A *Fluvioviridavis*-like bird from the Middle Eocene of Messel, Germany

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Abstract: A new avian taxon is described from the Middle Eocene of Messel in Germany. This bird closely resembles the Lower Eocene North American *Fluvioviridavis platyrhamphus* Mayr and Daniels, 2001. *Eurofluvioviridavis robustipes* n. gen. et sp. and *F. platyrhamphus* are classified in the new taxon **Fluvioviridavidae**. These birds exhibit a bauplan that is unknown among modern birds in combining a flycatcher-like beak with greatly abbreviated legs. *Eurofluvioviridavis* is distinguished from *Fluvioviridavis* by its much stronger toes, indicating that the new Messel species occupied a different ecological niche from its North American relative and that the Fluvioviridavidae were an ecologically diversified group in the Eocene. Despite their morphological distinctness, however, the phylogenetic affinities of the Fluvioviridavidae are still uncertain. Their phylogenetic affinities are evaluated in a cladistic analysis of 96 morphological characters, but the resulting position basal to a cluster of several modern higher level taxa is only weakly supported.

Résumé : La description est présentée d'un nouveau taxon avien de l'Éocène moyen de Messel, en Allemagne, qui ressemble de très près à *Fluvioviridavis platyrhamphus* (Mayr et Daniels 2001), de l'Éocène inférieur de l'Amérique du Nord. *Eurofluvioviridavis robustipes* gen. et sp. nov. et *F. platyrhamphus* sont affectés au nouveau taxon des **Fluvioviridavidae**. Ces oiseaux montrent un plan de construction inconnu chez les oiseaux modernes en cela qu'il allie un bec de type moucherolle à des pattes très écourtées. *Eurofluvioviridavis* se distingue de *Fluvioviridavis* par ses doigts de patte beaucoup plus forts, ce qui indique que la nouvelle espèce de Messel occupait une niche écologique différente de celle de son parent nord-américain et que les Fluvioviridavidae constituaient un groupe varié sur le plan écologique durant l'Éocène. Toutefois, en dépit de ces différences morphologiques, les affinités phylogénétiques des Fluvioviridavidae demeurent incertaines. Ces dernières ont été évaluées à l'aide de l'analyse cladistique de 96 caractères morphologiques, mais les assises de l'interprétation qui en découle de leur position basale par rapport à plusieurs taxons modernes de plus haut niveau sont faibles.

[Traduit par la Rédaction]

Introduction

The Early Eocene avian species *Fluvioviridavis platyrhamphus* was described from the North American Green River Formation by Mayr and Daniels (2001). It is a short-legged bird about the size of a roller (Coraciidae), which exhibits a fairly wide, tyrant flycatcher-like beak (Fig. 1). The original description of *F. platyrhamphus* was based on a single skeleton on a slab, but Mayr and Daniels (2001) also tentatively referred to *Fluvioviridavis* an isolated skull from the Middle Eocene of Messel in Germany (Fig. 2) and three-dimensionally preserved bones from the Lower Eocene London Clay in England. Subsequently, however, the Messel skull was connected with the enigmatic Eocene *Palaeopsittacus* Harrison, 1982 by Mayr (2003), who identified a postcranial skeleton of this taxon from Messel and noted similarities to *Fluvioviridavis*.

Olson (1985, p. 126) considered the holotype of *Fluvioviridavis* to be similar to modern rollers (Coraciidae) but later assigned it to the putative oilbird (Steatornithidae) *Prefica nivea* (Olson 1987). However, Mayr and Daniels (2001) showed that *Fluvioviridavis* does not belong to *Prefica* and classified it Aves incertae sedis, noting similarities to the paraphyletic (Mayr 2002a; Mayr et al. 2003) "Caprimulgiformes" (nightjars and allies).

The morphologically similar (Mayr 2003) *Palaeopsittacus* was originally described as a parrot by Harrison (1982), but this assignment is not supported by the more completely preserved remains described by Mayr and Daniels (1998) and Mayr (2003).

Here I describe a well-preserved skeleton of the above-mentioned *Fluvioviridavis*-like bird from Messel, which belongs to a new taxon and displays previously unknown features of these birds. The new specimen confirms original assignment of the isolated skull described by Mayr and Daniels (2001) (pro Mayr and Daniels 2001, contra Mayr 2003). It is shown that *Fluvioviridavis* and the new Messel species belong to a previously unrecognized taxon of widespread Paleogene birds, the phylogenetic affinities of which are for the first time evaluated in a cladistic analysis.

Material and methods

Osteological terminology follows Baumel and Witmer (1993). The fossil specimens are deposited in Forschungsinstitut Senckenberg, Frankfurt am Main, Germany (SMF) and

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Fig. 1. *Fluvioviridavis platyrhamphus*, holotype (SMNK.PAL.2368a) from the Lower Eocene Green River Formation, Wyoming, USA. Scale bar = 10 mm.


Staatliches Museum für Naturkunde Karlsruhe, Germany (SMNK).

Ninety-six characters for 35 ingroup taxa (see character matrix in Appendix B, Table B1) were coded for a phylogenetic analysis with PAUP 3.1 (Swofford 1993). The character matrix is based on the revised and emended matrix of Mayr et al. (2003). The most parsimonious trees were found with the heuristic search option. Two characters (69 and 75 in Appendix A) were coded as "ordered," the consistency index (CI), retention index (RI), and rescaled consistency index (RC) were calculated. The robustness of the resulting trees was evaluated with a bootstrap analysis of 100 replicates.

Fluvioviridavis and the new taxon from Messel share derived similarities only with taxa of the "land bird assemblage" sensu Olson (1985), and selection of the ingroup rep-

Fig. 2. *Eurofluvioviridavis robustipes* n. gen. et sp., isolated skull from the type locality (SMF-ME 10783a + 10783b) in ventral ((A) SMF-ME 10783a) and dorsal ((B) SMF-ME 10783b) view. ?ax, ?axis; ent, os entoglossum; iof, interorbital section of os frontale; lar, larynx and tracheal rings; man, mandible; nar, narial opening; pal, processus maxillaris of palatinum; pt, pterygoid; qu, quadratum. Coated with ammonium chloride to enhance contrast. Scale bar = 10 mm.
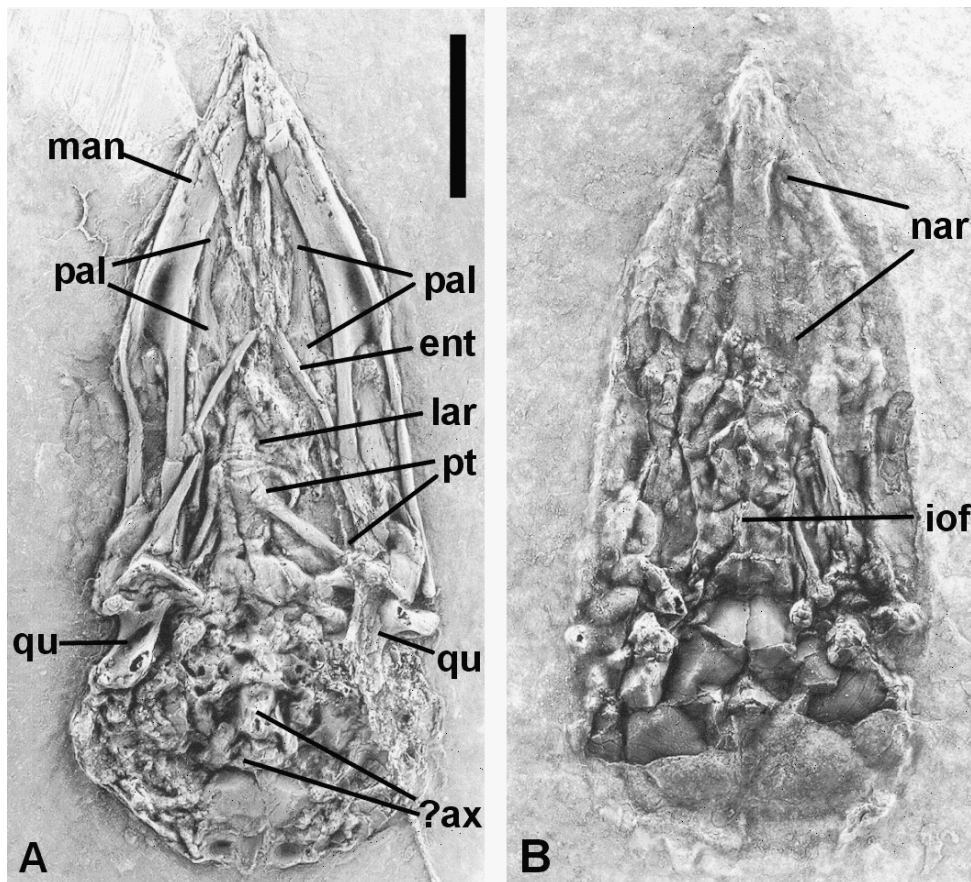
resentatives is thus focused on members of this group. The character matrix of Mayr et al. (2003) has been expanded by Sagittariidae (secretary bird) and Cathartidae (New World vultures). In addition, stem group representatives of Psittaciformes (parrots) and Coliiformes (mousebirds) were included that display a more plesiomorphic morphology than the crown group taxa, as well as the Early Eocene *Palaeopsittacus* (see Introduction).

