coraciidae and Brachypteraciidae (Olson, 1985; Houde & Olson, 1989; Feduccia, 1999; Mayr & Mourer-Chauviré, 2000; Mayr *et al.*, 2004; Mourer-Chauviré & Sigé, 2006; Fig. 1). 'Coraciiformes' was proposed to possibly comprise the dominant small arboreal birds of the Eocene (e.g. Feduccia, 1999), filling ecological roles today occupied by the most speciose group of the avian crown clade, the Passeriformes. Arising from both taxonomic issues (i.e. varied application of the name Coraciiformes) and phylogenetic uncertainty, this fossil record has had widely varying interpretations. The most recent review of this record (Mayr *et al.*, 2004) identified only specimens from early Eocene Green River deposits of Wyoming, from middle Eocene deposits from Messel, Germany, from late Eocene deposits of Quercy, France, and from the early Miocene of the Czech Republic as stem parts of Mayr's 'Coraciiformes *sensu stricto*' (i.e. Coracii of this paper).

All Palaeogene material has so far been placed outside the crown clade, Coracioidea. The earliest allies of true rollers (Coraciidae) were originally considered to be the Geranopteridae from the late Eocene

of Quercy, France (Feduccia, 1999), but this placement was recently found to be unsupported (Mayr & Mourer-Chauviré, 2000). Kirchman *et al.* (2001) cited undescribed fossils attributed to the Brachypteraciidae from the middle Eocene of Europe as a calibration point for the Coraciidae/Brachypteraciidae split in divergence estimates for the timing of ground roller diversification. These authors concluded that, given the antiquity of the lineage inferred from these fossil calibrations, there was a notable lack of sequence divergence within Brachypteraciidae relative to other groups of birds. However, they did note that this referral could be questionable and proposed that the fossils could be found to be outside the roller crown clade. Such a placement was indeed confirmed for the middle Eocene Messel roller referenced by Kirchman *et al.* (2001) now named *Eocoracias brachyptera* (Mayr & Mourer-Chauviré, 2000, 2003).

Mayr & Mourer-Chauviré (2000) described new material of *Geranopterus alatus* Milne-Edwards (1892) and a new species (*Geranopterus milneedwardsi*) from deposits within the Quercy fissure fills (dated to approximately 35 Myr; Legendre & Lévêque, 1997), identifying these as part of the coraciiform stem lineage. More recently, further isolated material has been referred to Geranopteridae from these late Eocene deposits (Mourer-Chauviré & Sigé, 2006). Intriguingly, Mourer-Chauviré (1999) reassigned a tarsometatarsus described as a fossil jacana by Mlíkovsky (*Nupharanassa bohémica* Mlíkovsky, 1999) to *Geranopterus bohemicus*. If this referral is correct, it represents a significant extension in stratigraphical range for *Geranopterus* as the holotype of *Geranopterus bohemicus* is from the early Miocene (~17 Mya; Kempf *et al.*, 1997) of the Czech Republic.

'Primobucconidae' (Feduccia & Martin, 1976) was originally coined for several small landbird species from the early Eocene Green River Formation later found to be polyphyletic (Houde & Olson, 1989; Mayr *et al.*, 2004). Subsequently, the name-bearing species *Primobucco mcgrewi*, whose holotype (UWGM 3299, right wing) was described by Brodkorb (1970), was proposed to have affinities with ground rollers (Houde & Olson, 1989). A second specimen (USNM 336284), comprising a nearly complete skeleton, constituted important further evidence confirming a New World record for Coracii [mentioned by Houde & Olson (1989); described by Mayr *et al.* (2004)]. Two closely related species, *Primobucco perneri* and *Primobucco frugilegus*, were proposed from the middle Eocene of Messel, Germany (Mayr *et al.*, 2004). The latter species preserves direct evidence of a seed diet (Mayr *et al.*, 2004). By contrast, crown clade rollers feed almost exclusively on insects and small vertebrates (Fry *et al.*, 1992). Thus, only comparatively recently was the first evidence for a significant shift in diet

and distribution in the stem lineage leading to Coracioidea recognized.

Mayr *et al.* (2004) undertook the first phylogenetic analysis including fossil and extant Coracii (Coraciiformes *sensu stricto* of Mayr, 1998) taxa as well of other taxa traditionally included in Coraciiformes *sensu lato*. Geranopteridae was found to be the sister taxon of the crown clade Coracioidea (note different usage of this name by Mayr *et al.*, 2004), whereas Primobucconidae and Eocoraciidae were part of a polytomy placed outside the clade Geranopteridae + Coracioidea. These results are consistent with the hypothesis of Mayr & Mourer-Chauviré (2000).

Here, we describe a new stem Coracii species from the Eocene Green River Formation and evaluate the phylogenetic position of this species relative to extant and extinct species using an expanded morphological dataset and molecular sequence data.

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York, NY, USA; FMNH, Department of Geology, Field Museum of Natural History, Chicago, IL, USA; NCSM, North Carolina Museum of Natural Sciences, Raleigh, NC, USA; SMF, Forschungsinstitut Senckenberg, Frankfurt, Germany; UWGM, University of Wyoming Geological Museum, Laramie, WY, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

SYSTEMATIC PALEONTOLOGY

AVES, LINNAEUS, 1758

CORACIIFORMES, FORBES, 1884

CORACII, WETMORE & MILLER, 1926

PARACORACIAS OCCIDENTALIS GEN. ET SP. NOV.

Holotype specimen: AMNH 30572, a nearly complete skeleton lacking only the distal left hind limb (i.e. tarsometatarsus and pedal phalanges; Figs 2–7; Table 1).

Etymology: ‘*Paracoracias*’ from the Greek affix ‘para’ for nearby or beside and to reflect phylogenetic placement in Coracii. ‘*occidentalis*’ reflects the New World or ‘Western’ provenience of the new species.

Locality: The holotype is from the Eocene Green River Formation. The Green River Formation represents an ancient and extensive lake system and has also yielded exquisite specimens of snails and insects as well as an exceptional record of vertebrates including birds, mammals, fish, and squamates (Colbert, 1955; Grande, 1980; Bartels, 1993). Further provenience information on this fossil is not available.

Diagnosis: The new species is differentiated from other Coracii below. Characters supporting placement in the Coracii are treated in the Discussion. Varying levels of completeness in material of other extinct Coracii and homoplasy across crown and stem Coracii prevented the optimization of unambiguous autapomorphies in the analysis. Species diagnosis is as for the taxon *Paracoracias*.

Paracoracias occidentalis differs from all parts of crown Coracioidea in the lack of an expanded descending process of the lacrimal (Character 11; Appendix 3). It is differentiated from both Coracioidea and *Geranopterus alatus* in the absence of an anterior projection on the postorbital process (Character 16; Appendix 3). It is further differentiated from these two taxa and *Geranopterus milneedwardsi* in the absence of an intermetacarpal process (Character 47; Appendix 3). The states for these characters in *Paracoracias* are presently optimized as plesiomorphies for Coracii.

Paracoracias occidentalis can be further differentiated from Coraciidae as the narial opening is not divided by an osseous bridge (Character 6; Appendix 3). Additionally, the posterior margin of the palatine is convex (concave in Coraciidae; Character 18; Appendix 3), and the humeral bicipital crest is shorter in distal extent (Character 42; Appendix 3). *Paracoracias occidentalis* is differentiated from Brachypteraciidae, *Geranopterus alatus*, and *G. milneedwardsi* by subequal projection of metacarpals II and III (Character 50; Appendix 3), and it is further differentiated from Brachypteraciidae by a weakly projected anterior cnemial crest of the tibiotarsus (Character 61; Appendix 3). *Geranopterus bohemicus* is known only from a single tarsometatarsus; it was not used in differentiating *Paracoracias occidentalis* from *Geranopterus* or Geranopteridae.

Paracoracias occidentalis is differentiated from *Eocoracias brachyptera* (the sole species in Eocoraciidae) in possessing plesiomorphically broad nares. *Eocoracias brachyptera* is described as having a distinct slit-like narial opening (Mayr & Mourer-Chauviré, 2000; although see also comments in the description below). *Paracoracias* further differs from *Eocoracias* in proportions of the limb elements. Manual phalanx I:1 is shorter relative to total carpometacarpus length. The tarsometatarsus is also slightly longer relative to femoral and tibiotarsal proportions. The rostrum is proportionally broader than in *Eocoracias* and longer relative to hind limb elements (i.e. femur and tibiotarsus; see Table 1 and Mayr & Mourer-Chauviré, 2000). Finally, the ventral ramus (crus longus) of the ulnare is significantly longer than the dorsal ramus (crus breve; Character 45; Appendix 3) in *Paracoracias* but the rami of the ulnare are subequal in *E. brachyptera* (Mayr &

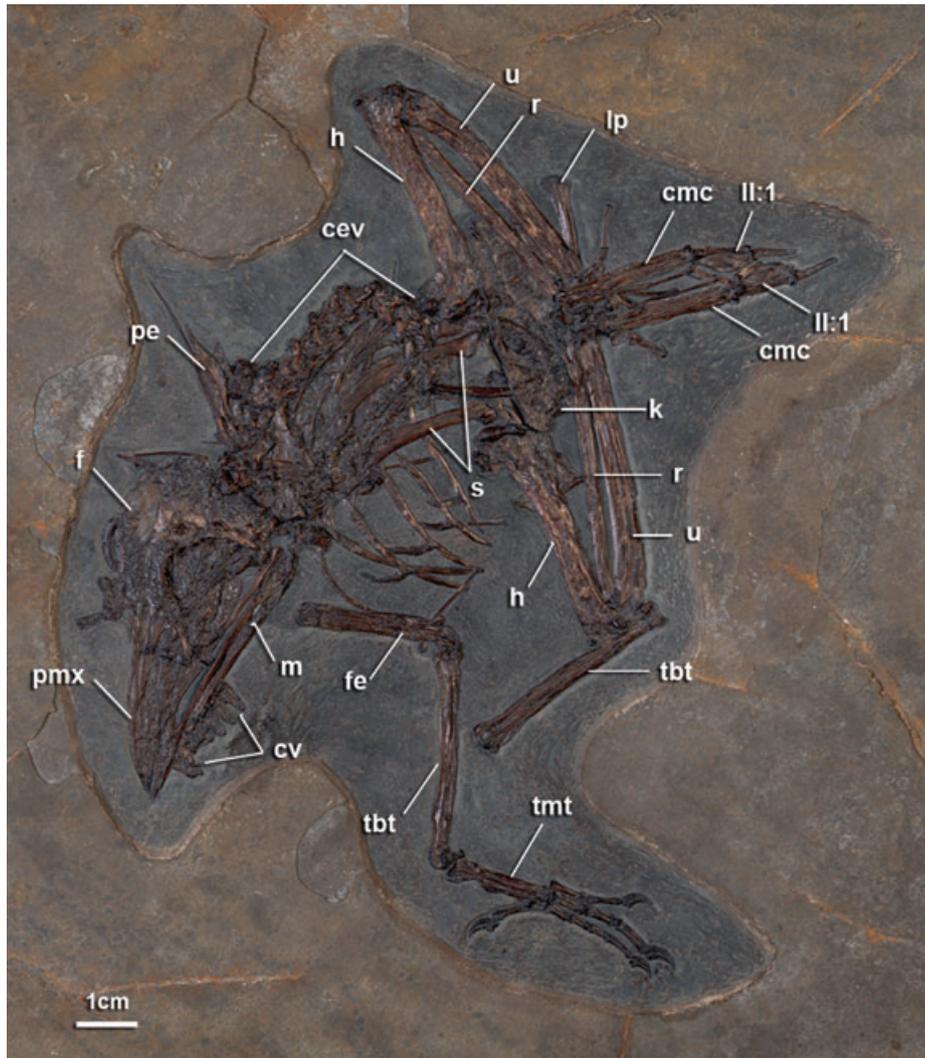


Figure 2. Holotype specimen of *Paracoracias occidentalis* (AMNH 30572). Anatomical abbreviations: II:1, manual phalanx II:1; cev, cervical vertebrae; cmc, carpometacarpus; cv, caudal vertebrae; f, frontal; fe, femur; h, humerus; k, keel; lp, lateral process of sternum; m, mandible; pe, pelvis; pmx, premaxilla; r, radius; s, scapulae; tbt, tibiotarsus; tmt, tarsometatarsus; u, ulna.

Mourer-Chauviré, 2000). The condition seen in *Paracoracias* is also seen in *Primobucco* and Coraciidae, but not Brachypteraciidae.

Relative to all named *Primobucco* species, *Paracoracias occidentalis* differs in possessing a significantly broader beak, nares triangular with a flat ventral margin (ovoid in *Primobucco*; Character 2; Appendix 3), more elongate processus postorbitalis (Character 15; Appendix 3); and significantly larger size (see Table 1). Support for the monophyly of Primobucconidae, or *Primobucco*, is not recovered in the phylogenetic analysis (see *Discussion*).

Description: The skull is broad and large relative to overall body size (e.g. significantly longer than either the humerus or tibiotarsus; Fig. 2). Beak length is

just slightly greater than half of the skull length. The beak is curved in lateral view, with the peak curvature located anterior to the external nares. In this morphology the beak shape is more similar to *Eurysotomus* than *Coracias*, Brachypteraciidae, *Primobucco*, or *Eocoracias*.

The external nares are large and broaden posteriorly. The long axis of the exposed left naris is approximately half the total length of the beak. The subtriangular shape of the naris approaches the condition developed in Coracioidea. The nares would be significantly broader dorsoventrally than in *Eocoracias* in which they are described as slit-like (Mayr & Mourer-Chauviré, 2000). It is possible that this condition observed in *Eocoracias* may be a result of the plastic deformation common to birds from the Grube

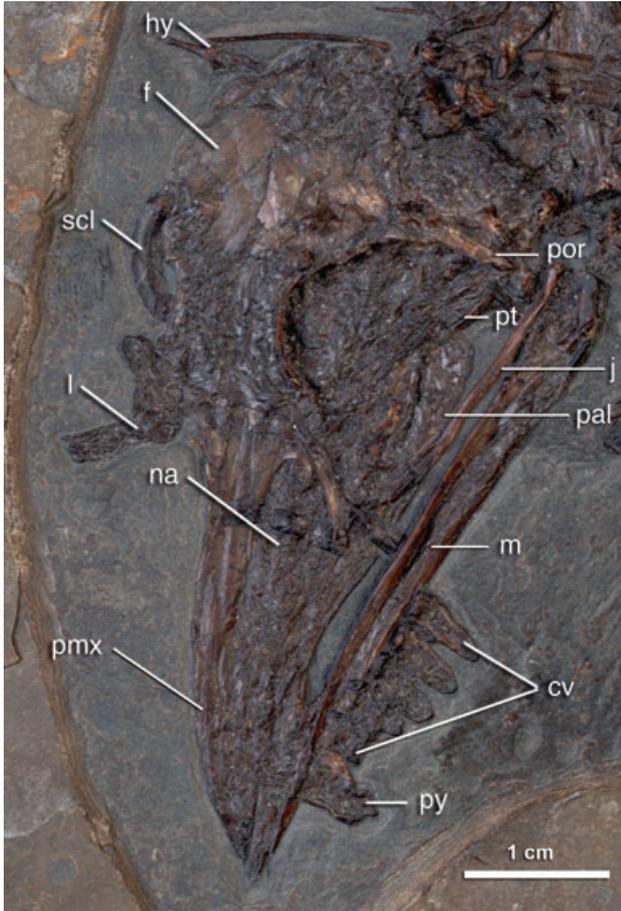


Figure 3. Skull of *Paracoracias*. Anatomical abbreviations: cv, caudal vertebrae; f, frontal; hy, hyoid; j, jugal; l, lacrimal; m, mandible; na, naris; pal, palatine; pmx, premaxilla; por, postorbital process; pt, pterygoid; py, pygostyle; scl, sclerotic ring.

