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THE POSTCRANIAL OSTEOLOGY AND PHYLOGENETIC POSITION OF THE MIDDLE EOCENE *MESSELASTUR GRATULATOR* PETERS, 1994—A MORPHOLOGICAL LINK BETWEEN OWLS (STRIGIFORMES) AND FALCONIFORM BIRDS?

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ABSTRACT—An articulated skeleton of *Messelastur gratulator* Peters, 1994, from the middle Eocene of Messel in Germany is described. This species was hitherto known from two skulls with associated vertebrae only, and has been tentatively classified in the Accipitridae (hawks). The new specimen shows that *M. gratulator* closely resembles the Lower Eocene *Tynskya eocaena* Mayr, 2000a, which is known from an articulated skeleton from the North American Green River Formation and isolated bones from the London Clay in England. Both species, *M. gratulator* and *T. eocaena*, are assigned to the new taxon Messelasturidae. The new specimen exhibits previously unknown osteological details bearing on the phylogenetic position of the Messelasturidae, most notably the absence of an ossified supratendineal bridge on the distal tibiotarsus. Cladistic analysis of 110 characters supports sister-group relationship between *Messelastur* and *Tynskya*, and shows the Messelasturidae to be the sister taxon of owls (Strigiformes). The clade (Messelasturidae + Strigiformes) is shown to be the sister group of the clade (Falconidae [falcons] + Accipitridae). Among the known fossil raptorial birds, the Messelasturidae most substantially differ from the extant taxa. They provide a morphological link between Strigiformes and Falconiformes (diurnal birds of prey), and support the highly disputed falconiform affinities of owls in combining derived tibiotarsus and tarsometatarsus characters of owls with a more plesiomorphic, 'falcon-' or 'hawk-like', skull morphology.

INTRODUCTION

Messelastur gratulator Peters, 1994, is a raptorial bird from the middle Eocene of Messel in Germany, that was previously known only from two isolated skulls with associated vertebrae (Fig. 1A). The species has been assigned tentatively to the falconiform Accipitridae (hawks) in the original description (Peters, 1994), but its exact phylogenetic affinities remained uncertain owing to the lack of postcranial bones.

Here, I describe the first skeleton of *M. gratulator*, recently discovered during excavations by Forschungsinstitut Senckenberg at the Messel fossil site. The new specimen can be unambiguously assigned to *Messelastur* as it clearly shows the characteristic, derived skull features of this taxon, i.e., a very short beak with a markedly hooked tip, well-developed processus supraorbitales, and unusually deep rami mandibulae (Fig. 1). Among the known avian taxa from Messel only *Messelastur* exhibits the combination of these characters. Although the new specimen is larger than the holotype (length of mandible 29.2 versus 24.6), this size difference is in the range of many extant raptorial birds where, due to sexual dimorphism, females are distinctly larger than males.

The postcranial osteology of the new skeleton shows *M. gratulator* to be very similar to another raptorial bird, *Tynskya eocaena* Mayr, 2000a. This species is known from a single skeleton from the Lower Eocene Green River Formation of North America (Fig. 2), and isolated bones from the Lower Eocene London Clay in England (Mayr, 2000a). The tarsometatarsus of *T. eocaena* exhibits a derived morphology similar to that of owls (Strigiformes, see below), but the species is otherwise distinguished from strigiform birds in many osteological features (Mayr, 2000a, and below). Its exact phylogenetic affinities could not be determined so far, because important osteological features remained unknown. As shown in this study, *Messelastur* and *Tynskya* are sister taxa, and a new name is proposed for the clade including these two taxa.

MATERIAL AND METHODS

Osteological terminology follows Baumel and Witmer (1993); measurements are in millimeters and refer to the maximum length of the bone along its longitudinal axis. The specimen of *Messelastur* was transferred into a slab of artificial resin, and details of the skeleton are visible through the reverse side of the transparent slab. Examinations of extant taxa are based on skeletons in the collection of Forschungsinstitut Senckenberg; additional information on the osteology of falconiform birds was taken from Jollie (1976, 1977a–c) and Sushkin (1905).

Phylogenetic Analysis—110 characters for 22 taxa (see character matrix in Appendix 2) were coded using the modified character matrix of Mayr and Clarke (2003). Mesozoic non-neornithine taxa, ratites, and most aquatic/semi-aquatic birds were excluded. Characters from the Mayr and Clarke (2003) character matrix that show no variation within the taxa analyzed in the present study were excluded, and six new/modified ones (characters 52, 73, 78–80, 82 in Appendices) added in order to resolve the position of the fossil taxa that were not included in the Mayr and Clarke (2003) analysis. The character matrix was analyzed with PAUP 3.1 (Swofford 1993). The search was performed with the heuristic search option. Four characters (64, 74, 75, and 79 in Appendix 1) 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 1000 replicates. Outgroup comparisons were made with the paleognathous Tinamidae (tinamous) and the Galliformes (landfowl), one of the most basal lineages of neognathous birds (e.g., Sibley and Ahlquist 1990, Mayr and Clarke 2003).