Coding of the extant taxa is based on skeletons in the collection of SMF. The psittaciform Quercypsittidae and Pseudasturidae were coded after Mourer-Chauviré (1992) and Mayr (1998, 2002*b*) respectively, Sandcoleidae after Houde and Olson (1992), Mayr (2000*a*), and Mayr and Peters (1998), and *Palaeopsittacus* after Harrison (1982) and Mayr (2003).

Outgroup comparisons were made with the palaeognathous Tinamidae (tinamous) and with Anseriformes (waterfowl), one of the most basal lineages of neognathous birds (e.g., Sibley and Ahlquist 1990; Mayr and Clarke 2003; Fain and Houde 2004).

Systematic paleontology

Aves Linnaeus, 1758

Fluvioviridavidae n. fam.

TYPE GENUS: *Fluvioviridavis* Mayr and Daniels, 2001.

INCLUDED GENERA: *Eurofluvioviridavis* n. gen.

DIAGNOSIS: Characterized by the combination of the following characters: (1) beak wide and flattened, of similar shape to that of some extant tyrant flycatchers; (2) sternum with four shallow notches; (3) coracoid with concave cotyla scapularis, (4) foramen nervi supracoracoidei present; (5) crista deltopectoralis of humerus with concave caudal surface; (6) tarsometatarsus short (< 2/3 of length of carpometacarpus) and without crista medianoplantaris, (7) trochlea metatarsi III reaching farther distally than other trochleae metatarsorum, trochleae metatarsorum II et IV plantarly deflected, and and tr. mt. IV bearing a plantarly directing wing-like flange; (8) hallux long (first phalanx longer than first phalanx of third toe). I consider characters (1) and (8) to be autapomorphies of the Fluvioviridavidae n. fam.

Eurofluvioviridavis n. gen.

TYPE SPECIES: *Eurofluvioviridavis robustipes* n. sp., by monotypy.

DIAGNOSIS: Characterized by the unusually strong legs, which have the proximal phalanges of all three anterior toes abbreviated and robust claws that lack a sulcus neurovascularis. Differs from *Fluvioviridavis* Mayr and Daniels, 2001 in a

Table 1. Maximum length of the skull and major limb bones (left/right, in mm) of *Eurofluvioviridavis robustipes* n. gen. et sp., and *Fluvioviridavis platyrhamphus* Mayr and Daniels, 2001 in comparison.

	Skull	Humerus	Ulna	Carpometacarpus	Femur	Tibiotarsus	Tarsometatarsus
Eurofluvioviridavis robustipes **n. gen. et sp.**							
SMNK.PAL.3835	~50	48.3/48.6	54.4/—	—/~25.9	—/~25	—/~29–36	~15.0/~15.4
Fluvioviridavis platyrhamphus **Mayr and Daniels 2001**[a]							
SMNK.PAL.2368a	~62	50.1/49.5	56.3/56.0	27.7/27.5	24.3/—	—/34.2	13.5/13.5

Note: Length differences between the left and right side of the skeleton are of diagenetic origin due to the preservation of the skeleton.
[a]after Mayr and Daniels (2001).

stouter but proportionally longer tarsometatarsus (15.0 mm versus 13.5 mm in the slightly larger *Fluvioviridavis*; see Table 1), and from *Palaeopsittacus* Harrison, 1982 in a stouter coracoid, phalanx digiti alulae without claw, phalanx digiti minoris proportionally smaller, stouter tarsometatarsus, hypotarsus without marked sulcus for tendon of musculus flexor perforatus digiti II.

ETYMOLOGY: The genus name refers to the European provenance of the new taxon and its morphological similarity to *Fluvioviridavis*.

Eurofluvioviridavis robustipes n. sp.

2001   ?*Fluvioviridavis* sp. Mayr and Daniels, 2001, fig. 3.

HOLOTYPE: SMNK.PAL.3835 (Figs. 3–5). There exists a counter slab of this specimen in the private collection of the late T. Burkhardt (Auchel, France) which was, however, not available for study.

DIAGNOSIS: As for genus.

TYPE LOCALITY AND HORIZON: Messel near Darmstadt, Hessen, Germany; lower Middle Eocene, MP 11 (Schaal and Ziegler 1988; Legendre and Lévêque 1997).

DIMENSIONS OF THE HOLOTYPE: pedal phalanges (in parentheses the dimensions of *Fluvioviridavis platyrhamphus*, after Mayr and Daniels 2001): dI p1, 7.6 (7.5); dI p2, 6.9 (4.8); dII p1, 4.0 (6.4); dII p2, 7.2 (5.2); dII p3, ~7.8 (4.4); dIII p1, 3.0 (7.1); dIII p2, 3.9 (5.3); dIII p3, 7.3 (6.3); dIII p4, ~8.7 (5.1); dIV p1, 2.9 (4.9); dIV p2, ~2.9 (4.0); dIV p3, 3.3 (4.4); dIV p4, 6.8 (4.4); dIV p5, ~7.4 (5.5); other measurements see Table 1.

REFERRED SPECIMEN: SMF-ME 10783a + 10783b, isolated skull from the type locality and horizon (Fig. 2).
Dimensions of the referred specimen: length of skull, 50.3; length of mandible, 35.

ETYMOLOGY: The species name is derived from robustus (Latin): strong and pes (Latin): foot, and refers to the unusually strong feet of the new taxon.

REMARKS: In the holotype, there is an accumulation of small quartz grains in the area of the stomach, which may have been ingested by the bird. The distal end of the right tibiotarsus further exhibits a distinct fracture which probably caused its death (limb bone fractures are common among Messel birds, see Mayr 2000*b*).

Description and comparison

Skull

The flattened and wide beak exhibits the characteristic shape of the beak of *Fluvioviridavis* and some extant passeriform tyrant flycatchers (Tyrannidae) as, e.g., *Tolmomyias* and *Empidonax*. It is about as long as the cranium, and of nearly constant width in its proximal half, before it gradually tapers. The narial openings (SMF-ME 10783a + 10783b) are large.

The interorbital section of the os frontale is slightly narrower than in *Fluvioviridavis*. Contrary to other taxa with a flat and wide beak, e.g., extant Podargidae (frogmouths), the processus maxillares of the palatinum are widely separated and the palate is not heavily ossified. The pterygoid (Fig. 2, SMF-ME 10783a+ 10783b) is slender and does not exhibit a facies articularis basipterygoidea, which indicates the absence of basipterygoid processes. The processus oticus of the quadratum is wide, with a shallow incisura intercapitularis; there are no pneumatic foramina along the dorsal margin of its caudal surface. The processus mandibularis quadrati (SMF-ME 10783b, left side) resembles that of modern rollers (Coraciidae).

The rami mandibulae are of equal depth over most of their length, the pars symphysialis is short, fenestrae mandibulae cannot be discerned.

In specimen SMF-ME 10783a the apparatus hyobranchialis and parts of the larynx are preserved but do not allow a meaningful comparison.

Vertebral column

Only few details of the vertebrae are discernible. The corpus of the caudalmost thoracic vertebrae is mediolaterally compressed as, e.g., in extant Falconidae (falcons) and Podargidae. Eight free caudal vertebrae can be counted, whereas there are only six or seven caudal vertebrae in *Fluvioviridavis*. The pygostyle is of similar shape to that of *Fluvioviridavis* but proportionally smaller. It is mediolaterally narrow, without a discus pygostyli, but with a craniocaudally wide lamina pygostyli and a perforated caudoventral end.