Messel (G. Mayr, pers. comm.). Currently known specimens may provide insufficient evidence to resolve this question with confidence.

An internarial septum is preserved as a sheet of bone visible through the left naris and inferred from the indistinct anterior edge of this opening (Fig. 3). In the new species and in *Coracioidea* this septum grades smoothly into the anterior margin of the naris. In *Coraciidae*, an additional thin osseous sheet divides each naris, but this feature is absent in *Paracoracias occidentalis*. In *Brachypteraciidae*, a small osseous sheet rises from the posteroventral margin of the naris but does not contact the narial bar to divide the opening. The zone of the craniofacial hinge is slightly depressed but not strongly lineate. This condition appears also to be present in *Eocoracias* and was noted within crown *Coracioidea* (Livezey & Zusi, 2006, 2007). The morphology of this region is highly variable, and is lineate in other traditional

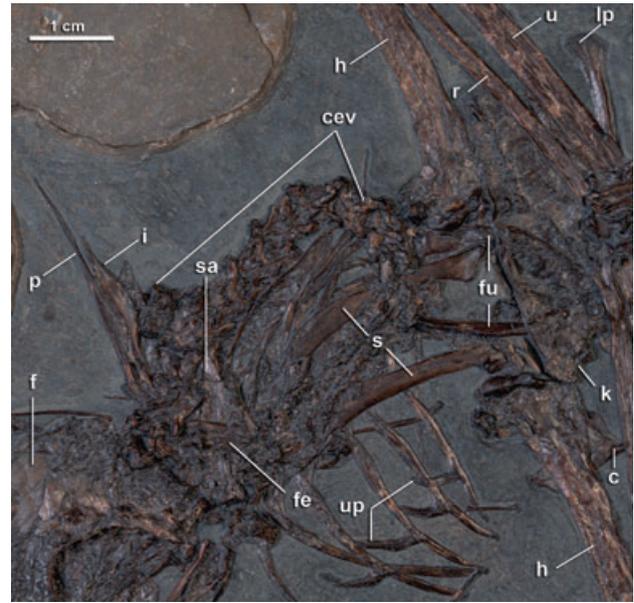


Figure 4. Cervical series, thoracic region, and sacrum of *Paracoracias*. Anatomical abbreviations: c, coracoid; cev, cervical vertebrae; f, frontal; fe, femur; fu, furcula; h, humerus; i, ischium; k, keel; lp, lateral process of sternum; p, pubis; r, radius; s, scapulae; sa, sacrum; u, ulna; up, uncinate processes.

Coraciiformes recovered close to *Coracii* (e.g. some *Alcedinidae* and *Momotidae*).

The postorbital processes are elongate; they closely approach the jugal bar and possibly contacted this element in life (Fig. 3). Such a morphology is seen in *Eocoracias*, *Geranopterus*, and *Coracioidea* (Mayr *et al.*, 2004). The lacrimal head is expanded, a synapomorphy of *Coracii* known from all stem taxa except for *Geranopterus* for which it cannot be evaluated. *Paracoracias* also lacks an anterior projection of the postorbital process, a feature developed in all *Coracioidea* with the exception of polymorphism exhibited in *Eurystomus orientalis* (two of nine adult specimens of examined in this study lacked this process). The zygomatic process is elongate as in other *Coracii*.

The left palatine and posterior portion of the left pterygoid are exposed in the orbital region in oblique dorsolateral view (Fig. 3). Anteriorly the pterygoid is overlain by the palatine, and posteriorly it is in contact with the remains of the quadrate base. In the new species, some *Brachypteraciidae* (*Atelornis crossleyi* and *Brachypteracias leptosomus*), and *Primobucco mcgrewi* (Ksepka & Clarke, in press) this margin is slightly convex. By contrast, the posterior margin of the palatines is concave in ventral or dorsolateral view in *Coraciidae* and other *Brachypteraciidae* (*Atelornis pittoides* and *Uratelornis chimaera*). The frontal processes of the premaxillae are fused,

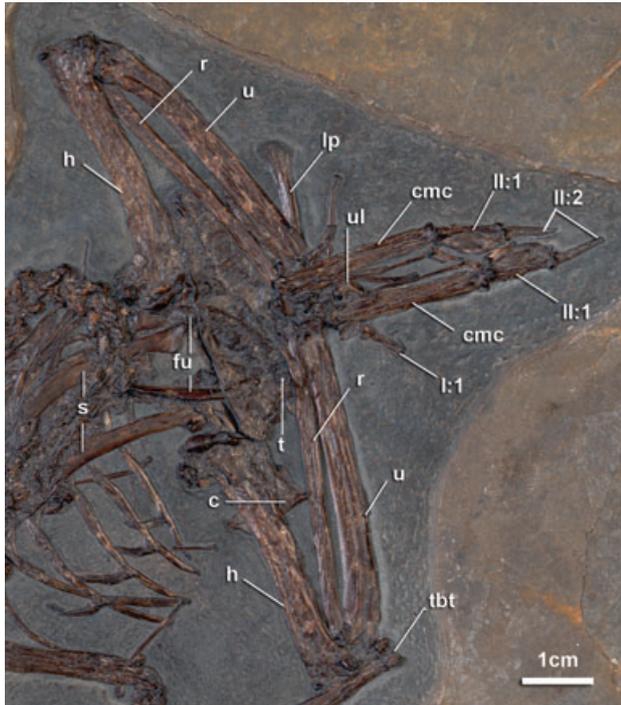


Figure 5. Pectoral girdle and limbs of *Paracoracias*. Anatomical abbreviations: I:1, manual phalanx I:1; II:1, manual phalanx II:1; II:2, manual phalanx II:2; c, coracoid; cmc, carpometacarpus; fu, furcula; h, humerus; lp, lateral process of sternum; r, radius; s, scapulae; t, tracheal ring; tbt, tibiotarsus; u, ulna; ul, ulnare.

although the suture between them remains visible posteriorly. The frontals are relatively broad, and rectangular in dorsal view (Fig. 3). An interorbital septum is present. Remains of the right sclerotic ring are visible.

The mandible is partially exposed in oblique left dorsolateral view. The symphysis is relatively short, approximately one-fifth of total jaw length (Fig. 3). A diminutive coronoid process is present. The broadly confluent lateral and posterior cotylae are partially exposed, whereas the medial portion of the articular is obscured by portions of the quadrate and jugal.

Portions of the hyoid apparatus are well preserved, but they appear to have been twisted such that the urohyal projects anteriorly (Fig. 3). One ceratobranchial element is preserved in articulation with the fused urohyal and basihyal. Between the later elements the suture is incompletely obliterated. The paraglossale in the fossil appears to have been cartilaginous or absent. The urohyal is a well-developed elongate rod-like element similar to that in *Brachypteracias leptosomus*. In the specimens of *Coracias garrulus* and *Coracias benghalensis* examined, the urohyal was very poorly projected. This appears to be the result of a lack of complete ossi-

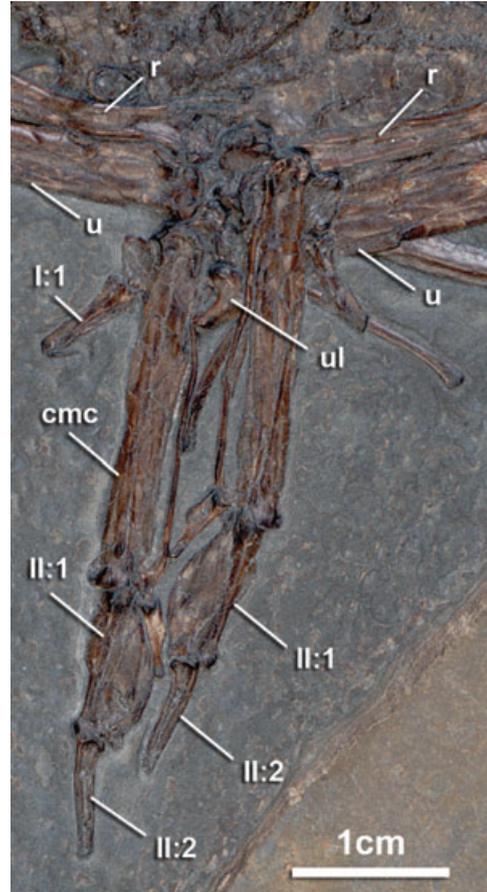


Figure 6. Distal wing elements of *Paracoracias* in dorsal view. Anatomical abbreviations: I:1, left manual phalanx I:1; II:1, manual phalanx II:1; II:2, manual phalanx II:2; cmc, carpometacarpus; r, radius; u, ulna; ul, ulnare.

fication, as much of this element remains cartilaginous in the specimen of *C. benghalensis* depicted by Burton (1984: fig. 25). The basihyal is expanded at the contact with the ceratobranchials in both the new species and in extant Coracioidea, more so than in Meropidae and Todidae but less so than in Alcedinidae (Burton, 1984). There is a slight depression on the midline of the urohyal at its contact with the basihyal and a midline groove on the basihyal with two lateral depressions on the mediolaterally expanded area just distal to the inferred position of the ceratobranchial articulations. Several tracheal rings are preserved near the right side of the base of the sternal keel as well as between the right scapula and the right furcular ramus.

The presacral vertebral series is articulated and forms a tight U-shape from the back of the skull to terminate near the lower jaw where the sacrum is also located (Figs 2, 4). Eighteen presacral vertebrae are visible, although additional elements may have



Figure 7. Pelvic limb of *Paracoracias* in lateral view. Anatomical abbreviations: I:1, pedal phalanx I:1; II:1, pedal phalanx II:1; fb, fibula; fe, femur; h, humerus; tbt, tibiotarsus; tmt, tarsometatarsus; u, ulna.

been present. There is an osseous extension from the transverse processes to the postzygopophyses perforated by a small foramen in the third cervical vertebra (Mayr & Clarke, 2003: character 52), a feature present in all taxa evaluated for the phylogenetic analysis except Trogonidae. The posterior thoracic vertebrae contain ovoid lateral excavations. The sacrum is exposed in ventral view but is largely obscured by overlying anterior cervical vertebrae and posterior skull fragments (Fig. 4). At least one costal strut is present, which is developed in the part of the series correspondent with the area of the acetabulum. Four ribs bear fused, recurved uncinat processes.

Five free caudal vertebrae and the pygostyle are preserved in articulation. This portion of the caudal series is displaced and lies near the mandibular symphysis (Fig. 3). Two caudal vertebrae are preserved separately and are partially overlain by the anterior end of the sacrum. Additional free caudal vertebrae may have been present as well. Pygostyle morphology is nearly identical to Coracioidea in that the anterior margin is convex in lateral view with a conspicuous notch, the posterior margin is straight to slightly concave, and a projected discus is developed.

The right coracoid is preserved in ventral view but is mostly obscured by the proximal end of the right humerus and parts of the sternum and furcula (Figs 4, 5). A well-projected, pointed lateral process is

Table 1. Measurements of the holotype specimen of *Paracoracias occidentalis* (AMNH 30572) in mm

Skull	
Maximum length	60.0
Rostrum, length (nasofrontal hinge to premaxilla tip)	30.6
Orbit, diameter at midpoint	13.2
External nares, maximum length	12.6
Mandible, maximum length	50.0
Mandibular symphysis, maximum length	13.6
Vertebral column	
Sacrum, length (estimated)	26.6
Pygostyle, midpoint anteroposterior diameter	4.3
Pygostyle, maximum height	9.6
Pectoral girdle	
Sternum, length on midline, anterior base of carina to terminus	35.5
Scapula, maximum length (left, estimated)	36.0
Coracoid, maximum height (right, estimated)	26.2
Furcula, distance from apophysis to omal tips on midline	21.5
Furcula, diameter at omal tip (left)	3.3
Pectoral limb	
Humerus, maximum length (left/right)	43.7/43.6
Humerus, deltapectoral crest length (right side)	12.0
Ulna, maximum length (right, estimated)	52.7
Radius, maximum length (right)	49.0
Carpometacarpus, maximum length (left)	25.9
Phalanx I.1 length (left/right)	7.4/7.5
Phalanx II.1 length (left/right)	10.6/10.9
Phalanx II.2 length (left/right)	8.4/8.4
Phalanx III.1 length (left/right)	5.3/5.3
Pelvic girdle	
Ischium, maximum length from margin of obturator foramen (left)	20.3
Pubis, maximum length from margin of obturator foramen (left/right)	30.1/29.3
Pelvic limb	
Femur, maximum length (left/right)	29.5/29.3
Tibiotarsus, maximum length (left/right)	39.8/39.6
Tarsometatarsus, maximum length (right)	19.2
Metatarsal I, maximum length (right)	5.4
Phalanx I.1 length (right, estimated)	8.1
Phalanx I.2 length (right)	5.8
Phalanx II.1 length (right)	7.0
Phalanx II.2 length (right)	6.4
Phalanx II.3 length (right)	5.3
Phalanx III.1 length (right)	6.6
Phalanx III.2 length (right)	5.3
Phalanx III.3 length (right)	7.4
Phalanx III.4 length (right)	5.9
Phalanx IV.1 length (right)	4.6
Phalanx IV.2 length (right)	4.0
Phalanx IV.3 length (right)	3.7
Phalanx IV.4 length (right)	5.6
Phalanx IV.5 length (right)	5.2

present. The medial coracoid margin flares slightly omally from its sternal contact and is distinctly notched at approximately the same level as the tip of the lateral process. The right scapula is visible in dorsal view, whereas the left is exposed in ventral view (Fig. 5). The scapula is shorter than the humerus and close in aspect to those of Coracioidea. The blade is recurved and expands slightly before tapering towards the distal end. The scapular glenoid facet is subcircular and projected from the shaft. The acromion may have been bifid. However, its medial surface is embedded in matrix so this feature cannot be verified.

The furcular apophysis is covered by the sternum, although its outline remains discernable (Fig. 5). The exposed omal tips are compressed mediolaterally. The sternum is exposed in right ventrolateral view. A spina externa is present. The apex of the sternal keel is projected anterior to the coracoidal sulci and extends to the posterior margin of the sternum. Lateral and medial posterior trabeculae are developed, with the lateral flared distally (Fig. 5).

The humeri are exposed in posterior view. The humerus is conspicuously shorter than the ulna (Fig. 5). The head is narrow and oblate with a well-defined distal margin in posterior view. This condition is developed in ground rollers but not in Coraciidae or in *Geranopterus* (Mayr & Mourer-Chauviré, 2000: fig. 8J). In Brachypteraciidae, the secondary tricipital fossa is relatively broad dorsoventrally excavating the humeral head and contributing to this well-defined margin. The deltopectoral crest is short, extending less than one-third of the total shaft length, and its dorsal margin is rounded (Fig. 5). The pit-shaped fossa for m. supracoracoideus insertion on the dorsal tubercle is conspicuous and deep. This fossa appears to be anteriorly directed, however, this orientation may be exaggerated by slight compression. The capital incisure is open and broad. The bicipital crest is relatively short, and its distal margin angles sharply into the shaft, more closely resembling the condition in Brachypteraciidae than Coraciidae. The shaft exhibits very little curvature. Distally, the m. scapulotriceps groove and a projected dorsal supracondylar process are visible (Fig. 5).

The radii, ulnae, and carpometacarpi are preserved in dorsal view (Figs 5, 6). A tuberculated muscular attachment is present on the ulna between the olecranon process and the dorsal cotyla. The radius is robust, approaching nearly one half of the diameter of the ulna. The ulnare and radiale are in partial articulation with the carpometacarpus on both sides. The dorsal ramus (*crus brevis*) of the ulnare is markedly shorter than the ventral (*crus longus*; Figs 5, 6). In *E. brachyptera*, these rami are subequal in length.

The hand is shorter relative to the proximal wing elements when compared to Coraciidae or Brachypteraciidae but is comparable to *E. brachyptera* (Mayr & Mourer-Chauviré, 2000; Table 1). The extensor process is low and weakly projected in dorsal view (Fig. 6). Although it is with certainty less projected than Coraciidae, its relative lack of projection appears slightly exaggerated by the orientation of metacarpal I. The intermetacarpal space is narrow, with metacarpal III extremely thin and subparallel to metacarpal II (Fig. 6). Metacarpal III just surpasses metacarpal II in distal extent as in Coraciidae, *Eocoracias*, and *Primobucco*. By contrast, metacarpal III significantly surpasses metacarpal II in distal extent in *Geranopterus*, Brachypteraciidae, and most groups of 'higher landbirds' (i.e. Meropidae, Momotidae, Todidae, Alcedinidae, Upupidae, Piciformes, Passeriformes). The intermetacarpal process is developed as a small tubercle rather than the large triangular process present in Coracioidea. On the dorsal surface of metacarpal II, the extensor groove is well developed, and a large tubercle is associated with the retinaculum attachment. A small spike-like chip of bone distal to left phalanx I:1 may be homologous to the small alular claw documented for *Primobucco perneri* (Mayr *et al.*, 2004; Fig. 6). However, no such element is visible associated with the right digit I, and this claw is absent in extant Coraciidae (Stephan, 1992). Phalanx II:1 bears a small internal index process comparable in development to that in Coraciidae and *Eocoracias brachyptera* but more projected than in *Primobucco* and Brachypteraciidae. Phalanx III:1 has a well-developed flexor tubercle.

The synsacrum is covered by the posterior skull elements, proximal cervical vertebrae, and left femur (Figs 2, 3). Only its left postacetabular portion is well exposed. The ischium tapers to a pointed terminal ischial process that conspicuously surpasses the dorso-lateral iliac spine. The pubis is straight, extremely narrow, and tapering toward its distal extreme; it is not appreciably medially deflected (Fig. 3). No pectineal process is developed, and the obturator foramen is small.

The right leg is articulated and exposed primarily in lateral view (Fig. 7). The disarticulated left limb is represented by the poorly exposed femur covered by the cervical series, and a tibiotarsus exposed in dorsal view near the wing elements (Fig. 7). The femur is straight. A free, ovoid ossification lies near the proximal end of the patellar groove. A small intratendinous ossification was also observed in articulated specimens of Coraciidae, Meropidae, and Alcedinidae. It is likely to be widely distributed, although easily lost in the maceration of skeletons. The cnemial crests are weakly projected as in Coraciidae, whereas in Brachypteraciidae they are significantly anteriorly pro-

jected. The distal condyles have approximately the same mediolateral extent. The fibula is elongate, extending just over two-thirds of the length of the tibia.

The right tarsometatarsus is abbreviated as in Coracii other than Brachypteraciidae (Fig. 7). It is preserved in oblique anterolateral view with digit I artefactually appressed to its lateral side. The tubercle for *m. tibialis cranialis* is very large and positioned towards the medial margin of the tarsometatarsus, a condition also seen in *Primobucco*. By contrast, this tubercle is less prominent and located closer to the midline of the tarsometatarsus in Coracioidea. The shape of the well-projected lateral hypotarsal crest and development of the lateral parhypotarsal fossa closely match the corresponding morphologies in Coracioidea. The trochlea of metatarsal IV closely approaches that of metatarsal III in distal extent. The trochlea of metatarsal II is not exposed. However, based on the position of the articulated proximal phalanges of this digit, it is likely to have obtained approximately the same distal extent as III. A dorsal sulcus at the fused contact between metatarsals III and IV extends the length of the element. The distal vascular foramen is not discernable.

Pedal digits III and IV are longer than the tarsometatarsus, and phalanx III:3 is longer than the proximal phalanges of this digit (Fig. 7, Table 1). The foot is anisodactyl and the third digit is longest.

PHYLOGENETIC ANALYSIS

The dataset for the phylogenetic analysis comprises 133 morphological characters evaluated for 49 taxa. Characters were coded from direct observation for all taxa (see Appendix 1). The osteological character set is based on the work of Cracraft (1971), Simpson & Cracraft (1981), Prum (1988), Mayr (1998, 2000), Mayr & Mourer-Chauviré (2000), Mayr & Clarke (2003), and Mayr *et al.* (2003, 2004). Soft tissue characters were drawn in large part from the studies of Maurer & Raikow (1981), Swierczewski & Raikow (1981), and McKittrick (1991, 1993). Three characters (13, 15, 69) were considered ordered. However, unordering these characters does not affect the position of *Paracoracias occidentalis*.

Sequence data for two nuclear genes (*RAG-1* and *c-myc*) and one mitochondrial gene (*NADH dehydrogenase subunit 2*) generated by previous studies (see Appendix 2) were included in the combined dataset. Sequences for each gene were aligned in ClustalX (Thompson *et al.*, 1997) and checked visually in MacClade (Maddison & Maddison, 1992). The alignments were then concatenated to produce a total of 4411 bp

of sequence data. GenBank accession numbers and citations are provided in Appendix 2.

The broad taxonomic sample included species exemplars from groups traditionally included in or considered to have affinities with Coraciiformes, including Coraciidae, Brachypteraciidae, Alcedinidae, Meropidae, Momotidae, Todidae, Upupidae, Bucrotidae, and Trogonidae. We also included multiple taxa of Piciformes, which are hypothesized to be most closely related to some subset of these taxa (e.g. Ericson *et al.*, 2006; Hackett *et al.*, 2008). Including Piciformes also allowed for an additional test of the original hypothesis of Brodkorb (1970) and Feduccia & Martin (1976) that *Primobucco mcgrewi* represented a member of the piciform clade Galbulae.

We did not include the cuckoo roller, *Leptosomus discolor*, in our analysis. Assessing its relationships would have required an even more inclusive taxonomic sample. Recent molecular studies have identified this taxon as comparatively distantly related to Coracioidea as an outgroup of a major neoavian clade comprising either most traditional Coraciiformes and Piciformes (Hackett *et al.*, 2008), or these taxa plus Strigiformes and Falconiformes (Ericson *et al.*, 2006). *Leptosomus discolor* has also been historically allied with an array of other neoavian taxa (e.g. Falconidae and Cuculidae; Mayr *et al.*, 2003, 2004, Mayr, 2008 and discussion therein). A major morphological study (Livezey & Zusi, 2006, 2007) intriguingly did recover a sister group relationship between Leptosomidae and Brachypteraciidae, placing *L. discolor* not only as allied with Coracii but also within crown Coracioidea. However, because *L. discolor* was scored for this analysis as lacking features such as a zygodactyl foot and supracoracoideus nerve foramen that the species possesses, it has been suggested that a specimen of ground roller *Brachypteracias leptosomus* could have been mistakenly evaluated, making these results problematic (Mayr, 2008). We found no characters supporting close ties to Coracii, and other morphological datasets have also failed to recover any (e.g. Mayr *et al.*, 2003, 2004). Given the disparate proposed systematic placements of *Leptosomus*, a rigorous attempt to estimate its relationships would necessitate an analysis of all Neoaves, which is outside the scope of this study.

Immediate outgroups of Coracii were determined through analysis. Thirty-five were included given the lack of consensus regarding the nearest sister taxa to the lineage. Caprimulgidae was used to root the recovered phylogeny in the primary analysis. Caprimulgidae is well supported to belong outside the clade including all other taxa in our analysis (Mayr *et al.*, 2003; Cracraft *et al.*, 2004; Fain & Houde, 2004; Ericson *et al.*, 2006; Hackett *et al.*, 2008). Some recent large-scale molecular analyses of birds have supported

division of Neoaves into two large clades, Coronaves and Metaves (Fain & Houde, 2004; Ericson *et al.*, 2006). Caprimulgidae has been placed in the Metaves by these studies, whereas all other taxa included in our analyses were placed in the Coronaves. Other studies have not recovered this large basal split, but nonetheless consistently place Caprimulgidae near but outside our ingroup taxa (Espinosa de los Monteros, 2000). Morphological analyses by Mayr *et al.* (2003) and Livezey & Zusi (2006, 2007) also found Caprimulgidae to belong outside a clade containing all other higher taxa included in our analysis.

There is historical support and a recent growing consensus for a clade including Coracii, Alcedinidae, Momotidae, Meropidae, and Todidae. A clade including the former four taxa (Todidae not included in all analyses) has been recovered by both morphological and major molecular datasets (Mayr *et al.*, 2003; Ericson *et al.*, 2006; Livezey & Zusi, 2007; Hackett *et al.*, 2008). Therefore, an additional analysis included just this restricted taxonomic sample to look at potential effects on character optimization within Coracii and the new fossil.

All searches were conducted in PAUP*4.0b10 (Swofford, 2002) with all characters equally weighted. Search strategy included 5000 random taxon addition sequences [tree bisection-reconnection branch swapping, random starting trees]. Branches with minimum length 0 were collapsed and multistate codings were used only for polymorphism. Bootstrap support values were calculated from 1000 replicates with ten random addition sequences per replicate using the same settings as the primary analysis. Bremer support values were calculated manually in PAUP*4.0b10.

RESULTS

Topologies of recovered trees from of the combined and morphology-only analyses are largely congruent. Strict consensus cladograms of the most parsimonious trees from each analysis are presented in Figures 8 and 9, respectively. The combined analysis resulted in two trees of 4882 steps, whereas the morphology-only analysis resulted in 24 trees of 345 steps. Differences amongst resultant strict consensus cladograms include slightly better resolution in the combined tree and shifts in the position of *Atelornis pittoides* and *E. orientalis*. One area of conflict between these two analyses is the placement of Meropidae. It is the sister taxon of Alcedinidae in the morphological analysis but the sister taxon to Upupiformes + Bucrotiformes in the combined analysis.

Phylogenetic placement of *Paracoracias* as part of Coracii is robust to unordering included characters and in analyses of a taxonomic sample restricted to

Coracii, Meropidae, Todidae, Momotidae, and Alcedinidae that explore the effect of outgroups on character polarity within the Coracii stem. Of all stem Coracii, the basal *Primobucco* taxa are predictably most weakly supported as part of the lineage. Monophyly of *Primobucco* is not recovered. Only one previous phylogenetic analysis sampled multiple extinct parts of Coracii (Mayr *et al.*, 2004). This analysis used a similar broad set of outgroup taxa. However, these taxa were included as supraspecific terminals that did not probe their monophyly or sample variation within these taxa. Lack of support for a *Primobucco* clade may be expected because of missing data issues arising from sampling of species as terminals in the present analysis as well as homoplasy for evaluated characters within candidate sister taxa to Coracii. Alternatively, given the phylogenetic results, it is possible that *Primobucco* species may comprise a paraphyletic assemblage of basal stem Coracii.

Monophyly of Coracii is supported by an expanded lacrimal head, elongation of the postorbital process, and presence of a ventrally projecting flange on the proximal portion of metacarpal III. Mayr *et al.* (2004) identified these features as synapomorphies of Coracii (his Coraciiformes *sensu stricto*) and also listed an additional diagnostic character: distal interosseal canal (canalis interosseus distalis) not ossified plantarly and forming a deep narrow sulcus between trochleae III and IV. These authors reported this canal in an isolated tarsometatarsus from the Eocene of France referred to *Primobucconidae* gen. et sp. indet. The character is not determinable in other *Primobucco* specimens. If the primobucconid referral can be confirmed with more complete material, this character would also support Coracii monophyly.

Two features support a clade including *Paracoracias*, *Eocoracias*, *Geranopterus*, and Coracioidea to the exclusion of *Primobucco*: postorbital process contacting or nearly contacting jugal bar and projection of internal index process of phalanx II-1 surpassing the distal articular surface for phalanx II-2 (reversed in Brachypteraciidae). *Eocoracias* is placed as the sister taxon to a clade comprising *Paracoracias*, *Geranopterus*, and Coracioidea. This recovered position for *Paracoracias*, as more closely related to Coracioidea than *Eocoracias*, is supported by one unambiguous synapomorphy: i.e. external nares triangular with a flat ventral margin. In *Primobucco*, the nares are distinctly ovoid (Mayr *et al.*, 2004), whereas in *E. brachyptera* the nares are ovoid but narrow (Mayr & Mourer-Chauviré, 2000). However, the placement of *Paracoracias* is retained even if the observed slit-like *Eocoracias* morphology is treated as noncomparable, because *Paracoracias* shares the crown condition.

Geranopterus is supported as more closely related to Coracioidea relative to *Eocoracias* by the presence

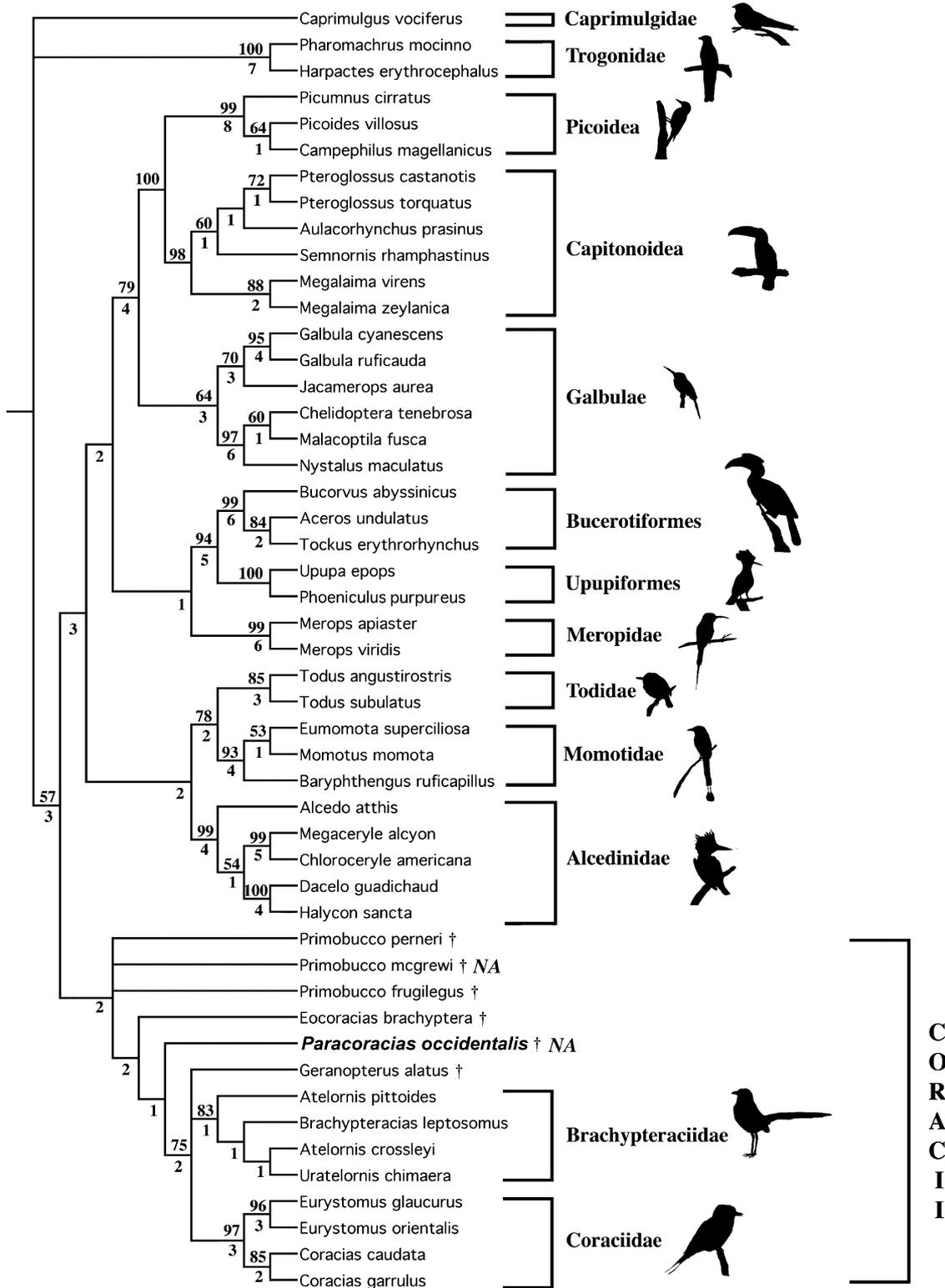


Figure 8. Strict consensus cladogram of two most parsimonious trees (length = 4882; consistency index = 0.424; retention index = 0.798; rescaled consistency index = 0.340) from the combined analysis using all morphological and sequence data (*ND2*, *RAG-1*, and *c-myc*). Bootstrap support values are presented above and Bremer support values are presented below the branch they refer to. Note that the crown clade Coracioidea (Coraciidae + Brachypteraciidae) is not labelled; the position of *Geranopterus alatus* with respect to this clade is unresolved. †, extinct taxa; NA, North American Coracii.