Pectoral girdle

As in *Fluvioviridavis*, the coracoid exhibits a foramen nervi supracoracoidei. The extremitas omalis is not preserved in the holotype, but in its proportions the bone otherwise is similar to that of the London Clay Fluvioviridavidae figured by Mayr and Daniels (2001, fig. 4). As in the latter, there is a shallow indentation on the medial margin of the shaft, just at the beginning of the extremitas sternalis (Fig. 4), and the

Fig. 3. *Eurofluvioviridavis robustipes* n. gen. et sp., holotype (SMNK.PAL.3835). Coated with ammonium chloride to enhance contrast. Scale bar = 10 mm.
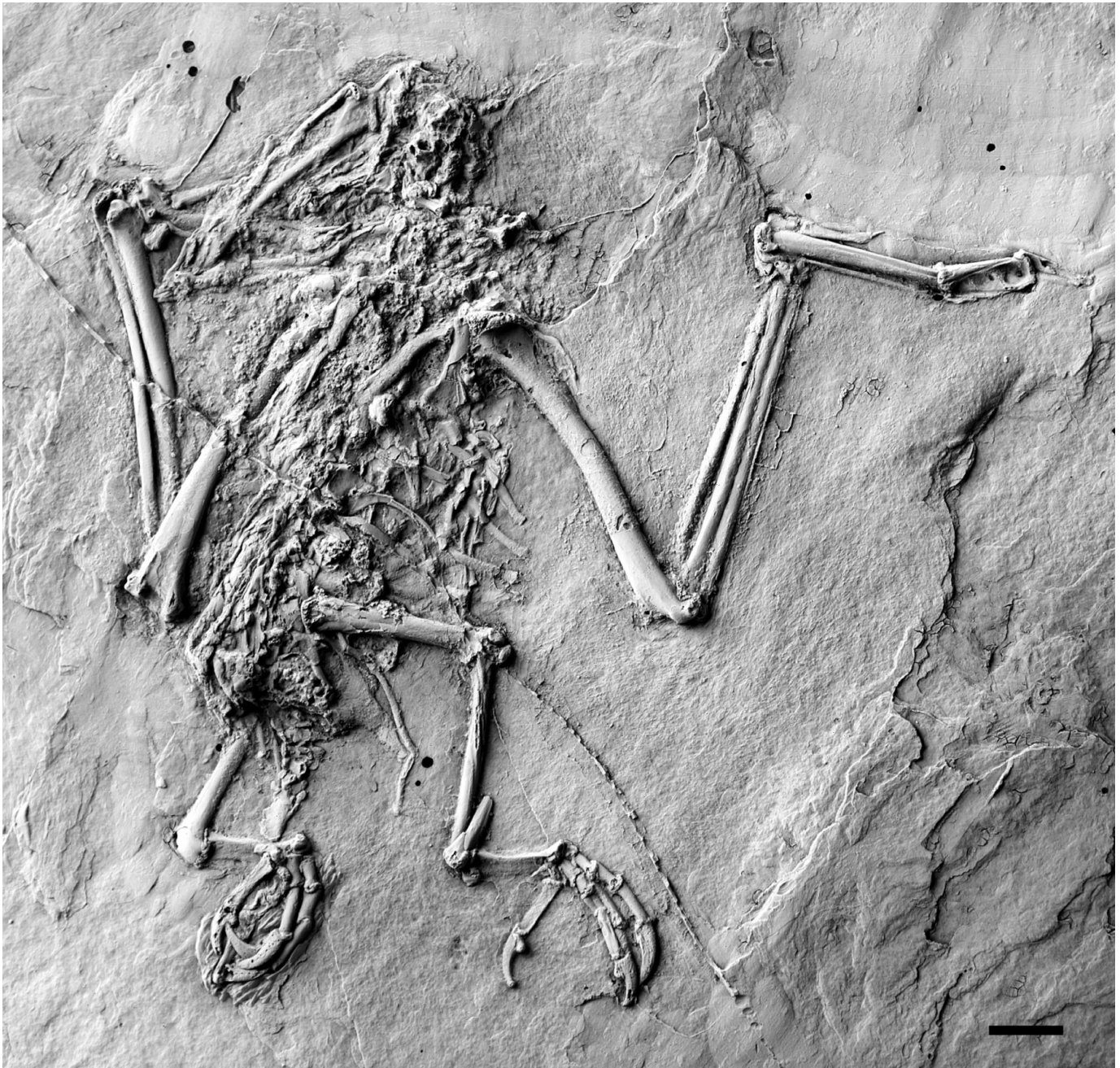
processus lateralis forms a small hook (Fig. 4). The coracoid of *Palaeopsittacus* is proportionally more elongated and exhibits a shallower facies articularis scapularis than at least *Fluvioviridavis* (Fig. 6; this part of the coracoid is unknown for *Eurofluvioviridavis*).

The corpus of the scapula is strongly angled, as in *Fluvioviridavis* and the London Clay Fluvioviridavidae. Details of the furcula and the sternum cannot be discerned in the specimen.

Humerus

The humerus corresponds well with the corresponding bone of *Fluvioviridavis* and the London Clay Fluvioviridavidae figured by Mayr and Daniels (2001). Compared with extant birds, it is similar to the humerus of some Falconidae (*Falco* spp.) in its proportions, from which it however differs in some osteological details as, e.g., the less-pronounced crista bicipitalis. The proximal end of the bone is fairly wide. The well-developed crista deltopectoralis is of similar proportions to that of modern Falconidae; as in the latter its caudal surface is concave. The shaft is curved and, also as in modern Falconidae (and several other taxa), the caudal surface of its proximal part is sharply angled. The sulcus humerotricipitalis is wide and deep, with a well-developed fossa olecrani, whereas

Fig. 4. *Eurofluvioviridavis robustipes* n. gen. et sp., holotype (SMNK.PAL.3835), right wing (A), right coracoid and proximal end of right humerus (B), and distal end of left humerus (C). cla, claw on phalanx digiti alulae; cor, coracoid; del, crista deltopectoralis; dep, depression; fns, foramen nervi supracoracoidei; hu, humerus; min, phalanx digiti minoris; no, notch; pdm, phalanx proximalis digiti majoris; pla, processus lateralis; shu, sulcus humerotricipitalis; ssc, sulcus scapulotricipitalis. Coated with ammonium chloride to enhance contrast. Scale bars = 5 mm.

the sulcus scapulotricipitalis is shallow. The epicondylus dorsalis is proximodistally low but dorsally protruding, and bears a distinct pit on its dorsal surface.

Ulna

The ulna exceeds the humerus in length. Eight papillae remigales can be counted, the total number probably was < 13, thus indicating a low number of secondaries. There is no marked depressio radialis on the distal end of the bone. The tuberculum carpale is very small, as in modern *Podargus* (Podargidae).

Carpometacarpus

The carpometacarpus is fairly long, of similar proportions to that of, e.g., extant Psittacidae and Falconidae, with a narrow spatium intermetacarpale. The fovea carpalis cranialis is well developed, the processus extensorius of average size. There

is a weakly developed projection at the insertion area of musculus extensor carpi ulnaris.

Other elements of the wing

As in *Fluvioviridavis*, the phalanx digiti alulae bears a rudimentary claw (Fig. 4). The dorsal surface of the phalanx proximalis digiti majoris exhibits a deep depression in its distal half (Fig. 4), a marked sulcus for the tendon of musculus interosseus dorsalis, and a notch on the distal end of the margo cranialis (Fig. 4) as, for example, in modern Falconidae and Podargidae. There is no processus internus indicis (terminology after Stegmann 1963), and this process is also very short in *Fluvioviridavis*. Further, as in *Fluvioviridavis*, the phalanx digiti minoris is very short.

Pelvis

The alae ischii of the pelvis are somewhat wider than in *Fluvioviridavis*. A spina dorsolateralis ilii that is well developed