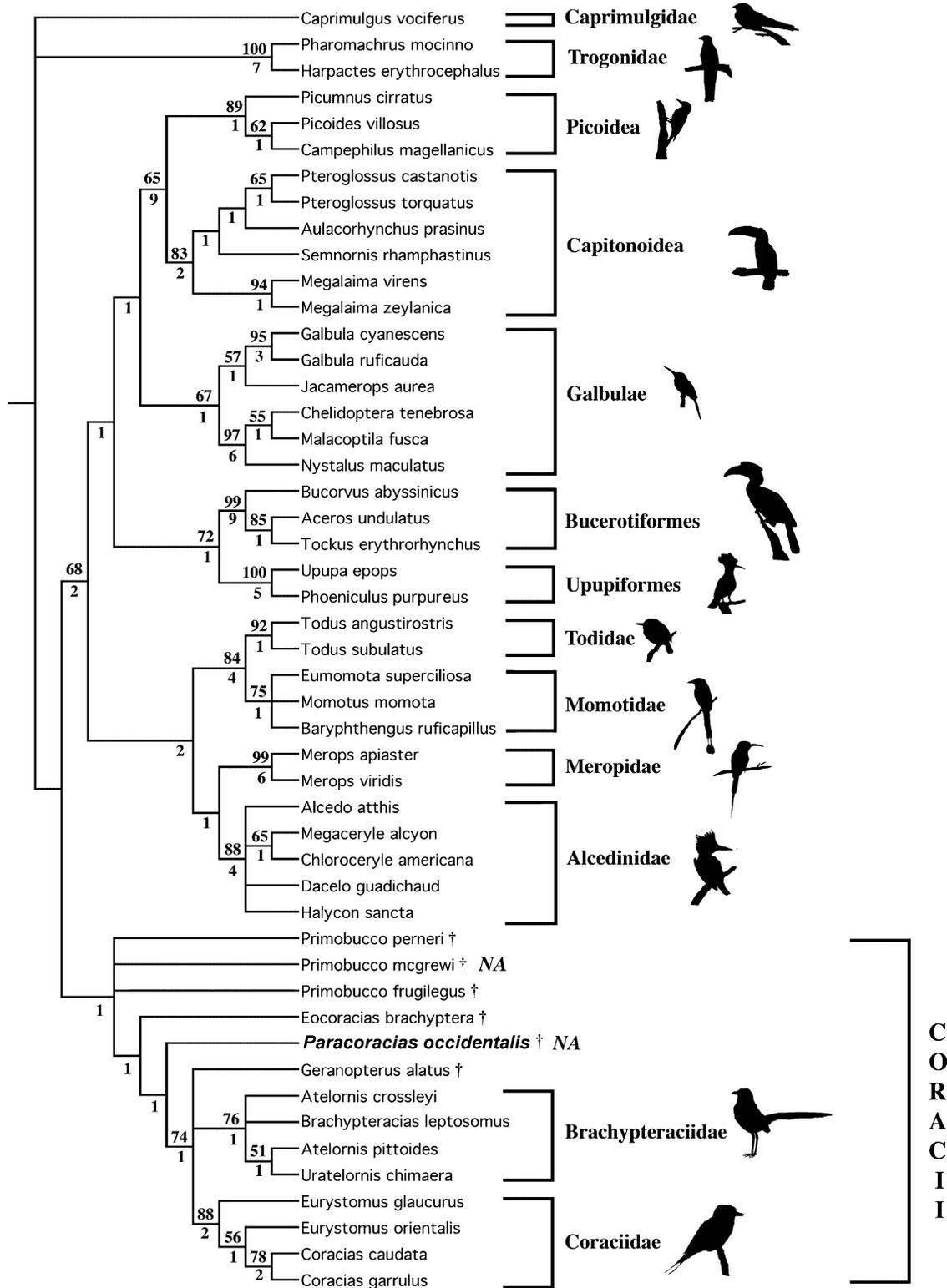


Figure 9. Strict consensus cladogram of 24 most parsimonious trees (length = 345; consistency index = 0.499; retention index = 0.474; rescaled consistency index = 0.237) from the analysis using the morphological data set. Bootstrap support values are presented above and Bremer support values are presented below the branch they refer to. Note that the crown clade Coracioidea (Coraciidae + Brachypteraciidae) is not labelled; the position of *Geranopterus alatus* with respect to this clade is unresolved. †, extinct taxa; NA, North American Coracii.

of an anterior process on the postorbital process (Mayr & Mourer-Chauviré, 2000; Mayr *et al.*, 2004). This character is an apomorphy relative to *Paracoracias* as well; its absence in the new species and presence in all crown Coracioidea supports placement outside of the crown clade. *Geranopterus alatus* is placed in an unresolved trichotomy with Coraciidae and Brachypteraciidae, as opposed to the sister taxon to the crown Coracioidea. Mayr *et al.* (2004) found only one synapomorphy uniting Coraciidae and Brachypteraciidae to the exclusion of Geranopteridae: presence of a foramen perforating the base of a ventral process on proximal metacarpal III. We were able to examine a large number of skeletons of Brachypteraciidae and found this foramen to be absent in two ground roller species (*Atelornis pittoides* and *Uratelornis chimera*), variable in *Atelornis crossleyi*, and present in *Brachypteracias leptosomus*. Because of this distribution, the character is not unambiguously optimized as a synapomorphy of a Coraciidae + Brachypteraciidae clade excluding *Geranopterus* in our analysis. Its optimization depends on recovered relationships within ground rollers.

The distal extent of metacarpal III in *G. alatus* is described as comparable to Brachypteraciidae (in which III markedly surpasses II) and figured as such (Mayr & Mourer-Chauviré, 2000: fig. 8M and N). Thus, we coded the marked distal projection as present in *G. alatus*, in contrast to Mayr *et al.* (2004: character 22). This character supports placement of *Geranopterus* as part of the ground roller stem in some of the resultant most parsimonious trees, contributing to diminished phylogenetic resolution. The plesiomorphic lack of a projection of the carpal trochlea of the carpometacarpus, which gives it a hooked appearance in ventral view (Mayr & Mourer-Chauviré, 2000: fig. 10), excludes *Geranopterus* from comprising part of crown Brachypteraciidae.

Basal divergences amongst ground rollers vary in the current analyses. In the morphology-only analysis they are unresolved (Fig. 9), whereas in the combined dataset *Atelornis pittoides* is placed as basal (Fig. 8). By contrast, Mayr & Mourer-Chauviré (2000) and some of the analyses of Kirchman *et al.* (2001) found *Brachypteracias leptosomus* to be the sister taxon of all other Brachypteraciidae. Monophyly of *Atelornis* is not recovered. Although *Atelornis* monophyly has been supported by other mitochondrial sequence data (Kirchman *et al.*, 2001), the two *Atelornis* species differed in three included morphological characters (e.g. the shape of the palatine, the development of the dentiform process, and the absence, presence, or polymorphism for the foramen in metacarpal III). Further data is needed to achieve consensus on ground roller relationships. However, both analyses place *Uratelornis* as derived relative to the other Brachypteraciidae

species, a placement recovered by Mayr & Mourer-Chauviré (2000) and by some analyses of Kirchman *et al.* (2001).

Coracii is placed as the sister taxon to a large clade including Piciformes and many of the traditional components of Coraciiformes in the primary analyses. Most recovered relationships, e.g. the monophyly of Piciformes, the division of Piciformes into Galbulae and Pici (Capitonoidea + Picoidea), the monophyly of a Upupiformes + Bucerotiformes clade, and the recovery of a clade of alcediniform birds (Momotidae, Alcedinidae, and Todidae), are supported by most other morphological and/or molecular analyses (e.g. Prum, 1988; Mayr *et al.*, 2003, 2004; Cracraft *et al.*, 2004; Ericson *et al.*, 2006; Livezey & Zusi, 2007; Hackett *et al.*, 2008). Lack of congruence with some previously recovered deep relationships of major subclades (e.g. of a clade including alcediniform birds and Coracii) is expected to be related to inclusion of species exemplars rather than superspecific terminals. Although necessary for inclusion of molecular sequence data, this approach also samples crown homoplasy for the morphological characters. Differences may also stem from rooting with *Caprimulgus*, which recent analyses suggest may be comparatively distantly related to these taxa (Ericson *et al.*, 2006; Livezey & Zusi, 2007; Hackett *et al.*, 2008).

The present dataset, constructed with the aim of evaluating characters variable within Coracii for a comprehensive set of potential outgroup taxa, will need to be expanded to address more fully coraciiform and piciform interrelationships. Sampling fossil stem taxa for other major lineages is necessary to better estimate basal morphological character states for these lineages. The character optimizations relevant to placing the new fossil and interrelationships in Coracii are, however, robust to analysis of a less inclusive clade recovered in recent molecular analyses (i.e. of Coracii, alcediniform birds, and Meropidae; Ericson *et al.*, 2006; Hackett *et al.*, 2008).

DISCUSSION

The presence of successive outgroups of Coracioidea in North America and Europe supports a widespread early Eocene distribution for stem Coracii, with subsequent restriction of the lineage to the Old World. The occurrence of *Primobucco mcgrewi* (a basal Coracii species) and *Paracoracias occidentalis* (more closely related to the crown clade) in the Green River Formation is consistent with at least two dispersals between Europe and North America by the early-middle Eocene. Similarities between the Eocene avifaunas of Europe and North America have been extensively commented on (e.g. Houde & Olson, 1989; Blondel & Mourer-Chauviré, 1998; Mayr *et al.*, 2004;

Mayr, 2005). *Paracoracias* further supports this proposed pattern and provides new insight into the early biogeography and diversity in Coracii.

In bill shape, wing proportions, and the abbreviated tarsometatarsus, *Paracoracias* is most similar to the broad-billed extant roller taxon *Eurystomus* (Coraciidae). Diet in extant Coracioidea is varied, but most species feed on insects and small vertebrates. Only *Eurystomus* rollers, however, have a modified broad rostrum and gape for aerial insect capture (Fry *et al.*, 1992). Given support for placement of *Paracoracias* outside of the crown clade, this bill shape and inferred ecology must have evolved at least twice within Coracii. *Primobucco mcgrewi*, the only previously described North American representative of Coracii, has a comparatively narrow rostrum, as do the European *Primobucco* species. Although lacking most of the beak, a skull referred to *Geranopterus* (Mayr & Mourer-Chauviré, 2000: fig. 8v) is also narrower at the orbit than *Eurystomus*, indicating a relatively narrow rostrum. As a result of flattening and orientation, no described specimens of *Eocoracias* permit a precise evaluation of beak width. Based on current character optimizations, the broad bill of *Paracoracias* represents convergence on extant *Eurystomus* morphologies and evidence of further ecological diversity in early Coracii.

Distribution of forested tropical environments to 50° N latitude are indicated in the late Palaeocene–early Eocene (e.g. Frakes, Francis & Syktus, 1992). A tropical to subtropical environment is strongly supported specifically for the Green River lake complex during the Eocene by the fossil flora and fauna (MacGinitie, 1969; Grande, 1994). The placement of Eocene Coracii in current and previous analyses (Mayr *et al.*, 2004) is consistent with a pattern observed in many other major avian clades, in which taxa now restricted to lower-latitude tropical forested environments were present in higher latitudes (and possibly widespread) during the Eocene (e.g. Peters, 1991; Blondel & Mourer-Chauviré, 1998; James, 2005). So far, no younger fossils speak to the timing of the disappearance of Coracii from North America. Other taxa show a similar pattern of diminishing range resulting in a relict extant distribution. Coliiformes (mousebirds) are restricted to Africa today, but were diverse during the Palaeogene and are now known to have persisted in North America until at least the latest Eocene, just prior to major Eocene/Oligocene global cooling (Ksepka & Clarke, 2009), and into the Miocene of Europe (Ballmann, 1969).

Some authors, from both fossil data alone and molecular divergence dates, have proposed major shifts in avian distributions from the early Eocene to the present, but they identify these dynamics within crown clades of major lineages (e.g. Brachypteraciidae

in Blondel & Mourer-Chauviré, 1998; Alcedinidae in Moyle *et al.*, 2006). As new Palaeogene fossils have come to light from the Eocene of North America and Europe, we have instead found increasing diversity in stem lineages of these groups (e.g. Mayr & Weidig, 2004; Mayr, 2005; Ksepka & Clarke, 2009). Given limited global sampling for Eocene localities, fossils cannot yet speak to an area of origin for Coracii. We can also not exclude the possibility that extant families were once more widespread but their fossils are as yet unrecovered from deposits outside their extant range. However, so far it is equally probable that the distribution of the crown clade Coracioidea is driven by late Palaeogene or even Neogene dynamics (Mayr, 2005). The low mitochondrial sequence divergence between Brachypteraciidae and Coraciidae noted by Kirchman *et al.* (2001) was also considered consistent with a comparatively recent origin for crown Coracioidea (Mayr & Mourer-Chauviré, 2003).

Phylogenetic and biogeographical data for Coracii perhaps best fit a proposal explored by Mittelbach *et al.* (2007, citations and discussion therein) that Cenozoic diversification may have followed an irregular pattern with considerable early Palaeogene species diversity in warm-adapted stem clades and subsequent climate-driven restriction and extinction within these clades. Diversification of crown lineages would be driven by different dynamics, climatic or otherwise, occurring over the late Palaeogene and even the Neogene. In contrast to birds, northern hemisphere biogeographical patterns in plants have received considerable attention. Prominent in this discussion has been the proposal of a broadly distributed early Tertiary northern hemisphere flora with subsequent differential extinction in North America and fragmentation associated with global cooling explaining many disjunctive extant distributions (boreotropical forest hypothesis; Wolfe, 1975; Tiffney, 1985). Although patterns are more complex for animals and for some plant clades (Sanmartín, Enghof & Ronquist, 2001; Donoghue & Smith, 2004), the potential for there being related drivers in the evolution of avian distributions deserves further consideration. The discovery of further North American Coracii diversity underscores the importance of considering extinct as well as extant taxa when investigating major biogeographical shifts in the history of avian biodiversity.

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REFERENCES

- Ballmann P. 1969.** Les oiseaux miocènes de la Grive-Saint-Alban (Isère). *Geobios* **2**: 157–204.
- Bartels WS. 1993.** Niche separation of fluvial and lacustrine reptiles from the Eocene Green River and Bridger Formations of Wyoming. *Journal of Vertebrate Paleontology* **13**: 25a.
- Baumel J, Witner LM. 1993.** Osteologia. In: Baumel JJ, King AS, Breazile JE, Evans HE and Vandern Berge JC, eds. *Handbook of Avian Anatomy: Nomina Anatomica Avium*. Cambridge, MA: Nuttall Ornithology Club, 45–132.
- Benz BW, Robbins MB, Peterson AT. 2006.** Evolutionary history of woodpeckers and allies (Aves: Picidae): placing key taxa on the phylogenetic tree. *Molecular Phylogenetics and Evolution* **40**: 389–399.
- Blondel J, Mourer-Chauviré C. 1998.** Evolution and history of the western Palaearctic avifauna. *Trends in Ecology and Evolution* **13**: 488–492.
- Bostwick KS, Brady MJ. 2002.** Phylogenetic analysis of wing feather taxis in birds: Macroevolutionary patterns of genetic drift? *The Auk* **119**: 943–954.
- Brodkorb P. 1970.** An Eocene puffbird from Wyoming. *Contributions to Geology* **9**: 13–15.
- Burton P. 1984.** Anatomy and evolution of the feeding apparatus in the avian orders Coraciiformes and Piciformes. *Bulletin of the British Museum (Natural History) Zoology Series* **47**: 331–443.
- Colbert EH. 1955.** *Evolution of the vertebrates*. New York: Wiley and Sons.
- Cracraft J. 1971.** The relationships and evolution of the rollers: Families Coraciidae, Brachypteraciidae, and Leptosomatidae. *The Auk* **88**: 72–752.
- Cracraft J. 1981.** Toward a phylogenetic classification of the recent birds of the world (Class Aves). *The Auk* **98**: 681–714.
- Cracraft JF, Barker K, Braun J, Harshman J, Dyke GJ, Feinstein J, Stanley S, Cibois A, Schikler P, Beresford P, García-Moreno J, Sorenson MD, Yuri T, Mindell DP. 2004.** Phylogenetic relationships among modern birds (Neornithes): towards an avian tree of life. In: Cracraft J, Donoghue MJ, eds. *Assembling the tree of life*. New York: Oxford University Press, 468–489.
- Donoghue M, Smith J. 2004.** Patterns in the assembly of temperate forests around the Northern Hemisphere. *Philosophical Transactions of Royal Society of London. Series B, Biological Sciences* **359**: 1633–1644.
- Ericson PGP, Anderson CL, Britton T, Elzanowski A, Johansson US, Källersjö M, Ohlson JI, Parsons TJ, Zuccon D, Mayr G. 2006.** Diversification of Neoaves: integration of molecular sequence data and fossils. *Biology Letters* **4**: 543–547.
- Espinosa de los Monteros A. 2000.** Higher-level phylogeny of Trogoniformes. *Molecular Phylogenetics and Evolution* **14**: 20–34.
- Fain MG, Houde P. 2004.** Parallel radiations in the primary clades of birds. *Evolution* **58**: 2558–2573.
- Feduccia A. 1975a.** Morphology of the bony stapes (columella) in the Passeriformes and related groups: evolutionary implications. *University of Kansas Museum of Natural History Miscellaneous Publications* **63**: 1–34.
- Feduccia A. 1975b.** The bony stapes in Upupidae and Phoeniculidae: new evidence for common ancestry. *Wilson Bulletin* **87**: 416–417.
- Feduccia A. 1999.** *The origin and evolution of birds*, 2nd edn. New Haven, CT: Yale University Press.
- Feduccia A, Martin LD. 1976.** The Eocene zygodactyl birds of North America (Aves: Piciformes). *Smithsonian Contributions to Paleontology* **27**: 101–110.
- Forbes WA. 1884.** Final ideas as to the classification of birds. *Ibis* **26**: 119–120.
- Frakes LA, Francis JE, Syktus JI. 1992.** *Climate modes of the Phanerozoic*. Cambridge: Cambridge University Press.
- Fry CH, Fry K, Harris A. 1992.** *Kingfishers, bee-eaters and rollers*. Princeton, NJ: Princeton University Press.
- Fuchs J, Ohlson JI, Ericson PGP, Pasquet E. 2007.** Synchronous intercontinental splits between assemblages of woodpeckers suggested by molecular data. *Zoologica Scripta* **36**: 11–25.
- Fürbringer M. 1888.** *Untersuchungen zur Morphologie und Systematik der Vögel, zugleich ein Beitrag zur Anatomie der Stütz- und Bewegungsorgane*, 2 volumes. Amsterdam: T. J. Van Holkema.
- Gadow H. 1892.** On the classification of birds. *Proceedings of the Zoological Society of London* **1892**: 229–256.
- George JC, Berger AJ. 1966.** *Avian myology*. New York: Academic Press.
- Grande L. 1980.** Paleontology of the Green River Formation, with a review of the fish fauna. *Bulletin of the Geological Survey of Wyoming* **63**: 1–333.
- Grande L. 1994.** The Tertiary Green River Lake Complex, with comments on paleoenvironments and historical biogeography. Symposium volume on Early Tertiary paleontology and environments in Wyoming. *Contributions to Geology* **30**: 3–14.
- Groth JG, Barrowclough GF. 1999.** Basal divergences in birds and the phylogenetic utility of the nuclear RAG-1 gene. *Molecular Phylogenetics and Evolution* **12**: 115–123.
- Hackett SJ, Kimball RT, Reddy S, Bowie RCK, Braun EL, Braun MJ, Chojnowski JL, Cox WA, Han K-L, Harshman J, Huddleston CJ, Marks BD, Miglia KJ, Moore WS, Sheldon FH, Steadman DW, Witt CC, Yuri T. 2008.** A phylogenomic study of birds reveals their evolutionary history. *Science* **320**: 1763–1768.
- Höflich E, Alvarenga HMF. 2001.** Osteology of the shoulder

- girdle in the piciformes, passeriformes and related groups of birds? *Zoologischer Anzeiger* **240**: 196–208.
- Houde P, Olson S. 1989.** Small arboreal non-passerine birds from the early Tertiary of western North America. In: Ouellet H, ed. *Acta XIX congressus internationalis ornithologici*. Ottawa: University of Ottawa Press, 2030–2036.
- Irestedt M, Johansson US, Parsons TJ, Ericson PGP. 2001.** Phylogeny of major lineages of suboscines (Passeriformes) analysed by nuclear DNA sequence data. *Journal of Avian Biology* **32**: 15–25.
- James HF. 2005.** Paleogene fossils and the radiation of modern birds. *The Auk* **122**: 1049–1054.
- Johansson US, Ericson PGP. 2003.** Molecular support for a sister group relationship between Pici and Galbulae (Piciformes sensu Wetmore 1960). *Journal of Avian Biology* **34**: 185–197.
- Johansson US, Parsons TJ, Irestedt M, Ericson PGP. 2001.** Clades within the 'higher land birds', evaluated by nuclear DNA sequences. *Journal of Zoological Systematics and Evolutionary Research* **39**: 37–51.
- Johnston DW. 1988.** A morphological atlas of the avian uropygial gland. *Bulletin of the British Museum of Natural History (Zoology)* **54**: 199–259.
- Kempf O, Bolliger T, Kälän D, Engesser B, Matter A. 1997.** New magnetostratigraphic calibration of Early to Middle Miocene mammal biozones of the North Alpine foreland basin. In: Aguilar J-P, Legendre S, Michaux J, eds. *Actes du Congrès BiochroM'97. Mémoires et Travaux de l'Ecole Pratique des Hautes Etudes, Institut de Montpellier* **21**: 547–561.
- Kirchman JJ, Hackett SJ, Goodman SM, Bates JM. 2001.** Phylogeny and systematics of ground rollers (Brachypteraciidae) of Madagascar. *The Auk* **118**: 849–863.
- Ksepka DT, Clarke JA. 2009.** Affinities of *Palaeospiza bella* and the phylogeny and biogeography of mousebirds. *Auk* **126**: 245–259.
- Ksepka DT, Clarke JA.** In press. *Primobucco mcgrewi* (Aves: Coraci) from the Eocene Green River Formation: new anatomical data and the earliest definitive record of stem rollers. *Journal of Vertebrate Paleontology*.
- Langrand O. 2001.** Family Brachypteraciidae (ground-rollers). In: del Hoyo J, Elliott A, Sargatal J, eds. *Handbook of the birds of the world, vol. 6: mousebirds to hornbills*. Barcelona: Lynx Edicions, 378–388.
- Legendre S, Lévêque F. 1997.** Etalonnage de l'échelle biochronologique mammalienne du Paleogene d'Europe occidentale: vers une integration a l'échelle globale. In: Aguilar J-P, Legendre S, Michaux J, eds. *Actes du Congrès BiochroM'97. Mémoires et Travaux de l'Ecole Pratique des Hautes Etudes, Institut de Montpellier* **21**: 461–473.
- Linnaeus C. 1758.** *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. ed. 10, tom. 1–2. Holmiae: Impensis L. Salvii.
- Livezey BC, Zusi RL. 2006.** Higher-order phylogenetics of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. I. Methods and characters. *Bulletin of the Carnegie Museum of Natural History* **37**: 1–544.
- Livezey BC, Zusi RL. 2007.** Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. II. Analysis and discussion. *Zoological Journal of the Linnean Society* **149**: 1–95.
- MacGinitie HD. 1969.** The Eocene Green flora of northwestern Colorado and northeastern Utah. *University of California Publications in Geological Science* **83**: 1–149.
- Maddison WP, Maddison DR. 1992.** *MacClade: analysis of phylogeny and character evolution*. 4.08 edn. Sunderland, MA: Sinauer Associates.
- Marks BD, Weckstein JD, Moyle RG. 2007.** Molecular phylogenetics of the bee-eaters (Aves: Meropidae) based on nuclear and mitochondrial DNA sequence data. *Molecular Phylogenetics and Evolution* **45**: 23–32.
- Maurer DR, Raikow RJ. 1981.** Appendicular mycology, phylogeny, and classification of the avian order Coraciiformes (including Trogoniformes). *Annals of Carnegie Museum* **50**: 417–434.
- Mayr E, Amadon D. 1951.** A classification of recent birds. *American Museum Novitates* **1496**: 1–42.
- Mayr G. 1998.** 'Coraciiforme' und 'piciforme' Kleinvögel aus dem Mittel-Eozän der Grube Messel (Hessen, Deutschland). *Courier Forschungsinstitut Senckenberg* **205**: 1–101.
- Mayr G. 1999.** A new trogon from the Middle Oligocene of Céreste, France. *The Auk* **116**: 427–434.
- Mayr G. 2000.** Tiny hoopoe-like birds from the Middle Eocene of Messel (Germany). *The Auk* **117**: 964–970.
- Mayr G. 2004.** The phylogenetic relationships of the early Tertiary Primoscenidae and Sylphornithidae and the sister taxon of crown group piciform birds. *Journal of Ornithology* **145**: 188–198.
- Mayr G. 2005.** The Paleogene fossil record of birds in Europe. *Biology Review* **80**: 515–542.
- Mayr G. 2008.** Avian higher-level phylogeny: well-supported clades and what we can learn from a phylogenetic analysis of 2954 morphological characters. *Journal of Zoological Systematics and Evolutionary Research* **46**: 63–72.
- Mayr G, Clarke J. 2003.** The deep divergences of neornithine birds: a phylogenetic analysis of morphological characters. *Cladistics* **19**: 527–553.
- Mayr G, Manegold A, Johansson US. 2003.** Monophyletic groups within higher land birds – comparison of morphological and molecular data. *Journal of Zoological Systematics and Evolutionary Research* **41**: 233–248.
- 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). *Journal of Vertebrate Paleontology* **20**: 553–546.
- Mayr G, Mourer-Chauviré C. 2003.** Phylogeny and fossil record of the Brachypteraciidae: a comment on Kirchman et al. (2001). *The Auk* **120**: 202–203.
- Mayr G, Mourer-Chauviré C, Weidig I. 2004.** Osteology and systematic position of the Eocene Primobucconidae (Aves, Coraciiformes sensu stricto), with first records from Europe. *Journal of Systematic Paleontology* **2**: 1–12.
- Mayr G, Weidig I. 2004.** The Early Eocene bird *Gallinuloides wyomingensis* – a stem group representative of Galliformes. *Acta Palaeontologica Polonica* **49**: 211–217.