Fig. 5. *Eurofluvioviridavis robustipes* n. gen. et sp., holotype (SMNK.PAL.3835), right (A) and left (B) foot in comparison to (C) the right foot of the holotype of *Fluvioviridavis platyrhamphus* (SMNK.PAL.2368a). The toes are numbered (1–4). for, foramen on caudoventral end of pygostyle; hyp, hypotarsus; omI, os metatarsale I; mtII, trochlea metatarsi II; mtIV, trochlea metatarsi IV; pyg, pygostyle. (A) and (B) coated with ammonium chloride to enhance contrast. Scale bars = 5 mm.
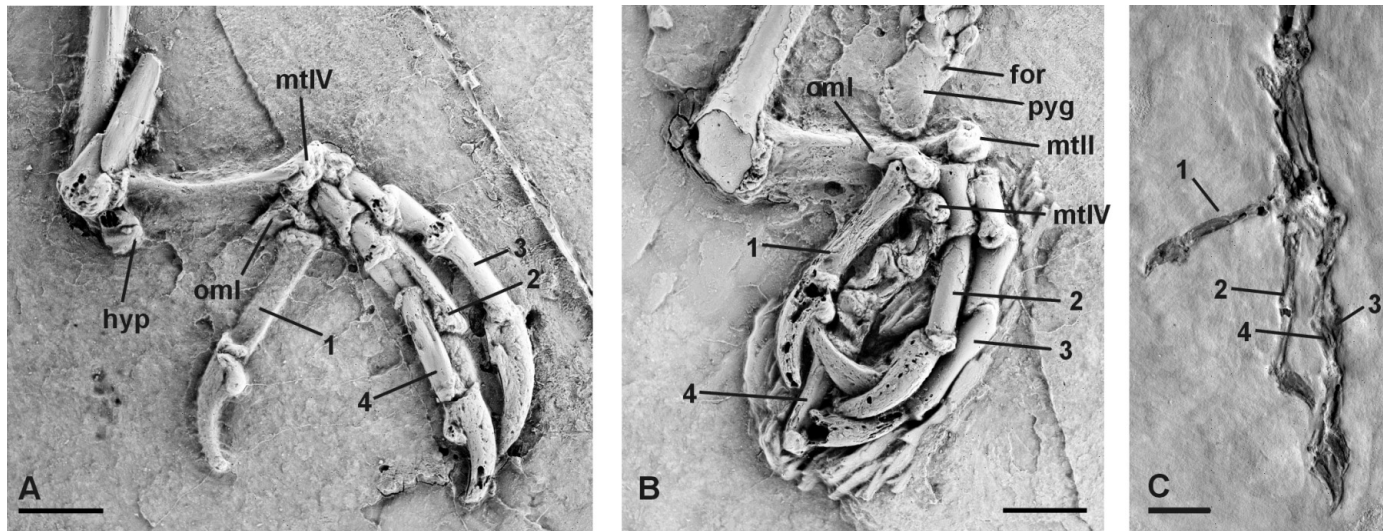
in *Fluvioviridavis* cannot be discerned in the specimen. The alae praeacetabulares ilii appear to have had a similar length to the alae postacetabulares ilii.

Femur

A meaningful description of the rather short and stout femur is not possible.

Tibiotarsus

The original length of the tibiotarsus is difficult to estimate, because the bone is fractured and the degree to which the broken ends are displaced from their original position cannot be clearly discerned. The fibula is of average length.

Tarsometatarsus

The tarsometatarsus (Fig. 5) is stouter than that of *Fluvioviridavis* and *Palaeopsittacus*, and appears to have been of similar proportions to that of the Eocene Quercypsittidae Mourer-Chauviré, 1992 (Fig. 6). Because of its great similarity to that of Podargidae, Leptosomidae (cuckoo-roller), Cuculidae (cuckoos), and Psittacidae (parrots), the hypotarsus of the new taxon most likely enclosed two canals as in these modern groups; its plantar surface exhibits two shallow sulci. Two hypotarsal canals are also present in the isolated bones of the London Clay Fluvioviridavidae figured by Mayr and Daniels (2001) (M. Daniels, personal communication, 2001). On the left tarsometatarsus, the medial foramen vasculare proximale is situated close to the margo medialis of the bone, a lateral foramen vasculare proximale appears to be absent. There is no crista medianoplantaris. The trochlea metatarsi (tr. mt.) II (Fig. 5) is unusually large, exhibits a furrow on its plantar surface, and lacks a well-developed plantarly directing projection. In its shape, it most closely resembles the tr. mt. II of the Eocene stem group Psittaciformes Quercypsittidae (Mourer-Chauviré 1992). The tr. mt. IV (Fig. 5) does not reach as far distally as the tr.

mt. III and is also shorter than the trochlea for the second toe; it bears a well developed wing–like flange.

Toes

The toes of the right foot are preserved in an anisodactyl position, whereas the fourth toe of the left foot is preserved in a semizygodactyl position (i.e., appears to have been spread laterally when embedded in the sediment), its claw directs forward and not backwards as do the claws of the second and third toe (Fig. 5). The os metatarsale I is small. The hallux is long as in *Fluvioviridavis* but the proximal phalanges of the three anterior toes are more strongly abbreviated than in the latter. The claws are further much larger and more robust, and lack a sulcus neurovascularis. The tuberculum flexorium is moderately developed, there is no pair of canals lateral and medial to it (Mayr and Clarke 2003, fig. 9F). The plantar surface of at least the claw of the third toe is flat.

Results of phylogenetic analysis

Analysis of the character matrix in Appendix B yielded 108 most parsimonious trees (Length = 324, consistency index (CI) = 0.34, retention index (RI) = 0.59, rescaled consistency index (RC) = 0.20), the consensus tree of which is shown in Fig. 7A. This analysis did not result in monophyly of the neoavian taxa included in the study (all taxa except Tinamidae and Anseriformes). Because monophyly of Neoaves, i.e., a clade including all neognathous birds, except Galloanseres, is supported by several independent studies of molecular and morphological data (e.g., Sibley and Ahlquist 1990; Livezey and Zusi 2001; Mayr and Clarke 2003; Cracraft et al. 2004; Fain and Houde 2004), a second analysis was run with a topological constraint enforced to retain a clade (Tinamidae + (Anseriformes + neoavian taxa)). This analysis resulted in 18 most parsimonious trees (Length = 326, CI = 0.33, RI = 0.58, RC = 0.19), the consensus tree of which is shown in Fig. 7B.

In both analyses, the resulting clades of modern birds

Discussion

The flycatcher-like beak and long wings of the Fluvio-viridavidae indicate an aerial way of living (Mayr and Daniels 2001), and these birds may have caught small to medium-sized insects either by sallying flights from a perch or on the wing. *Eurofluvioviridavis* differs from *Fluvioviridavis* in its strong feet which exhibit greatly abbreviated proximal phalanges and stronger claws (Fig. 5), and certainly the new taxon occupied a different ecological niche than its North American relative. As there is no modern bird that combines a flycatcher-like beak with such strong feet, it is difficult to speculate what *Eurofluvioviridavis* might have used its feet for. These may have been adapted for manipulation of prey; for a special way of locomotion, such as climbing; or for other behavioral characteristics, such as digging nest cavities, in which case it has to be assumed that the new taxon had a different breeding strategy than *Fluvioviridavis*.

In any case, the significant differences in foot morphology of the new taxon described in this study and *Fluvioviridavis* provide evidence for the presence of a previously unrecognized, ecologically diversified group of birds that appears to have been widespread in the early Eocene of the Northern Hemisphere.

Unfortunately, the higher level relationships of birds are still very poorly resolved (e.g., Mayr et al. 2003; Mayr and Clarke 2003; Cracraft et al. 2004), and it is difficult to evaluate the phylogenetic affinities of fossil taxa that do not belong to the stem lineage of a modern "order," as appears to be the case in the Fluvioviridavidae (Mayr and Daniels 2001). Accordingly, the position of Fluvioviridavidae, as resulting from the present analysis (Fig. 7), is only weakly supported.

Fluvioviridavids are distinguished from most extant "higher land birds" (sensu Olson 1985) by the presence of a claw on the digitus alulae (Fig. 4) and a coracoid with both a cup-like facies articularis scapularis and a foramen nervi supracoracoidei (Fig. 6). These features are probably plesiomorphic for neornithine (crown clade) birds, as a cup-like facies articularis scapularis and a foramen nervi supracoracoidei occur in Mesozoic non-neornithine birds, such as *Ichthyornis* (e.g., Clarke 2004), and wing claws are present in most non-neornithine birds (e.g., Chiappe and Witmer 2002). Wing claws and the previously mentioned features of the coracoid appear to have been lost independently several times within neornithine birds, and a foramen nervi supracoracoidei is, for example, present in stem group Psittaciformes (Pseudasturidae) and Coliiformes (Sandcoleidae) but absent in crown group representatives of these taxa.