- McKittrick MC. 1991.** Phylogenetic analysis of avian hindlimb musculature. *University of Michigan, Museum of Zoology Miscellaneous Publications* **179**: 1–85.
- McKittrick MC. 1993.** Trends in the evolution of hindlimb musculature in aerial-foraging birds. *The Auk* **110**: 189–206.
- Milne-Edwards A. 1892.** Sur les oiseaux fossiles des dépôts éocènes de phosphate de chaux du Sud de la France. In: Sclater PL, ed. *Comptes Rendus du Second Congrès Ornithologique International*. Budapest, 60–80.
- Mittelbach G, Schemske D, Cornell HV, Allen AP, Brown JM, Bush MB, Harrison SP, Hurlbert AH, Knowlton N, Lessios HA, McCain CM, McCune AR, McDade LA, McPeck MA, Near TJ, Price TD, Ricklefs RE, Roy K, Sax DF, Schluter D, Sobel JM, Turelli M. 2007.** Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* **10**: 315–331.
- Mlíkovský J. 1999.** A new jacana (Aves: Jacanidae) from the early Miocene of the Czech Republic. *Comptes Rendus de l'Académie des Sciences (Paris), Sciences de la Terre et des Planètes* **328**: 121–123.
- Mourer-Chauviré C. 1999.** Position systématique de *Nuphar-*ranassa bohemica** Mlíkovský, 1999. *Comptes Rendus de l'Académie des Sciences de Paris, série IIa* **329**: 149–152.
- Mourer-Chauviré C, Sigé B. 2006.** Une nouvelle espèce de Jungornis (Aves, Apodiformes) et de nouvelles formes de Coraciiformes s.s. dans l'Éocène supérieur du Quercy. *Strata* **13**: 151–159.
- Moyle RC, Chesser T, Prum R, Schikler P, Cracraft J. 2006.** Phylogeny and evolutionary history of Old World suboscine birds (Aves, Eurylaimides). *American Museum Novitates* **3544**: 1–22.
- Moyle RG. 2005.** Phylogeny and biogeographic history of Trogoniformes, a pantropical bird order. *Biological Journal of the Linnean Society* **84**: 725–738.
- Moyle RG. 2006.** A molecular phylogeny of kingfishers (Aves: Alcedinidae) with insights into early biogeographic history. *The Auk* **123**: 487–499.
- Moyle RG, Fuchs J, Pasquet E, Marks BD. 2007.** Feeding behavior, toe count, and the phylogenetic relationships among alcedinine kingfishers (Alcedininae). *Journal of Avian Biology* **38**: 317–326.
- Olson SL. 1976.** Oligocene fossils bearing on the origins of the Todidae and Momotidae (Aves: Coraciiformes). *Smithsonian Contributions to Paleobiology* **27**: 111–119.
- Olson SL. 1985.** The fossil record of birds. In: Farner DS, King JR, Parkes KC, eds. *Avian biology*, Vol. 8. Orlando, FL: Academic Press, 79–238.
- Pereira SL, Johnson KP, Clayton DH, Baker AJ. 2007.** Mitochondrial and nuclear DNA sequences support a cretaceous origin of columbiformes and a dispersal-driven radiation in the paleogene. *Systematic Biology* **56**: 656–672.
- Peters DS. 1991.** Zoogeographical relationships of the Eocene avifauna from Messel (Germany). In: Bell BD, Cossee RO, Flux JEC, Heather BD, Hitchmough RA, Robertson CJR, Williams MJ, eds. *Acta congressus internationalis ornithologici*. Christchurch: Ornithological Congress Trust Board, 572–577.
- Prum RO. 1988.** Phylogenetic interrelationships of the barbets (Capitonidae) and toucans (Ramphastidae) based on morphology with comparisons to DNA-DNA hybridization. *Zoological Journal of the Linnean Society* **92**: 313–343.
- Sanmartín I, Enghof H, Ronquist F. 2001.** Patterns of animal dispersal, vicariance and diversification in the Holarctic. *Biological Journal of the Linnean Society* **73**: 345–390.
- Sclater PL. 1865.** On the structure of *Leptosoma discolor*. *Proceedings of the Zoological Society (London)* **1865**: 682–689.
- Sibley CG, Ahlquist JE. 1990.** *Phylogeny and classification of birds: a study in molecular evolution*. New Haven, CT: Yale University Press.
- Sibley CG, Ahlquist JE, Monroe BL. 1988.** A classification of the living birds of the world based on DNA-DNA hybridization studies. *The Auk* **105**: 409–423.
- Simpson SF, Cracraft JL. 1981.** The phylogenetic relationships of the Piciformes. *The Auk* **98**: 481–494.
- Sorenson MD, Oneal E, García-Moreno J, Mindell DP. 2003.** More taxon, more characters: the hoatzin problem is still unresolved. *Molecular Biology and Evolution* **20**: 1484–1498.
- Stegmann B. 1963.** Der Processus internus indicis im Skelett des Vogelflügels. *Journal für Ornithologie* **104**: 413–423.
- Stephan B. 1970.** Eutaxie, diastataxie and andere probleme der Befiederung des Vogelflügels. *Mitteilungen aus dem Zoologischen Museum in Berlin* **46**: 339–437.
- Stephan B. 1992.** Vorkommen und Ausbildung der Fingerkrallen bei rezenten Vögeln. *Journal für Ornithologie* **133**: 251–277.
- Stresemann E. 1959.** The status of avian systematics and its unsolved problems. *The Auk* **76**: 269.
- Swierczewski EV, Raikow RJ. 1981.** Hind limb morphology, phylogeny and classification of the Piciforms. *The Auk* **98**: 466–480.
- Swofford DL. 2002.** *PAUP*: phylogenetic analysis using parsimony (*and other methods), Version 4*. Sunderland, MA: Sinauer Associates.
- Thompson JD, Gibson TG, Plewniak F, Jeanmougin F, Higgins DG. 1997.** The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* **25**: 4876–4882.
- Tiffney BH. 1985.** The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the Northern Hemisphere. *Journal of the Arnold Arboretum, Harvard University* **66**: 243–273.
- Weckstein JD. 2005.** Molecular phylogenetics of the Ramphastos toucans: implications for the evolution of morphology, vocalizations and coloration. *Auk* **122**: 1191–1209.
- Wetmore A. 1960.** A classification for the birds of the world. *Smithsonian Miscellaneous Collections* **139**: 1–37.
- Wetmore A, Miller WW. 1926.** The revised classification for

the fourth edition of the AOU Check-list. *The Auk* **43**: 337–346.

Whitfield P, ed. 1988. *The MacMillan illustrated encyclopedia of birds*. New York: Macmillan Publishing Company.

Wolfe JA. 1975. Some aspects of plant geography of the Northern Hemisphere during the late Cretaceous and Tertiary. *Annals of the Missouri Botanical Garden* **62**: 264–279.

APPENDIX 1

COMPARATIVE MATERIALS

Comparative material examined for the phylogenetic analysis [note: we follow Moyle (2006) in recognizing 'Ceryle' *alcyon* as *Megaceryle alcyon*]: *Aceros undulatus* USNM19687; *Alcedo atthis* AMNH 23570, AMNH 25222; *Atelornis crossleyi* FMNH 363795; FMNH 427362; USNM 223864; *Atelornis pittoides* FMNH 384701; FMNH 384760; FMNH 427333; FMNH 438663; *Aulacorhynchus prasinus* AMNH 7088; *Baryphthengus ruficapillus* AMNH 6669; *Bucorvus abyssinicus* AMNH 1770; *Brachypteracias leptosomus* FMNH 384731; FMNH 431181; USNM 223863; *Campephilus magellanicus* AMNH 6704, AMNH 6706, AMNH 27756; *Caprimulgus vociferus* NCSM 15171, NCSM 16836; *Chelidoptera tenebrosa* AMNH 11938, AMNH 18009; AMNH 19269; *Chloroceryle americana* AMNH 8556, AMNH 10170; *Coracias benghalensis* AMNH 8562, AMNH 8561; *Coracias caudata*: AMNH 1471; AMNH 12811, SMF 6651, USNM 431908; *Coracias garrulus* AMNH 2141,

AMNH 457, USNM 553063; *Dacelo gaudichaud* AMNH 7551; *Eocoracias brachyptera* HMLD 10474; SMF 1452, SMF 11148; *Eurystomus glaucurus* USNM 347415; *Eurystomus gularis* USNM 292414; *Eurystomus orientalis* AMNH 7544, USNM 291382; *Eumomota superciliosa* AMNH 4602, AMNH 10295, AMNH 10297; *Halcyon sancta* AMNH 28154; *Harpactes erythrocephalus* AMNH 25537, AMNH 25539, AMNH 25539; *Galbula ruficauda* AMNH 25635; *Malacoptera fusca* AMNH 9134, AMNH 9143; *Megaceryle alcyon* AMNH 27237, NCSM 10089; *Megalaima zeylanica* AMNH 27076; *Merops apiaster* AMNH 450, AMNH 4209; *Merops ornatus* AMNH 9627, AMNH 9649; *Merops viridis* AMNH 449; *Momotus momota paretensis* AMNH 4807; *Momotus momota* AMNH 4807, AMNH 10868; *Nystalus maculatus* AMNH 25636, AMNH 25637; *Penelopides panini* USNM 613075; *Pharomachrus mocinno* AMNH 4673, AMNH 8734; *Phoeniculus purpureus* AMNH 10211; *Picoides villosus* AMNH 18859, AMNH 18860; *Primobucco fragileus* SMF 3507, SMF 3794; *Primobucco mcgrewi* USNM 336284, UWGM 3299; *Primobucco perneri* SMF 516; SMF 3546, SMF 3793; *Pteroglossus castanotis* AMNH 8599; *Pteroglossus torquatus* AMNH 2994; AMNH 4340; *Semnornis ramphastinus* AMNH 56581; *Tockus erythrorhynchus* USNM 321102; *Todus angustirostris* AMNH 25419; *Todus mexicanus* USNM 501845, *Todus subulatus* AMNH 25467, AMNH 25465, USNM 559682; *Todus todus* USNM 558882; *Uratelornis chimaera* SMF 4571; *Upupa epops* AMNH 15671, AMNH 27075, AMNH 87688.

APPENDIX 2

Original citations and GenBank accession numbers for sequences used in combined analysis.

Taxon	<i>cmyc</i>			<i>RAG-1</i>			<i>ND2</i>		
	Accession no.	Citation		Accession no.	Citation		Accession no.	Citation	
<i>Alcedo atthis</i>	AF295143	Johansson <i>et al.</i> (2001)		DQ1111792	Moyle (2006)		DQ640773	Moyle <i>et al.</i> (2007)	
<i>Atelornis crossleyi</i>							AF407455	Kirchman <i>et al.</i> (2001)	
<i>Atelornis pittooides</i>							AF407461	Kirchman <i>et al.</i> (2001)	
<i>Aulacorhynchus prasinus</i>							AY959857	Weckstein (2005)	
<i>Baryphthengus ruficapillus</i>	AF295146	Johansson <i>et al.</i> (2001)		AF294674	Johansson <i>et al.</i> (2001)				
<i>Brachypteracias leptosomus</i>				AF294676	Johansson <i>et al.</i> (2001)		AF407463	Kirchman <i>et al.</i> (2001)	
<i>Caprimulgus vociferus</i>				EF373497	Pereira <i>et al.</i> (2007)		EF373327	Pereira <i>et al.</i> (2007)	
<i>Chloroceryle americana</i>	AF295144	Johansson <i>et al.</i> (2001)		DQ111805	Moyle (2006)		DQ111844	Moyle (2006)	
<i>Coracias caudata</i>	AF295148	Johansson <i>et al.</i> (2001)		AF143737	Groth & Barrowclough (1999)				
<i>Coracias garrulus</i>									
<i>Dacelo gaudichaud</i>				DQ111824	Moyle (2006)		AF407465	Kirchman <i>et al.</i> (2001)	
<i>Eurystomus glaucurus</i>							DQ111863	Moyle (2006)	
<i>Eurystomus orientalis</i>							AF407469	Kirchman <i>et al.</i> (2001)	
<i>Galbula cyanescens</i>	AF295155	Johansson <i>et al.</i> (2001)		AF294682	Johansson <i>et al.</i> (2001)		AF407468	Kirchman <i>et al.</i> (2001)	
<i>Halcyon sancta</i>				DQ111817	Moyle (2006)				
<i>Harpactes erythrocephalus</i>				AY625242	Moyle (2005)		DQ111856	Moyle (2006)	
<i>Megaceryle alcyon</i>							AY625213	Moyle (2005)	
<i>Megalaima virens</i>	AY165829	Johansson & Ericson (2003)		DQ111803	Moyle (2006)		DQ111842	Moyle (2006)	
<i>Merops apiaster</i>				AY165793	Johansson & Ericson (2003)				
<i>Merops viridis</i>	AF295147	Johansson <i>et al.</i> (2001)		AF294675	Johansson <i>et al.</i> (2001)		EU021520	Marks <i>et al.</i> (2007)	
<i>Momotus momota</i>	AF295170	Irestedt <i>et al.</i> (2001)		DQ111789	Moyle (2006)		EU021528	Marks <i>et al.</i> (2007)	
<i>Nystaluis maculatus</i>	AF295153	Johansson <i>et al.</i> (2001)		AF294680	Johansson <i>et al.</i> (2001)		AY625193	Moyle (2005)	
<i>Picumnus cirratus</i>	AF295174	Irestedt <i>et al.</i> (2001)		DQ479153	Benz <i>et al.</i> (2006)		AF295195	Irestedt <i>et al.</i> (2001)	
<i>Picoides villosus</i>							DQ361290	Fuchs <i>et al.</i> (2007)	
<i>Pteroglossus castanotis</i>	AF295159	Johansson <i>et al.</i> (2001)		AF294686	Johansson <i>et al.</i> (2001)				
<i>Tockus erythrorhynchus</i>				AF294679	Johansson <i>et al.</i> (2001)		AY274055	Sorenson <i>et al.</i> (2003)	
<i>Todus angustirostris</i>				DQ111790	Moyle (2006)		DQ111829	Moyle (2006)	
<i>Upupa epops</i>									
<i>Uratelornis chimaera</i>	AF295151	Johansson <i>et al.</i> (2001)		AF294678	Johansson <i>et al.</i> (2001)		AF407470	Kirchman <i>et al.</i> (2001)	

APPENDIX 3

CHARACTER DESCRIPTIONS

1. Relationship of external naris and antorbital fenestra: do not overlap in lateral view (0); naris overlaps antorbital fenestra posteriorly (1).
2. External naris, shape, lateral view: ovoid (0); triangular with a flat ventral margin (1).
3. Temporal fossae, dorsal extent: widely separated (0); approach each other at midline (1).
4. Palatine, posterolateral margin, posteriorly directed spine-like processes: absent (0); present (1).
5. Skull, anterior wall of braincase: largely ossified (0); almost completely unossified (1). This character was used by Olson (1976) to support placement of the fossil *Palaeotodus* with Todidae.
6. External naris, division by a thin bony septum: undivided (0); divided (1; e.g. Cracraft, 1971: fig. 1). See discussion in Mayr & Mourer-Chauviré (2000: 534).
7. Internarial septum, largely or completely ossified: absent (0); present (1). See discussion in Mayr *et al.* (2004).
8. Beak grossly inflated: absent (0); present (1).
9. Upper beak, cutting edge of rhamphotheca finely serrated: absent (0); present (1).
10. Lacrimal, head: small (0); greatly enlarged (1).
11. Lacrimal, descending process: unexpanded (0); greatly medially expanded (1).
12. Lacrimal: present, unreduced (0); greatly reduced or absent (1).
13. Lacrimal, posterior margin of head in dorsal view: straight (0); concave, with small posterior point (1); concave with large posterior point (2). Ordered.
14. Ectethmoid, greatly expanded and plate-like, dorsal margin fused with frontals: no (0); yes (1).
15. Postorbital process: short (0); elongate, but well-separated from jugal bar (1); elongate, touching or nearly touching jugal bar (2). Ordered. See discussion in Mayr *et al.* (2004).
16. Postorbital process, development of an anterior process: absent (0); present (1). See discussion in Mayr *et al.* (2004) and Livezey & Zusi (2006: 40).
17. Zygomatic process, weak or absent: (0); long and thin (1); abbreviated and tab-like (2).
18. Palatine, posterior margin: concave (0); convex (1).
19. Columella, large hollow bulbous basal footplate area with large fenestra on one side: absent (0); present (1). Scorings are based on Feduccia (1975a, b). See also Mayr & Clarke (2003) and Livezey & Zusi (2006: 61).
20. Mandibular symphysis: short, approximately one-fifth of mandible length or less (0); moderate length, up to one-third of mandible length (1); extensive, more than one-third of mandible length (2).
21. Mandible, deep incision between medial process and retroarticular process in dorsal view (Olson, 1976: fig. 2): absent (0); present (1).
22. Mandible, posterior mandibular fenestra: absent or minute (0); large opening (1).
23. Atlas and axis: separate (0); fused into single element in adult (1).
24. Atlas, transverse foramen: absent (0); present (1).
25. Axis, transverse foramen: absent (0); present (1).
26. Presacral vertebrae: more than 19 (0); 19 (1); 18 (2).
27. Pygostyle, anterior border of lamina: absent (0); notch present (1); circular perforation with bony anterior rim (2).
28. Pygostyle, discus: unmodified (0); shield-like with sharply defined ridge-like lateral margins (1); discus enlarged, with large dorsal and ventral projections (this state encompasses the unique morphology seen in Coliiformes; 2). See Mayr, Manegold & Johansson (2003).
29. Furcula, apophysis: absent or small, blunt tubercle (0); blade-like projection (1); large sheet-like expansion (2).
30. Furcula, omal end: unmodified (0); widened with blunt, slightly convex and short acrocoracoid and acromion processes (1); acrocoracoid and acromion processes well developed and wide, forming plate-like omal extremity of subtriangular shape.
31. Scapula, acromion process: single (0); bifurcate, with additional medial process (1).
32. Scapula, pneumatic foramen on anterior part of acromion process: absent (0); present (1).
33. Coracoid, bony bridge connects procoracoid process and acromion process: absent (0); present (1).
34. Coracoid, procoracoid process: well developed (0); greatly reduced (1).
35. Coracoid, distinct process overhanging supraco-racoid sulcus: absent (0); present (1) See Mayr (1999) for discussion of this feature.
36. Sternum, clearly defined and strongly raised intramuscular line: absent (0); present (1). This character was discussed by Cracraft (1971).
37. Sternum, internal spine: absent (0); present (1).
38. Sternum, external spine: absent (0); present (1).
39. Sternum, posterior incisures: open (0); closed, forming fenestrae (1).
40. Sternum, posterior incisures: four (0); two (1).
41. Clavicles: fused, forming furcula (0); unfused (1).