The known specimens of the Fluvioviridavidae do not display derived features that would allow convincing assignment to any of the modern taxa. The most characteristic bone of *Eurofluvioviridavis* is the short and stout tarsometatarsus, which resembles that of the Eocene Quercypsittidae (Fig. 6). The latter occur in the Quercy fissure fillings and the London Clay and are known from an incomplete carpometacarpus, coracoids, distal tibiotarsi, and tarsometatarsi only (Mourer-Chauviré 1992; Mayr and Daniels 1998). Shared tarsometatarsal similarities include the shape of the large trochlea metatarsi II, as well as the presence of a wing-like flange on the trochlea metatarsi IV (Fig. 6). However, judging from the morphology of the large trochlea accessoria, quercy-

Fig. 6. Left coracoid (A–C) and left tarsometatarsus (D–F) in comparison. (A) Fluvioviridavidae indet. (after Mayr and Daniels 2001, fig. 4). (B) *Palaeopsittacus georgei* Harrison, 1982 (after Mayr 2003, fig. 1, reversed to facilitate comparison). (C) *Quercypsitta ivani* Mourer-Chauviré, 1992 (after Mourer-Chauviré 1992, pl. 2). (E) *Eurofluvioviridavis robustipes* n. gen. et sp. (holotype). (F) *Quercypsitta sudrei* Mourer-Chauviré, 1992 (after Mourer-Chauviré 1992, pl. 2). (G) *Palaeopsittacus georgei* Harrison, 1982 (after Mayr 2003, fig. 1). fas, facies articularis scapularis; fns, foramen nervi supracoracoidei; hyp, hypotarsus; mtII, trochlea metatarsi II; mtIV, trochlea metatarsi IV. Scale bars = 5 mm.
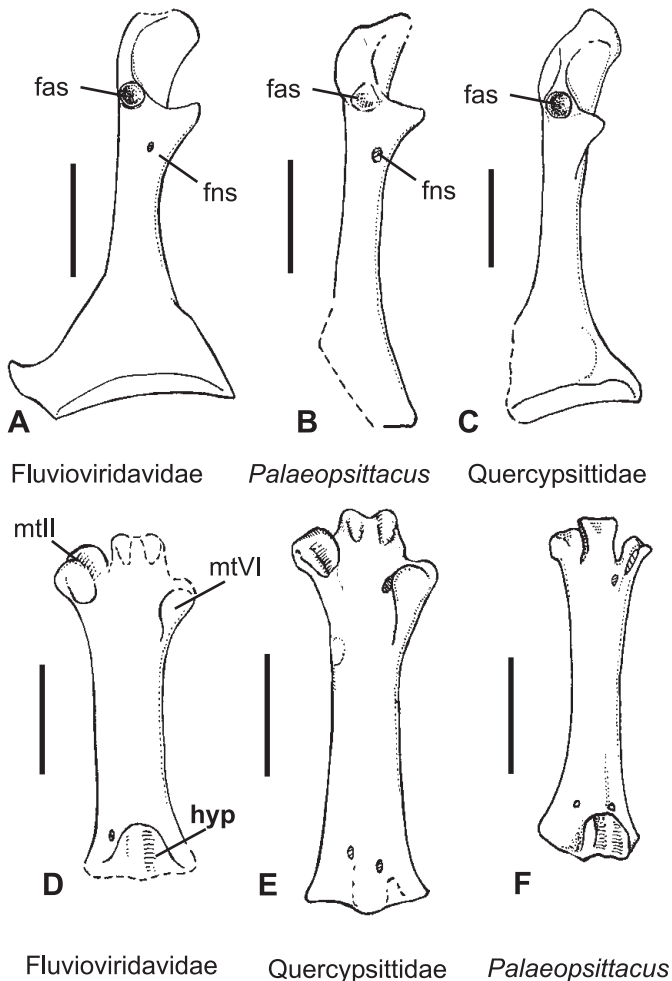
which received bootstrap support are in concordance with the morphological analysis of Mayr et al. (2003). Both analyses further supported psittaciform affinities of the extinct Quercypsittidae and Pseudasturidae, as well as sister group relationship between Coliidae and Sandcoleidae, as proposed by Mourer-Chauviré (1992), Mayr (2002b), and Mayr and Peters (1998), respectively.

The position of the Fluvioviridavidae received no bootstrap support in either of the two analyses. Whereas Fluvioviridavidae resulted as sister taxon of a large clade including various neoavian taxa in the primary search (Fig. 7A), they were placed in an unresolved polytomy in the strict consensus tree of the constrained analysis (Fig. 7B).

Fig. 7. (A) Strict consensus tree of 108 most parsimonious trees (Length = 324, CI = 0.34, RI = 0.59, RC = 0.20) resulting from the primary analysis of the character matrix in Appendix B. (B) 18 most parsimonious trees (Length = 326, CI = 0.33, RI = 0.58, RC = 0.19) resulting from a search that was constrained to trees that retained neoavian monophyly. Numbers indicate bootstrap support above 50% (100 replicates). Extinct taxa are indicated by a dagger.
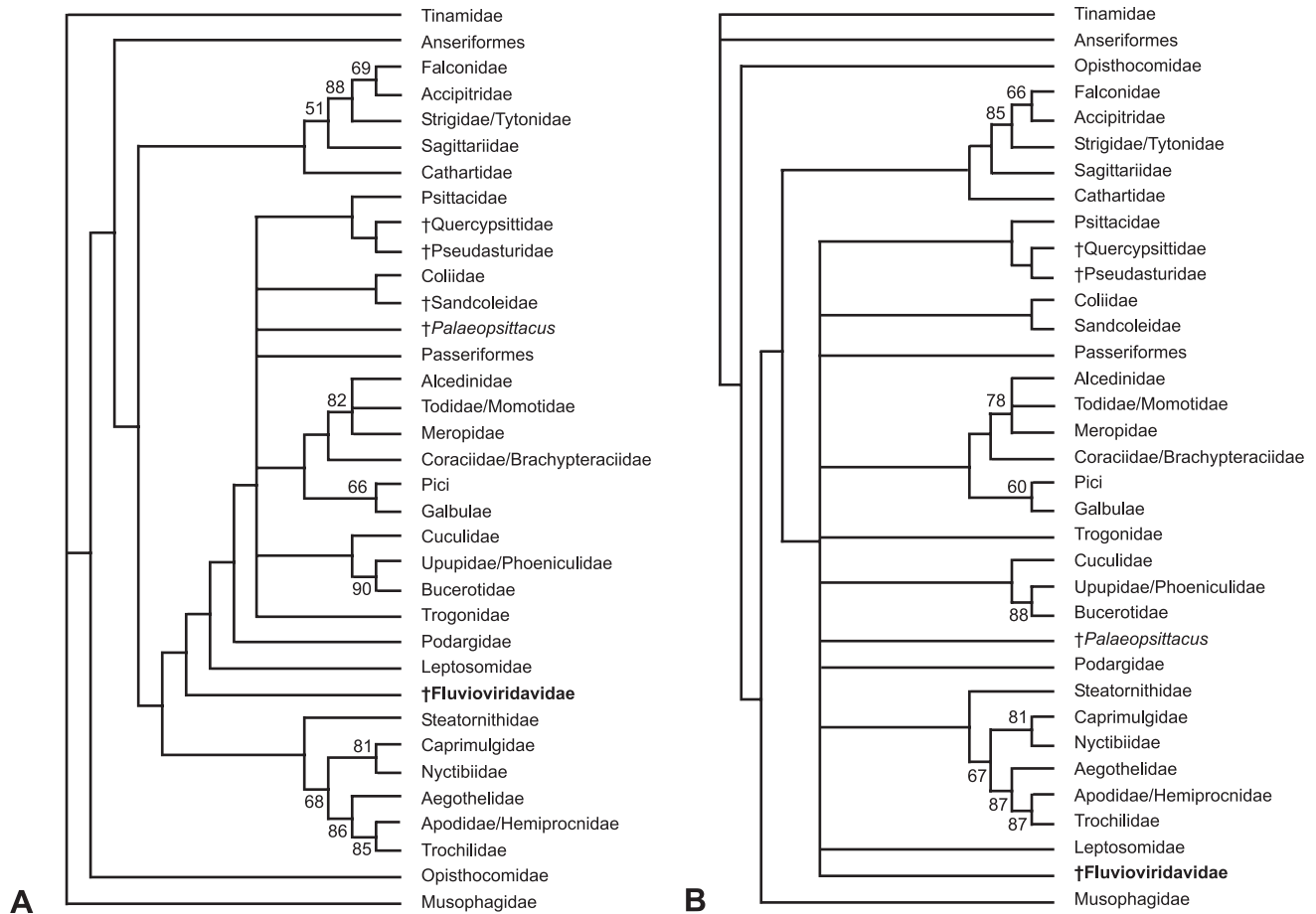
psittids appear to have been fully zygodactyl (i.e., the fourth toe was permanently retroverted), whereas *Eurofluvioviridavis*, as evidenced by the position of the feet of the holotype skeleton, was at best facultatively or semi-zygodactyl (i.e., the fourth toe was either spread laterally or could be turned forwards and backwards). The coracoid of quercypsittids exhibits a cup-like facies articularis scapularis as does the corresponding bone of the Fluvioviridavidae, but differs in the absence of a foramen nervi supracoracoidei (Fig. 6). Quercypsittidae were considered stem lineage Psittaciformes by Mourer-Chauviré (1992) and Mayr and Daniels (1998), and psittaciform affinities are here for the first time supported in a cladistic analysis. Psittaciform affinities of the Fluvioviridavidae are, however, not supported by the present analysis, which further neither supported nor convincingly refuted a closer relationship between Fluvioviridavidae and *Palaeopsittacus* (Fig. 7). Moreover, the poorly preserved tarsometatarsus of *Fluvioviridavis* (Fig. 5C) differs from that of *Quercypsitta* in its proportions and more closely resembles the corresponding bone of *Palaeopsittacus* (Fig. 6).

In displaying a bauplan that is unknown among modern birds and in possibly being the sister taxon of several modern "orders," the Fluvioviridavidae are of great potential interest concerning the early evolution and diversification of extant birds. It is to be hoped that future discoveries will provide additional osteological details that bear on the phylogenetic relationships of these birds.

Acknowledgments

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Appendix A. Character Descriptions

It is noted when character coding departs from Mayr et al. (2003) or new characters are added, see this reference for additional information on character coding in the extant taxa.

1. Skull, largely or completely ossified septum nasale: absent (0), present (1). The nasal septum is also ossified in few passeriform birds (e.g., *Rupicola* sp.), which is here considered to be an autapomorphy of these taxa.
2. Beak: not as follows (0), short and very wide at its base, with narial openings large and reaching far into its tip (1), "raptor-like," short and with sharply hooked tip (2). Character state (2) is newly added.
3. Proximodorsal part of narial openings covered by a thin osseous sheet: no (0), yes (1).
4. Beak with well-defined cere surrounding narial openings (feathered in some Psittacidae): no (0), yes (1).
5. Well-developed, caudally projecting processus supra-orbitales: absent (0), present (1). See Mayr et al. (2003) concerning coding of this character for Accipitridae and Strigiformes.
6. Os lacrimale (os praefrontale) vestigial or completely reduced: no (0), yes (1).
7. Os lacrimale, descending process greatly expanded medially: no (0), yes (1).
8. Os ectethmoidale, greatly expanded, plate-like, with dorsal margin largely fused with frontals: no (0), yes (1).
9. Vomer: not as follows (0), with truncate rostral and bifurcate caudal end (typical of the "aegithognathous"

palate) (1). This character is coded as unknown in taxa in which the vomer is vestigial or reduced.

10. Os palatinum, pars lateralis extremely craniolaterally expanded: no (0), yes (1).

11. Processus postorbitales strongly elongated, touching (or nearly touching) the jugals: no (0), yes (1). The presence of this character in few Strigiformes and Psittacidae, as well as in *Podargus* (Podargidae) is here considered autapomorphic for these taxa.

12. Os palatinum and os pterygoideum fused: yes (0), no (1). Newly added character.

13. Well-developed processus basipterygoidei that articulate with the ossa pterygoidea: yes (0), no (1).

14. Processus paroccipitales widely separated and strongly ventrally protruding; basis cranii concave: no (0), yes (1).

15. Cone-like bony protrusion at caudal margin of foramen nervi optici: absent (0), present (1).

16. Ossa quadratojugalia very stout, with wide caudal portion and dorsoventrally flattened distal part: no (0), yes (1). Newly added character.

17. Quadratum, processus orbitalis: not greatly reduced (0), greatly reduced (1).

18. Quadratum, condylus caudalis completely reduced, condylus lateralis separated from elongate condylus medialis by a deep but narrow furrow: no (0), yes (1).

19. Quadratum, processus oticus, dorsal margin of caudal surface with many small pneumatic foramina: no (0), yes (1).

20. Columella with large, hollow, bulbous basal and footplate area that exhibits a large fenestra on one side: no (0), yes (1).

21. Mandible, distal part of rami mandibulae very narrow, pars symphysialis very short: no (0), yes (1).

22. Mandible, area of pars symphysialis with rectangular cross section: absent (0), present (1).

23. Mandible with intraramal joint and caudal half of rami mandibulae greatly widened and dorsoventrally flattened: no (0), yes (1).

24. Mandible, proximal end unusually small, with very short cotyla lateralis and stout processus medialis: no (0), yes (1).

25. Atlas, incisura fossae: open (0), closed (1).

26. Axis, foramina transversaria: present (0), absent (1).

27. Pygostyle, corpus perforated at caudoventral end (Mayr and Clarke 2003, fig. 6G): yes (0), no (1). Newly added character.

28. Pygostyle with large, shield-like discus pygostyli with sharply defined, ridge-like lateral margins: no (0), yes (1).

29. Number of praesacral vertebrae (all vertebrae cranial to synsacrum) 19 or more (0), 18 (1), 17 (2). Nyctibiidae, Caprimulgidae, and Trochilidae have only 17 presacral vertebrae (contra Mayr et al. 2003). Atlas and axis of Bucerotidae are fused, but were counted as separate vertebrae. Note that coding of this character differs from Mayr et al. (2003).

30. Furcula, extremitas omalis with distinct, laterally protruding facies articularis acrocoracoidea: no (0), yes (1).

31. Coracoid, facies articularis scapularis excavated and cup-like: yes (0), no (1). Fluvioviridavidae were coded after *Fluvioviridavis*.

32. Coracoid, foramen nervi supracoracoidei: present (0), absent (1). I consider the presence of a foramen nervi supracoracoidei to be primitive for Anseriformes and accordingly coded it as present for that taxon.

33. Coracoid, extremitas sternalis with notch on margo medialis: no (0), yes (1). Note that coding of this character departs from Mayr et al. (2003) for Passeriformes.

34. Scapula, acromion distinctly bifurcate, i.e., with an additional medial process: no (0), yes (1).

35. Sternum, well-developed spina externa rostri: absent (0), present (1).

36. Sternum, spina interna rostri: absent (0), present (1).

37. Sternum, facies articularis coracoideus weakly saddle-shaped or convex: no (0), yes (1).

38. Caudal margin of sternum: with four notches or fenestrae (0), with two notches or fenestrae (1), or without notches or fenestrae (2).

39. Humerus, proximal end, sulcus transversus very deep, long, and rectangular-shaped: no (0), yes (1).

40. Humerus, distal end, fossa musculi brachialis deep and sharply delimited: no (0), yes (1). Within Pici, this character is present in Indicator which is here considered an autapomorphy of this taxon.

41. Humerus, processus flexorius strongly protruding in ventrodistal direction: no (0), yes (1).

42. Humerus, greatly abbreviated and stocky: no (0), yes (1).

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

44. Ulna, cotyla ventralis greatly enlarged, extending into olecranon: no (0), yes (1). Newly added character.

45. Ulna, proximal end, olecranon very long, narrow, and pointed; tuberculum ligamenti collateralis ventralis strongly protruding: no (0), yes (1).

46. Carpometacarpus, os metacarpale minus distinctly bowed, spatium intermetacarpale very wide: no (0), yes (1).

47. Carpometacarpus, processus intermetacarpalis: absent or small (0), well developed, reaching the os metacarpale minus (1), absent but tendon of musculus extensor carpi ulnaris inserts on the os metacarpale minus as it does in taxa with a processus intermetacarpalis (2). Note that coding of this character departs from Mayr et al. (2003) concerning Upupiformes and Bucerotiformes.

48. Carpometacarpus, os metacarpale minus distinctly exceeding os metacarpale majus in length: no (0), yes (1). Newly added character.

49. Os carpi ulnare with crus longum being much longer than crus breve: no (0), yes (1).

50. Os carpi ulnare with crus longum greatly abbreviated: no (0), yes (1).

51. Phalanx digiti alulae, claw: present (0), absent or rudimentary in adulthood (1); after Stephan (1992). Newly added character.

52. Fossa dorsalis of phalanx proximalis digiti majoris divided into two depressions by a distinctly raised oblique bulge: no (0), yes (1).

53. Phalanx proximalis digiti majoris, well-developed processus internus indicis: absent (0), present (1).

54. Phalanx proximalis digiti majoris, proximal end with large, proximally directing process on cranial side: no (0), yes (1).

55. Pelvis, foramen ilioischiadicum caudally closed: no (0), yes (1). Newly added character.

56. Pelvis wide in mediolateral direction, width across anti-trochanters as much or more than length of synsacrum: no (0), yes (1).

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

58. Pelvis, crista dorsolateralis ilii strongly developed, over-hanging a marked concavitas infracristalis and a marked sulcus antitrochantericus and convexly bowed if pelvis is viewed from its dorsal side, praeacetabular part much longer than postacetabular part, spina dorsolateralis ilii reduced: no (0), yes (1).

59. Pelvis, well-developed tubercula praeacetabularia: present (0), absent (1).

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

61. Femur, pneumatic foramen at craniolateral side of proximal end: absent (0), present (1). Newly added character.

62. Femur, distal end thickened, tuberculum musculi gastro-cnemialis lateralis large: no (0), yes (1). Newly added character.

63. Tibiotarsus, both cristae cnemiales and crista patellaris forming a ridge that circumscribes a groove on the cranial side of the bone: no (0), yes (1).

64. Tibiotarsus, crista cnemialis cranialis continuous with a ridge opposite to the crista fibularis: no (0), yes (1). Newly added character.