42. Humerus, bicipital crest: unenlarged (0); expanded, extending far distally (1). This character was discussed by Cracraft (1971).
43. Ulna, feather papillae: absent or faint (0); prominent raised knobs (1).
44. Ulna, olecranon: blunt (0); elongated and narrow (1).
45. Ulnare, rami: ventral ramus (*crus longus*) longer than dorsal ramus (*crus brevis*) (0); subequal (1); dorsal ramus longer than ventral ramus (2).
46. Carpometacarpus, metacarpal II, anterior protuberance at midshaft (*protuberantia metacarpalis*; Baumel & Witmer, 1993; dentiform process of Mayr, 2004): absent (0); present (1).
47. Carpometacarpus, intermetacarpal process: absent or weak (0); well developed (1); absent, but tendon of *m. extensor carpi ulnaris* inserting in position of intermetacarpal process (2). These character states, advocated by Mayr *et al.* (2004), distinguish between the taxa that lack an intermetacarpal process and retain a primitive insertion of the *extensor carpi ulnaris* tendon, and those that lack the process but show the apomorphic displaced insertion of the tendon. Stegmann (1963) provided a detailed discussion of this feature.
48. Carpometacarpus, metacarpal III with ventrally protruding projection on ventral side of proximal end: absent (0); present (1).
49. Carpometacarpus, foramen in ventrally protruding projection from metacarpal III: absent (0); present (1). See Mayr & Mourer-Chauviré (2000). This character is considered noncomparable for taxa lacking the projection.
50. Carpometacarpus: metacarpals II and III subequal in length (0); metacarpal III projects significantly distal to metacarpal II (1).
51. Carpometacarpus, portion of carpal trochlea proximal to metacarpal III: present (0); absent, creating concave distal margin to trochlea and giving the trochlea a hooked appearance in ventral view (1). See Mayr & Mourer-Chauviré (2000: fig. 10).
52. Carpometacarpus, metacarpals II and III: separated by moderate intermetacarpal space (0); metacarpal III strongly bowed, creating a wide space (1).
53. Carpometacarpus, ridge continuing distally from pisiform process to metacarpal III: absent (0); present (1). This character was discussed by Mayr (2000).
54. Carpometacarpus, posterior margin of metacarpal III: smooth (0); undulating (1).
55. Manual phalanx II:1, large proximally directed process on ventral side: absent (0); present (1).
56. Manual phalanx II:1, proximally hooked process projects from posterior edge of distal end (Mayr, 2004: fig. 5c): absent (0); present (1).
57. Manual phalanx II:1, internal index process: small, does not surpass the distal articular surface for phalanx II-2 (0); well developed, surpasses distal articular surface for phalanx II:2 (1).
58. Pelvis, pectineal tubercle: present, well developed (0); weak or absent (1).
59. Pelvis, anterior iliac blades: dorsal margin free from vertebrae (0); reduced in size and fused with vertebral transverse processes to form flat, horizontal surface (1). This character is discussed in Simpson & Cracraft (1981).
60. Femur, pneumatic foramen on anterolateral surface of proximal end: absent (0); present (1).
61. Tibiotarsus, anterior cnemial crest: weakly anteriorly projected (0); strongly projected (1). This feature was discussed by Cracraft (1971).
62. Tibiotarsus, anterior cnemial crest continuous with ridge along medial edge of the shaft, paralleling the fibular crest (1).
63. Tarsometatarsus, bony canal enclosing tendons of *m. flexor hallucis longus*: absent (0); present (1).
64. Tarsometatarsus, ossified extensor retinaculum: absent (0); present (1).
65. Tarsometatarsus: shorter than humerus/femur (0); elongate, surpassing humerus and femur in length (1).
66. Tarsometatarsus, well-developed medial plantar crest: absent (0); present (1).
67. Tarsometatarsus, distal vascular foramen: moderate size (0); greatly enlarged (1). Discussed in Mayr & Mourer-Chauviré (2000) and used in Mayr *et al.* (2004).
68. Tarsometatarsus, distal interosseal canal: present, canal open on plantar side, forming a deep narrow sulcus between trochlea III and IV (0); absent (1). Discussed in Mayr & Mourer-Chauviré (2000) and used in Mayr *et al.* (2004).
69. Tarsometatarsus, large accessory trochlea on trochlea IV: absent (0); present (1).
70. Tarsometatarsus trochlea IV reaching almost as far distally as trochlea III and rotund in lateral view: absent (0); present (1). See Mayr *et al.* (2004).
71. Pedal digit I, phalanx 1, proximal end: unexpanded (0); greatly medially expanded (1). See discussion in Mayr (1998: fig. 20).
72. Pedal digit I, phalanx 1 length relative to other proximal phalanges: moderate length, e.g. subequal to phalanx III:1 (0); elongate, twice the length of proximal phalanx of digit III.
73. Foot syndactyl: no (0); yes (1).

74. Foot heterodactyl: no (0); yes (1).
75. Pectoralis pars propatagialis, pars longus: fleshy (0); tendinous (1). Character 6 of Maurer & Raikow (1981).
76. Tensor propatagialis: single belly (0); two bellies (1). Character 7 of Maurer & Raikow (1981).
77. Tensor propatagialis, pars longus: present (0); absent (1). Character 8 of Maurer & Raikow (1981).
78. Deltoideus major, scapular anchor: present (0); absent (1). Character 10 of Maurer & Raikow (1981).
79. Deltoideus minor, insertion: anterior to supracoracoideus tendon (0); distal to supracoracoideus tendon (1); directly onto tendon (2). This character combines characters 11 and 12 of Maurer & Raikow (1981).
80. Scapulotriceps, ligamentum tricipitale: present (0); absent (1). Character 15 of Maurer & Raikow (1981).
81. Expansor secundariorum pars cubiti: present (0); absent (1). Character 16 of Maurer & Raikow (1981).
82. Flexor digitorum profundus: two heads (0); one head (1). Character 18 of Maurer & Raikow (1981).
83. Extensor carpi radialis, origin: one head (0); two heads (1). Character 19 of Maurer & Raikow (1981).
84. Extensor carpi ulnaris, origin: separate from ectepicondylo-ulnaris (0); origins fused (1). Character 20 of Maurer & Raikow (1981).
85. Extensor digitorum communis origin: from humerus only (0); from humerus and radius (1). Character 21 of Maurer & Raikow (1981).
86. Extensor digitorum communis insertion on alular phalanx: present (0); absent (1). Character 22 of Maurer & Raikow (1981).
87. Ectepicondylo-ulnaris, origin: single tendon (0); two tendons (1). Character 23 of Maurer & Raikow (1981).
88. Extensor longus digiti major pars distalis: present (0); absent (1). Character 24 of Maurer & Raikow (1981).
89. Extensor longus alulae, radial head: present (0); absent (1). Character 25 of Maurer & Raikow (1981).
90. Interosseus dorsalis: bipennate (0); unipennate (1); absent (2). This character combines characters 27 and 28 of Maurer & Raikow (1981).
91. Interosseus ventralis: bipennate (0); unipennate (1). Character 29 of Maurer & Raikow (1981).
92. Iliotibialis cranialis origin: single head (0); two heads (1). Character 1 of Swierczewski & Raikow (1981).
93. Femorotibialis externus pars distalis: present (0); absent (1). Character 8 of Swierczewski & Raikow (1981).
94. Femorotibialis internus: two bellies (0); one belly (1). Character 9 of Swierczewski & Raikow (1981).
95. Flexor cruris lateralis and flexor cruris medialis tendons of insertion: connected (0); separate (1). Character 12 of Swierczewski & Raikow (1981).
96. Flexor cruris medialis origin: from ischium (0); from ischium and pubis (1). Character 14 of Swierczewski & Raikow (1981).
97. Iliofemoralis internus: present (0); absent (1). Character 20 of Swierczewski & Raikow (1981).
98. Iliotibialis lateralis, acetabular part: fleshy (0); apneurotic (1); absent (2). This character combines characters 30 and 31 of Maurer & Raikow (1981).
99. Iliotrochantericus caudalis, origin: dorsal iliac crest (0); spinal crest of synsacrum (1). Character 32 of Maurer & Raikow (1981).
100. Flexor cruris lateralis pars accesoria femoralis: present (0); absent (1). Character 33 of Maurer & Raikow (1981).
101. Pubo-ischio-femoralis, pars medialis: undivided (0); divided (1). Character 35 of Maurer & Raikow (1981).
102. Pubo-ischio-femoralis: bellies separate (0); fused (1). Character 36 of Maurer & Raikow (1981).
103. Obturatorius lateralis pars dorsalis: present (0); absent (1). Character 37 of Maurer & Raikow (1981).
104. Obturatorius medialis: oval (0); triangular (1). Character 38 of Maurer & Raikow (1981).
105. Gastrocnemius pars medialis: single head (0); two heads (1). Character 39 of Maurer & Raikow (1981).
106. Gastrocnemius pars medialis: origin from medial surface of tibiotarsus (0); origin from posterior surface of tibiotarsus (1). Character 40 of Maurer & Raikow (1981).
107. Fibularis longus: present (0); absent (1). Character 42 of Maurer & Raikow (1981).
108. Fibularis longus, long branch, connecting to flexor perforatus digiti III tendon: present (0); absent (1). Character 41 of Maurer & Raikow (1981). This character is coded '?' in taxa lacking fibularis longus.
109. Fibularis brevis, tibiotarsal ligament: present (0); absent (1). Character 25 of Swierczewski & Raikow (1981).
110. Plantaris: present (0); absent (1). Maurer & Raikow (1981) coded this muscle as absent in Meropidae. However, McKittrick (1993) observed that in the lateral head of gastrocnemius, pars

- medialis may be fused to the plantaris in *Merops albicollis*. Given uncertainty of the homology of the plantaris in Meropidae, we code this taxon '?' for this character.
111. Plantaris, belly: short (0); long (1). Character 32 of Swierczewski & Raikow (1981).
 112. Popletius: present (0); absent (1). Character 43 of Maurer & Raikow (1981).
 113. Extensor digitorum longus tendon, first bifurcation: distal (0); proximal (1). Character 21 of Swierczewski & Raikow (1981).
 114. Extensor digitorum longus, tendinous slip to digit IV: absent (0); present (1). Character 22 of Swierczewski & Raikow (1981).
 115. Flexor perforatus digiti II, tendon: perforated by flexor perforans et perforatus digiti II and flexor hallucis longus tendons (0); not perforated (1). Character 26 of Swierczewski & Raikow (1981).
 116. Flexor perforatus digiti II: present (0); absent (1). Character 27 of Swierczewski & Raikow (1981).
 117. Flexor perforans et perforatus digiti II tendon perforated by flexor hallucis longus tendon: perforated (0); not perforated (1). Character 28 of Swierczewski & Raikow (1981). Maurer & Raikow (1981) and McKittrick (1993) reported different states of this character for *Galbula ruficauda*. Given the possibility that this represents either an error or intraspecific variation, we code this taxon '?' for present.
 118. Flexor perforatus digiti III: two tendons of origin (0); one tendon of origin (1). Character 30 of Swierczewski & Raikow (1981).
 119. Extensor brevis digiti III: present (0); absent (1). Character 49 of Maurer & Raikow (1981).
 120. Extensor brevis digiti IV: present (0); absent (1). Character 50 of Maurer & Raikow (1981).
 121. Abductor digiti II: present (0); absent (1). Character 47 of Maurer & Raikow (1981).
 122. Adductor digiti II: present (0); absent (1). Character 48 of Maurer & Raikow (1981).
 123. Abductor digiti IV: present (0); absent (1). Character 51 of Maurer & Raikow (1981).
 124. Vinculum of flexor perforatus digiti III and IV: absent (0); present (1). Character 52 of Swierczewski & Raikow (1981).
 125. Flexor hallucis brevis, tendon insertion: single (0); bifurcate (1). Character 37 of Swierczewski & Raikow (1981).
 126. Abductor digiti IV, retinaculum on trochlea IV: absent (0); present (1). Character 42 of Swierczewski & Raikow (1981).
 127. Deep plantar tendons, type (after George & Berger, 1966): type V (0); type VI (1); type VIII (2).
 128. Flexor hallucis longus: arises by one or two heads (0); arises by three heads (1).
 129. Flexor hallucis longus: supplies hallux (0); tendon excluded from hallux (1). Character 56 of Maurer & Raikow (1981).
 130. Wing feathering: diastataxic (0); eutaxic (1). Scorings are based on Stephan (1970) and Bostwick & Brady (2002).
 131. Rectrices highly stiffened: absent (0); present (1). Character 48 of Swierczewski & Raikow (1981).
 132. Central rectrices with racquet-shaped tips: absent (0); present (1).
 133. Uropygial gland: naked or minutely tufted (0); tufted (1). Scorings are based on Johnston (1988).

APPENDIX 4
MORPHOLOGICAL CHARACTER MATRIX

Multistate characters reflect polymorphism; ? denotes missing data.