65. Tibiotarsus, distal end, pons supratendineus: ossified (0), tendinous (1).

66. Fibula very long, extending over almost the entire length of the tibiotarsus, distal end fused to shaft: no (0), yes (1).

67. Tarsometatarsus, hypotarsus passing into a well-developed crista medianoplantaris; fossa parahypotarsalis medialis very marked, and proximal part of margo medialis forming a sharp ridge: no (0), yes (1).

68. Tarsometatarsus, hypotarsus without bony canals, crista lateralis separated from crista medialis by a wide sulcus: no (0), yes (1).

69. Tarsometatarsus, hypotarsus, not as follows (0), tendons of musculus flexor digitorum longus and m. flex. (musculus flexor) hallucis longus situated in deep furrows (1), tendons of musculus flexor digitorum longus and m. flex. hallucis longus enclosed in bony canals (2). This character was coded as ordered.

70. Tarsometatarsus, arcus extensorius (ossified retinaculum extensorium tarsometatarsi): absent (0), present (1). Presence of this character in some Anseriformes is here considered an apomorphy of these taxa.

71. Tarsometatarsus, canaliz interosseus distalis: present (0), absent (1).

72. Tarsometatarsus, incisurae intertrochleares very short: no (0); yes (1).

73. Tarsometatarsus, trochlea metatarsi III much wider in mediolateral than in dorsoplantar direction, with a distinct groove between the rims; its dorsal surface not being significantly raised above the dorsal surface of the shaft: no (0), yes (1). Newly added character.

74. Tarsometatarsus, furrow on distal end, between dorsal side of trochlea metatarsi IV and incisura intertrochlearis lateralis: no (0), yes (1). Newly added character.

75. Trochlea metatarsi IV: not as follows (0), with plantarly directing wing-like flange, feet semi-zygodactyl (1), with large trochlea accessoria, feet fully zygodactyl (2). This character was coded as ordered.

76. Hallux, proximal phalanx with proximal end greatly widened: no (0), yes (1).

77. Third and fourth toe coalescent at least over length of basal phalanx of third toe: no (0), yes (1).

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

79. Claws, pair of canals lateral and medial to tuberculum flexorium: absent (0), present (1).

80. Musculus splenius capitis with cruciform origin: no (0), yes (1).

81. Musculus ambiens: present (0), absent (1); after Mayr et al. (2003), coding of Sagittariidae and Cathartidae after McKitrick (1991).

82. Musculus iliofemoralis externus: present (0), absent (1); after Mayr et al. (2003), coding of Sagittariidae and Cathartidae after McKitrick (1991).

83. Musculus flexor cruris lateralis, pars pelvica: present (0), absent (1); after Mayr et al. (2003), coding of Sagittariidae and Cathartidae after McKitrick (1991).

84. Musculus flexor cruris lateralis, pars accessoria: present (0), absent (1); after Mayr et al. (2003), coding of Sagittariidae and Cathartidae after McKitrick (1991).

85. Musculus caudofemoralis, pars pelvica: present (0), absent (1); after Mayr et al. (2003), coding of Sagittariidae and Cathartidae after McKitrick (1991). Note that coding of this character departs from Mayr et al. (2003) concerning Anseriformes.

86. Musculus fibularis longus: present (0), absent (1); after Mayr et al. (2003), coding of Sagittariidae and Cathartidae after McKitrick (1991).

87. Musculus popliteus: present (0), absent (1); after Mayr et al. (2003), coding of Sagittariidae and Cathartidae after McKitrick (1991).

88. Vinculum between tendons of musculus flexor perforans et perforatus digiti III and m. perforatus digiti III: present (0), absent (1); after Mayr et al. (2003), coding of Sagittariidae and Cathartidae after McKitrick (1991). Note that coding of this character departs from Mayr et al. (2003) concerning Anseriformes.

89. Musculus flexor hallucis longus, origin with three heads, iliofibularis tendon passes lateral to lateral head: no (0), yes (1); after Mayr et al. (2003), coding of Sagittariidae and Cathartidae after McKitrick (1991).

90. Musculus flexor hallucis longus: tendon supplying hallux (0) tendon not supplying hallux (1); after Mayr et al. (2003), coding of Sagittariidae and Cathartidae after McKitrick (1991).

91. Musculus flexor hallucis longus and musculus flexor digitorum longus, type of arrangement. See George and Berger (1966, p. 447) for description of types I–VIII, and Berman (1984) for description of type X (coded 9, following McKitrick 1991); Trochilidae were coded 0, following McKitrick (1991); after George and Berger (1966), Maurer and Raikow (1981), McKitrick (1991). Newly added character.

92. Tendon of musculus extensor digitorum longus sending

branch to hallux: no (0), yes (1); after Mayr et al. (2003), coding of Sagittariidae and Cathartidae after McKitrick (1991).

93. Musculus abductor digiti II: present (0), absent (1); after Mayr et al. (2003), coding of Sagittariidae and Cathartidae after McKitrick (1991). Reduction of this muscle in some Anseriformes is here considered apomorphic for these taxa.

94. Oil gland: tufted (0) or minutely tufted (only vestigial feather remains present)/naked (1).

95. Wing: diastataxic (0), eutaxic (1).

96. Villi at the bases of the basalmost downy barbules of breast feathers: absent (0), present (1).

Appendix B. Character matrix

Appendix on following pages

Appendix B. Character matrix

Table B1 (*runs from p. 2034 to p. 2037*). Character matrix of 96 morphological characters for the 35 included in the analysis (see Appendix A for character definitions).

Taxa	Characters and character states																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Tinamidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Anseriformes	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Opisthocomidae	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0
Falconidae	1	2	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	01
Accipitridae	1	2	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Strigidae/Tytonidae	1	2	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Sagittariidae	1	2	0	1	1	0	0	0	?	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0
Cathartidae	0	2	0	1	0	0	0	0	?	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	1	2	0	1	0	0	0	0	?	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	01
Cuculidae	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	01	0	0	0	0	0	1
Musophagidae	1	0	0	0	0	0	0	01	0	0	0	1	1	0	0	0	0	0	01	0	0	0	0	0	0
Coliidae	1	0	0	0	0	0	0	1	?	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	01
Leptosomidae	1	0	0	0	0	0	0	1	?	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0
Alcedinidae	1	0	0	0	01	0	1	0	?	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	1
Meropidae	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	1
Todidae/Momotidae	1	0	0	0	0	0	01	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	1
Coraciidae/Brachypt.	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	01
Steatornithidae	1	2	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Podargidae	1	0	0	0	0	?	0	0	?	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0
Caprimulgidae	0	1	0	0	0	0	0	0	0	1	0	1	0	1	1	0	1	1	0	0	1	0	1	1	0
Nyctibiidae	0	1	0	0	0	1	0	0	0	1	0	1	0	1	1	0	1	1	0	?	1	0	1	1	0
Aegothelidae	0	1	0	0	0	1	0	0	1	0	0	1	1	0	0	0	1	1	1	0	1	0	0	0	0
Apodidae/Hemiproc.	0	1	1	0	0	1	0	1	1	0	0	1	1	0	0	0	1	1	1	0	1	0	0	0	1
Trochilidae	0	0	1	0	0	?	0	1	0	0	0	1	1	0	0	0	1	1	1	0	0	0	0	0	1
Upupidae/Phoenicul.	1	0	0	0	0	1	0	1	?	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1
Bucerotidae	1	0	0	0	0	?	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	1
Passeriformes	0	0	0	0	0	0	0	01	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1
Pici	01	0	0	0	0	?	0	1	0	0	0	1	1	0	0	0	0	0	01	0	0	0	0	0	1
Galbulae	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1
Trogonidae	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1
†Fluvioviridavidae	?	0	0	?	0	?	?	?	?	0	?	1	1	?	?	0	?	?	0	?	0	0	0	0	?
†Quercypsittidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†Pseudasturidae	?	0	0	?	1	0	?	?	?	0	0	1	1	0	?	0	?	0	?	?	0	0	0	0	?
†Sandcoleidae	0	0	0	?	0	0	?	?	?	0	0	1	1	0	?	0	0	?	?	0	0	0	0	0	?
†*Palaeopsittacus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Note: Polymorphic characters are coded as such, unknown character states are indicated by "?." Tinamidae and Anseriformes were used for outgroup comparison. Extinct taxa are indicated by a dagger.

Table B1 (*continued*).