Taxa	1	10	20	30	40	50	59	
<i>Caprimulgus vociferus</i>	1	0 0 0 0 0 0 0 0	0	0 0 0 0 0 1? 0 1	0	0 0 1 0 1 0 0 0 0 0	0	0 0 0 0 0 0 0 1 1
<i>Megalaima virens</i>	0	0 1 0 0 1 0 0 0	0	0? ? 1 1 0 0 0 0	1	1 0 0 1 0 0 0 1 0	0	0 0 0 0 1 0 0 1
<i>Megalaima zeylanica</i>	0	0 1 0 0 1 0 0 0	1	0 0 0 0 1 1 0 1 0	0	1 0 0 1 0 0 0 1 0	0	0 0 0 0 1 0 0 1
<i>Pteroglossus castanotis</i>	?	2 0 0 0 1? 1 0	?	0 0 0 0 0 1? 1 0	2	1 0 0 1 1 2 0 1 0?	?	0 0 0 0 1 0 0 1
<i>Pteroglossus torquatus</i>	?	2 0 0 0 1? 1 0	?	0 0 0 0 0 1? 1 0	2	1 0 0 1 1 2 0 1 0?	?	0 0 0 0 1 0 0 1
<i>Tadus angustirostris</i>	1	0 0 0 1 0 1 0 1	0	1 0 0 0 0 1 1 1	2	1 0 0 1 0 0 0 1 0	0	0 0 0 1 0 0 0 1
<i>Tadus subulatus</i>	1	0 0 0 1 0 1 0 1	0	1 0 0 0 0 1 1 1	2	1 0 0 1 0 0 0 1 0	0	0 0 0 1 0 0 0 1
<i>Galbula cyaneescens</i>	0	0 0 0 0 1 0 0 1	1	0 0 0 1 1 0 1 0	1	0 0 1 0 0 0 1 0	1	0 0 0 1 0 0 0 1
<i>Galbula ruficauda</i>	0	0 0 0 0 1 0 0 1	1	0 0 0 1 1 0 1 0	1	0 0 1 0 0 0 1 0	1	0 0 0 1 0 0 0 1
<i>Paracoracias occidentalis</i>	1	1 0 0 0 1 0 0 1	1	0 0 0 0 2 0 1 1 0	0	0 0 0 0 0 0 0 0 0	?	0 0 0 0 0 0 0 0
<i>Geranopterus alatus</i>	?	0? ? ? ? ? ? ?	?	? ? ? ? ? ? ? ?	?	1 0 0 0 ? ? ? ? ?	?	0? ? ? ? ? ? ?
<i>Eocoracias brachyptera</i>	?	0? ? ? ? ? ? ?	?	? ? ? ? ? ? ? ?	?	? ? ? ? ? ? ? ?	?	0 0 0 0 ? ? ? ?
<i>Primobucco perneri</i>	1	0? ? ? ? ? ? ?	1	0 0 0 0 0 1 0 0	0	0 0 0 0 0 0 0 0 0	?	0 0 0 0 0 0 0 0
<i>Primobucco mcgruei</i>	1	0? ? ? ? ? ? ?	1	0 0 0 0 0 1 0 0	0	0 0 0 0 0 0 0 0 0	?	0 0 0 0 0 0 0 0
<i>Primobucco fragilegus</i>	1	0? ? ? ? ? ? ?	1	0 0 0 0 0 1 0 0	0	0 0 0 0 0 0 0 0 0	?	0 0 0 0 0 0 0 0
<i>Eurystomus glaucurus</i>	1	1? 0 0 1 1 0 0	1	1 0 1 0 2 1 1 0 0	0	0 0 0 0 0 0 0 1 0	0	0 0 0 0 0 0 0 1
<i>Eurystomus orientalis</i>	1	1 0 0 0 1 0 0 1	1	1 0 1 0 2 0 0 1 0 0	0	0 0 0 0 1 1 1 0 0	0	0 0 0 0 0 0 0 1
<i>Coracias caudata</i>	1	1 1 0 0 1 1 0 0	1	1 0 1 0 2 1 1 0 0	1	0 0 0 0 1 1 1 0 1	0	0 0 0 0 0 0 0 1
<i>Coracias garrulus</i>	1	1 1 0 0 1 1 0 0	1	1 0 1 0 2 1 1 0 0	1	0 0 0 0 1 1 1 0 1	0	0 0 0 0 0 0 0 1
<i>Uratelornis chimacra</i>	?	1 1 0 0 0 1 0 0	1	1 0 0 0 2 1 1 0 0	?	0 0 0 0 1 1 1 0 1	0	0 0 0 0 0 0 0 1
<i>Brachypteryx leptosomus</i>	1	1 1 0 0 0 1 0 0	1	1 0 0 0 2 1 1 1 0	1	0 0 0 0 1 1 1 0 1	0	0 0 0 0 0 0 0 1
<i>Atelornis crossleyi</i>	1	1 1 0 0 0 1 0 0	1	1 0 0 0 2 1 1 1 0	1	0 0 0 0 1 1 1 0 1	0	0 0 0 0 0 0 0 1
<i>Atelornis pittoides</i>	1	1 1 0 0 0 1 0 0	1	1 0 0 0 2 1 1 1 0	1	0 0 0 0 1 1 1 0 1	0	0 0 0 0 0 0 0 1
<i>Merops apiaster</i>	0	0 1 0 0 0 0 0 0	0	0 0 0 0 0 0 0 1	2	0 0 0 0 1 1 0 0 0	0	0 0 0 0 0 0 0 1
<i>Merops viridis</i>	0	0 1 0 0 0 0 0 0	0	0 0 0 0 0 0 0 1	2	0 0 0 0 1 1 0 0 0	0	0 0 0 0 0 0 0 1
<i>Eumomota superciliosa</i>	1	0 0 0 0 0 0 0 1	?	? ? ? 0 1 0 1 1	2	1 0 0 0 1 1 0 0 0	0	0 0 0 0 0 0 0 1
<i>Momotus momota</i>	0	0 0 0 0 0 1 0 1	?	? ? ? 0 1 0 1 1	2	1 0 0 0 1 1 0 0 0	0	0 0 0 0 0 0 0 1
<i>Baryphthengus ruficapillus</i>	0	0 0 0 0 0 1 0 1	?	? ? ? 0 1 0 1 1	2	1 0 0 0 1 1 0 0 0	0	0 0 0 0 0 0 0 1
<i>Megaceryle alcyon</i>	0	0 1 1 0 0 1 0 0	1	1 0 1 0 0 0 0 1	2	0 0 0 0 1 1 0 0 0	0	0 0 0 0 0 0 0 1
<i>Alcedo athys</i>	0	0 1 1 0 0 1 0 0	1	1 0 1 0 0 0 0 1	2	0 0 0 0 1 1 0 0 0	0	0 0 0 0 0 0 0 1
<i>Halycon sancta</i>	0	0 1 1 0 0 1 0 0	1	1 0 1 0 1 0 1 0	2	0 0 0 0 1 1 0 0 0	0	0 0 0 0 0 0 0 1
<i>Dacelo guadichaud</i>	0	0 1 1 0 0 1 0 0	1	1 0 2 0 1 0 1 0	2	0 0 0 0 1 1 0 0 0	0	0 0 0 0 0 0 0 1
<i>Chloroceryle americana</i>	0	0 1 1 0 0 1 0 0	1	1 0 1 0 0 0 0 0	2	0 0 0 0 1 1 1 0 0	0	0 0 0 0 0 0 0 1
<i>Upupa epops</i>	1	0 0 1 0 1 1 0 0	?	? ? ? 1 0 0 0 0	2	0 0 0 0 0 2 0 1 0	1	0 1 1 0 1 1 0 1
<i>Phoeniculus porphyreus</i>	1	0 0 1 0 1 1 0 0	?	? ? ? 1 0 0 0 0	2	0 0 0 0 0 2 0 1 0	1	0 1 1 0 1 1 0 1
<i>Bucconus abyssinicus</i>	?	? 0 0 0 ? 1 ? 0	0	0 ? ? 1 1 0 1 1 0	2	0 0 1 0 0 1 0 1 0	1	0 0 0 0 0 0 0 0
<i>Toxechus erythrorhynchus</i>	?	? 0 0 0 ? 1 ? 0	0	0 ? ? 1 1 0 1 1 0	2	0 0 1 0 ? 1 ? 1 0	1	0 ? ? ? ? 0 0 ? ?
<i>Aceros undulatus</i>	?	? 0 0 0 1 ? 0	0	0 ? ? 1 1 0 1 1 0	1	0 1 0 0 0 1 1 0	1	0 0 0 0 0 0 0 1
<i>Sennormis rhamphastinus</i>	?	2 1 0 0 1 ? 0	?	? ? ? 1 0 0 1 1 0	1	0 0 0 0 1 1 ? 1 0	0	0 1 0 0 0 1 0 0
<i>Aulacorhynchus prasinus</i>	?	2 1 0 0 1 ? 0	?	? ? ? 1 1 0 1 1 0	2	1 1 0 1 0 0 0 1 0	0	0 1 0 0 1 0 0 1
<i>Picumnus cirratus</i>	1	0 0 0 0 0 0 0 0	?	? ? ? 1 1 0 ? 0 0	1	0 0 0 0 ? ? ? ? 0	0	0 0 0 0 1 0 0 1
<i>Picoides villosus</i>	0	0 0 0 0 0 0 0 0	?	? ? ? 1 1 0 1 0 0	1	? 1 0 1 1 1 0 1 0	0	0 0 0 1 1 0 0 1
<i>Campephilus magellanicus</i>	0	0 0 0 0 0 0 0 0	0	0 1 ? 1 1 0 1 0 0	1	1 0 0 0 0 1 ? 1 0	0	0 0 0 1 0 0 1 0
<i>Jacamerops aurea</i>	0	0 1 0 0 0 1 0 0	0	0 1 ? 1 1 0 1 1 0	2	1 1 0 1 0 0 0 1 0	0	0 0 0 1 1 1 0 1
<i>Pharomachus mocino</i>	0	0 0 0 1 0 1 0 0	0	0 0 0 0 0 0 2 1 1	0	0 0 0 0 0 1 0 1 0	0	0 1 0 0 0 0 0 1
<i>Harpactes erythrocephalus</i>	0	0 0 0 1 0 1 0 0	0	0 0 0 0 0 0 2 1 1	0	0 1 0 0 1 1 2 0 1	0	0 1 0 0 0 0 0 1
<i>Cheiloptera tenebrosa</i>	1	1 0 0 0 1 1 0 0	1	0 0 0 1 2 0 1 0 0	1	0 1 0 0 1 1 0 1 2	1	0 0 0 0 1 1 1 0
<i>Nystalus maculatus</i>	1	1 1 0 0 0 1 0 0	1	0 0 1 1 2 0 1 0 0	1	0 1 0 0 1 1 1 ? 1 2	0	0 0 0 0 1 1 1 0
<i>Malacoptila fusca</i>	1	1 0 0 0 1 1 1 0 0	1	0 0 0 1 2 1 1 0 0	1	1 0 0 0 1 1 1 ? 1 2	1	0 0 0 0 1 1 0 1

Taxa	60	70	80	90	100	110	120	130	
<i>Caprimulgus vociferus</i>	0	0 0 0 0 0 1 0 1 0 0	?	?	?	?	?	?	0 0 0 ? ? ? 0 0 0 0
<i>Megalania virens</i>	0	1 1 0 0 0 1 0 1 2 0	0	?	?	?	?	?	?
<i>Megalania zeylanica</i>	0	1 1 0 0 0 1 0 1 2 0	0	?	?	?	?	?	?
<i>Pteroglossus castanotis</i>	0	1 1 0 0 0 1 0 1 2 0	0	?	?	?	?	?	?
<i>Pteroglossus torquatus</i>	0	1 1 0 0 0 1 0 1 2 0	0	?	?	?	?	?	?
<i>Todius angustirostris</i>	0	0 0 0 ? 0 1 0 1 0 1	1	0 0 0 1 0 0 2 1 1 0	0 2 2 2 1 2 0 1 2 0	?	?	?	?
<i>Todius subulatus</i>	0	0 0 0 0 0 1 0 1 0 1	1	0 0 0 0 0 0 0 0 0 0	?	?	?	?	?
<i>Galbula cyanescens</i>	0	0 0 0 0 0 1 1 1 1 0	0	?	?	?	?	?	?
<i>Galbula ruficauda</i>	?	0 2 2 2 0 2 2 2 0 1	?	?	?	?	?	?	?
<i>Paracoracias occidentalis</i>	?	?	?	?	?	?	?	?	?
<i>Geranopterus alatus</i>	?	?	?	?	?	?	?	?	?
<i>Ecocoracias brachyptera</i>	?	0 2 2 2 0 1 0 0 0 1	?	?	?	?	?	?	?
<i>Primobucco perneri</i>	?	0 2 2 2 0 1 2 2 2 1	?	?	?	?	?	?	?
<i>Primobucco mcgrewi</i>	?	0 2 2 2 0 1 2 2 2 1	?	?	?	?	?	?	?
<i>Primobucco frugilegus</i>	?	?	?	?	?	?	?	?	?
<i>Eurystomus glaucurus</i>	0	0 0 0 0 0 1 1 0 0 1	0	?	?	?	?	?	?
<i>Eurystomus orientalis</i>	0	0 0 0 0 0 1 1 0 0 1	0	?	?	?	?	?	?
<i>Coracias caudata</i>	0	0 0 0 0 0 1 1 0 0 1	0	?	?	?	?	?	?
<i>Coracias garrulus</i>	0	0 0 0 0 0 1 1 0 0 1	0	?	?	?	?	?	?
<i>Uratelornis chimæra</i>	0	1 0 0 0 0 1 1 0 0 1	0	?	?	?	?	?	?
<i>Brachyptera ca? leptosomus</i>	0	1 0 0 0 0 1 1 0 0 1	0	?	?	?	?	?	?
<i>Aetolnis crossleyi</i>	0	1 0 0 0 0 1 1 0 0 1	0	?	?	?	?	?	?
<i>Aetolnis pittoides</i>	0	1 0 0 0 0 1 1 0 0 1	0	?	?	?	?	?	?
<i>Merops apiastr</i>	0	0 0 0 0 0 1 0 1 0 1	1	0 0 0 0 0 0 0 0 0 0	0 2 2 2 0 0 0 1 0 0 1	?	?	?	
<i>Merops viridis</i>	0	0 0 0 0 0 1 0 1 0 1	1	0 0 0 0 0 0 0 0 0 0	?	?	?	?	
<i>Eumomota superciliosa</i>	0	0 0 0 0 0 1 0 1 0 1	1	0 0 0 0 0 0 0 0 0 0	?	?	?	?	
<i>Momota momota</i>	0	0 0 0 0 0 1 0 1 0 1	1	0 0 0 0 0 0 0 0 0 0	?	?	?	?	
<i>Berypterus ca? ruficapillus</i>	0	0 0 0 0 0 1 0 1 0 1	1	0 0 0 0 0 0 0 0 0 0	?	?	?	?	
<i>Megaceryle alcyon</i>	0	0 0 0 0 0 1 1 1 0 1	1	0 0 0 0 0 0 0 0 0 0	?	?	?	?	
<i>Alcedo atthis</i>	0	0 0 0 0 0 1 1 1 0 1	1	0 0 0 0 0 0 0 0 0 0	?	?	?	?	
<i>Halycon sancta</i>	0	0 0 0 0 0 1 1 1 0 1	1	0 0 0 0 0 0 0 0 0 0	?	?	?	?	
<i>Dacelo guadichaud</i>	0	0 0 0 0 0 1 1 1 0 1	1	0 0 0 0 0 0 0 0 0 0	?	?	?	?	
<i>Chloroceryle americana</i>	1	0 0 0 0 0 1 1 1 0 1	1	0 0 0 0 0 0 0 0 0 0	?	?	?	?	
<i>Upupa epops</i>	1	0 0 0 0 0 1 1 1 0 1	1	0 0 0 0 0 0 0 0 0 0	?	?	?	?	
<i>Phoeniculus purpureus</i>	0	0 0 1 0 0 1 0 1 0 1	1	0 0 0 0 0 0 0 0 0 0	?	?	?	?	
<i>Bucconus abyssinicus</i>	0	0 0 1 0 0 1 0 1 0 1	1	0 0 0 0 0 0 0 0 0 0	?	?	?	?	
<i>Tokus erythrorhynchus</i>	0	0 0 1 0 0 1 0 1 0 1	1	0 0 0 0 0 0 0 0 0 0	?	?	?	?	
<i>Aceros undulatus</i>	0	0 0 1 0 0 1 0 1 0 1	1	0 0 0 0 0 0 0 0 0 0	?	?	?	?	
<i>Sennornis rhamphastinus</i>	0	0 1 0 1 1 0 1 0 1 2	0	?	?	?	?	?	?
<i>Autacorhynchus prasinus</i>	0	0 1 0 0 0 1 0 1 2 0	0	?	?	?	?	?	?
<i>Picaeides villosus</i>	0	0 1 0 1 0 0 0 1 2 0	0	?	?	?	?	?	?
<i>Campophilus megalanicus</i>	0	0 1 0 1 0 0 0 1 2 0	0	?	?	?	?	?	?
<i>Jacomerope aurea</i>	1	0 0 0 ? 0 0 1 0 1 1 0	0	?	?	?	?	?	?
<i>Pharomachus macino</i>	0	0 0 1 0 0 0 0 1 0 0	0	?	?	?	?	?	?
<i>Harpactes erythrocephalus</i>	0	0 0 1 0 0 0 0 1 0 0	0	?	?	?	?	?	?
<i>Chelidoptera tenebrosa</i>	0	1 0 0 0 0 1 0 1 1 0	0	?	?	?	?	?	?
<i>Nyctalus maculatus</i>	0	0 0 0 ? 0 1 0 1 1 0	0	?	?	?	?	?	?
<i>Malacoptila fusca</i>	0	1 0 0 ? 0 1 0 1 1 0	0	?	?	?	?	?	?