Taxa	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
	Characters and character states																								
Tinamidae	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Anseriformes	0	1	0	0	0	0	0	0	0	01	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Opisthocomidae	0	0	0	0	?	0	1	0	0	?	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0
Falconidae	1	0	0	0	1	1	0	0	0	1	01	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Accipitridae	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Strigidae/Tytonidae	1	0	0	0	01	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	01	0
Sagittariidae	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0
Cathartidae	01	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Psittacidae	01	1	0	0	0	1	1	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0
Cuculidae	01	1	0	1	0	1	1	0	0	1	01	0	01	0	0	1	0	0	0	0	1	0	1	0	1
Musophagidae	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1
Coliidae	1	0	1	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	1	0	1	1	1	0	0
Leptosomidae	0	1	0	1	1	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Alcedinidae	1	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Meropidae	1	1	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Todidae/Momotidae	1	1	0	0	0	1	1	01	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Coraciidae/Brachypt.	1	1	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	01	0	0
Steatornithidae	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	1	1	0
Podargidae	0	1	0	1	0	1	1	0	0	0	0	0	0	0	01	0	0	1	0	0	0	0	0	0	0
Caprimulgidae	0	0	0	2	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0
Nyctibiidae	0	0	0	2	1	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0
Aegothelidae	1	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0
Apodidae/Hemiproc.	1	1	0	1	1	0	0	0	0	0	0	1	2	1	0	0	1	1	0	0	0	0	0	1	0
Trochilidae	1	1	0	2	1	0	0	0	0	0	0	1	2	0	0	0	1	0	0	0	0	1	1	1	0
Upupidae/Phoenicul.	0	1	1	1	0	1	1	0	01	1	1	0	1	0	0	0	0	1	0	1	1	2	1	0	0
Bucerotidae	0	0	1	0	0	1	1	0	0	1	01	0	1	0	1	0	0	1	1	0	0	2	1	0	0
Passeriformes	1	1	0	0	0	1	1	01	01	1	0	0	01	0	0	0	0	1	0	1	0	1	1	0	01
Pici	01	1	1	0	0	1	1	1	01	1	0	0	0	0	0	1	0	1	0	1	0	1	1	0	0
Galbulae	1	1	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0
Trogonidae	1	1	0	1	0	1	1	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	1	1	0
†Fluvioviridavidae	?	0	0	?	0	0	0	0	?	?	?	0	0	?	?	0	0	1	?	0	0	0	0	?	?
†Quercypsittidae	?	?	?	?	?	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†Pseudasturidae	?	?	0	1	?	1	0	0	?	?	?	0	0	0	0	0	1	0	0	0	0	0	0	?	?
†Sandcoleidae	?	0	0	?	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	?	?
†*Palaeopsittacus*	?	?	?	?	?	1	0	0	0	1	?	0	?	0	?	?	0	0	0	0	0	0	0	?	?

Table B1 (*continued*).

Taxa	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
								Character and character states																	
Tinamidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	01	0	0	0	0	0	0	0	0	0
Anseriformes	0	1	0	0	1	0	0	0	01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opisthocomidae	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Falconidae	0	1	0	0	1	0	0	1	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Accipitridae	01	1	0	0	1	0	0	1	1	0	1	0	0	0	0	01	0	1	0	0	0	0	0	0	0
Strigidae/Tytonidae	1	1	0	0	1	0	0	1	1	0	0	0	0	0	1	1	0	1	0	01	0	0	0	0	1
Sagittariidae	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cathartidae	0	1	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psittacidae	1	1	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	2	0	1	0	1	1	2
Cuculidae	1	01	0	0	1	01	1	0	01	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	2
Musophagidae	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Coliidae	1	0	0	0	1	0	1	0	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	1
Leptosomidae	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1
Alcedinidae	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Meropidae	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Todidae/Momotidae	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Coraciidae/Brachypt.	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Steatornithidae	1	0	1	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Podargidae	1	1	0	0	1	01	0	0	1	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0
Caprimulgidae	1	1	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Nyctibiidae	?	1	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0
Aegothelidae	1	1	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Apodidae/Hemiproc.	0	1	1	0	1	1	0	0	1	1	0	0	0	01	0	0	0	01	0	1	1	0	0	0	0
Trochilidae	1	0	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Upupidae/Phoenicul.	1	0	0	0	1	0	1	0	1	1	1	0	0	0	0	0	1	0	2	1	1	1	0	0	0
Bucerotidae	1	0	0	0	1	0	01	0	1	1	1	0	0	0	1	0	1	0	2	0	1	1	0	0	0
Passeriformes	1	0	0	0	1	0	0	0	1	01	0	0	0	1	0	0	0	0	2	1	1	0	0	0	0
Pici	1	0	0	1	1	0	0	0	1	1	0	0	1	1	0	0	01	0	0	01	1	0	0	0	2
Galbulae	1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	2
Trogonidae	1	0	0	0	1	1	0	0	1	01	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0
†Fluvioviridavidae	0	1	0	0	1	0	?	0	1	0	?	?	0	0	?	0	0	0	2	?	?	0	?	?	?
†Quercypsittidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	0	1	0	1	0	1	?	2
†Pseudasturidae	1	1	0	0	1	0	0	0	1	?	0	0	0	1	0	0	0	0	1	0	1	0	1	1	2
†Sandcoleidae	0	0	0	0	1	0	0	0	1	1	0	1	1	1	0	0	0	0	2	0	0	0	0	0	1
†*Palaeopsittacus*	1	?	0	0	1	0	0	?	1	?	?	?	0	?	0	0	0	0	2	0	?	0	0	0	0

Table B1 (*concluded*).

| | Character and character states | | | | | | | | | | | | | | | | | | | | |
Taxa	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96
Tinamidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	1	?
Anseriformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	0	0	0	0	?
Opisthocomidae	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	?
Falconidae	0	0	1	1	0	0	0	1	1	1	0	0	1	0	0	3	0	0	0	0	?
Accipitridae	0	0	1	1	0	0	0	1	1	1	01	0	1	0	0	3	0	0	0	0	?
Strigidae/Tytonidae	0	0	1	1	0	1	0	1	1	1	1	0	1	0	0	1	0	0	1	0	?
Sagittariidae	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	?
Cathartidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	5	0	0	1	0	?
Psittacidae	0	0	0	01	0	01	0	0	0	1	1	1	1	0	0	9	1	1	0	0	0
Cuculidae	0	0	0	0	0	0	1	0	0	01	0	0	1	0	0	1	0	0	1	1	0
Musophagidae	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	1	0	0	0	1	0
Coliidae	0	0	1	0	0	1	0	0	0	1	0	1	1	0	0	5	1	1	0	1	0
Leptosomidae	0	0	0	0	0	1	1	0	?	1	0	0	?	0	0	5	0	0	1	0	?
Alcedinidae	1	1	0	0	0	1	1	0	1	1	0	1	1	0	1	5	0	1	0	01	0
Meropidae	1	1	0	0	0	1	1	?	0	1	1	1	?	0	1	5	0	1	1	1	0
Todidae/Momotidae	1	1	0	0	0	1	1	?	0	1	0	1	?	0	1	5	0	1	01	1	0
Coraciidae/Brachypt.	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	5	0	0	1	01	0
Steatornithidae	0	0	1	0	0	1	1	0	0	1	1	0	0	0	0	?	0	0	1	0	?
Podargidae	0	0	0	0	0	1	1	0	0	1	0	01	1	0	0	?	0	0	1	0	?
Caprimulgidae	0	0	0	0	0	1	1	0	0	1	0	0	01	0	0	5	0	0	1	0	0
Nyctibiidae	0	0	0	0	0	1	1	0	0	1	0	1	1	0	0	?	0	0	1	0	?
Aegothelidae	1	0	0	0	1	1	1	0	0	1	1	1	1	0	0	?	0	0	1	0	?
Apodidae/Hemiproc.	01	0	01	0	1	1	1	0	1	1	1	1	1	0	0	5	0	0	1	01	0
Trochilidae	0	1	1	0	1	1	1	?	1	1	1	1	1	0	0	0	0	1	1	01	1
Upupidae/Phoenicul.	01	1	0	0	0	1	1	0	0	1	1	1	1	0	0	?	0	1	0	1	0
Bucerotidae	0	01	0	0	0	1	1	0	0	1	1	1	1	0	0	5	0	0	0	1	0
Passeriformes	0	0	0	01	0	1	1	0	0	1	0	1	1	0	0	7	0	1	1	1	1
Pici	0	0	0	0	0	1	1	0	0	1	0	1	1	1	0	6	0	1	0	1	1
Galbulae	0	0	0	0	0	1	1	0	0	1	01	01	?	1	0	6	0	?	1	1	0
Trogonidae	0	1	0	0	0	1	1	0	1	1	0	1	1	0	0	8	0	0	1	1	0
†Fluvioviridavidae	0	?	01	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†Quercypsittidae	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†Pseudasturidae	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†Sandcoleidae	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Palaeopsittacus*	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?