Institutional Abbreviations—**SMF**, Forschungsinstitut Senckenberg, Frankfurt a. M., Germany; **BSP**, Bayerische Staatssammlung für Paläontologie und Historische Geologie, München, Germany.

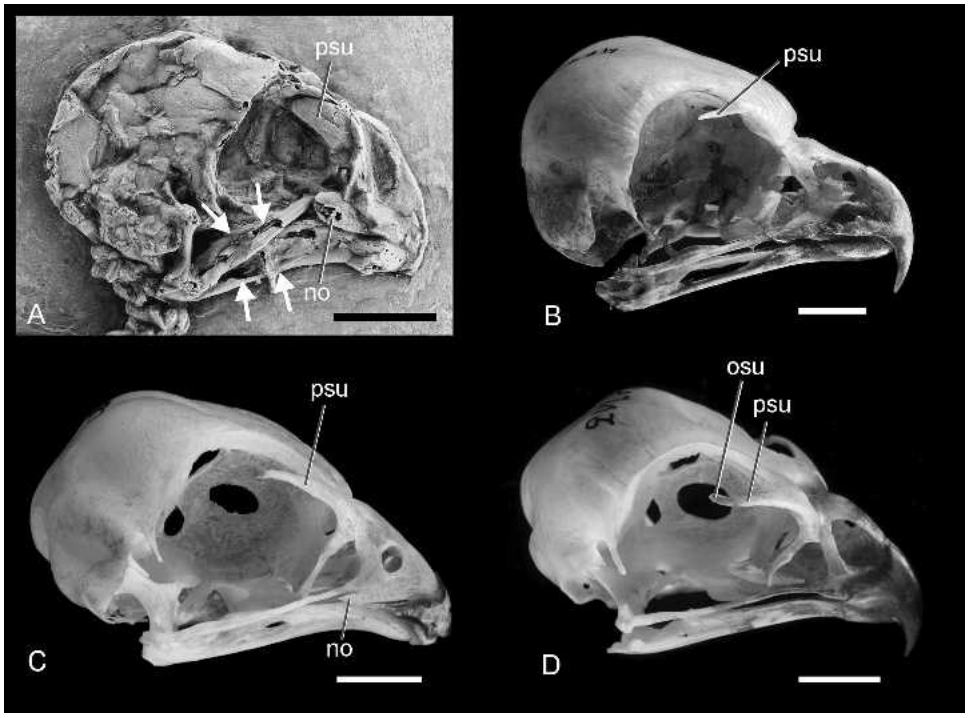

FIGURE 1. *Messelastur gratulator* Peters, 1994, skull of holotype (**A**, SMF-ME 2024) in comparison to the skull of **B**, extant Hawk-Owl, *Surnia ulula* (Strigidae, Strigiformes); **C**, Common Kestrel *Falco tinnunculus* (Falconidae, Falconiformes); **D**, European Sparrow-Hawk *Accipiter nisus* (Accipitridae, Falconiformes). **Abbreviations**: **no**, 'nose'-like projection ventral to caudal end of jugal bone; **psu**, processus supraorbitalis; **osu**, os supraorbitalis. The arrows indicate the unusually deep mandibular rami in *Messelastur*. Scale bars equal 10 mm.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758
MESSELASTURIDAE, fam. nov.

Type Genus—*Messelastur* Peters, 1994.

Included Genus—*Tynskya* Mayr, 2000a.

Diagnosis—(1) Beak short and raptor-like; (2) well-developed processus supraorbitales present; (3) mandible with very deep rami; (4) proximal end of humerus without foramen pneumaticum; (5) tibiotarsus without ossified pons supratendineus; (6) tarsometatarsus with well-developed cristae hypotarsi bordering a wide sulcus; (7) trochlea metatarsi II small; (8) trochlea metatarsi III very broad; (9) and trochlea metatarsi IV plantarly inflected.

Remarks—All of the above diagnostic characters are here considered to be derived within neornithine birds and are absent in basal Neornithes, such as Tinamidae (tinamous) and Galloanseres (land- and waterfowl) (e.g., Mayr and Clarke, 2003). Characters (2), (3), and (5) are unknown for *T. eocaena*, owing to the poor preservation of the holotype; the tarsometatarsal characters are unknown for *Messelastur*.

Messelastur Peters, 1994, mainly differs from *Tynskya* Mayr, 2000a, in a proportionally somewhat shorter tibiotarsus (tibiotarsus slightly longer than ulna in *Tynskya* but slightly shorter than ulna in *Messelastur*; see measurements below).

Differential Diagnosis—The Messelasturidae, fam. nov., differ: from the upper Eocene Horusornithidae Mourer-Chauviré, 1991, in characters (6)–(9) listed in the diagnosis, and in the tibiotarsus with much lower condyli and trochlea cartilaginis tibialis; from Accipitridae and Falconidae in characters (3)–(5) and (7)–(9) listed in the diagnosis, and the humerus with smaller crista bicipitalis; from Strigiformes in characters (2)–(4) and (7) listed in the diagnosis, and the humerus less slender and with smaller crista bicipitalis; and from early Eocene psittaciform Pseudasturidae Mayr, 1998, in characters (1), (3), and (6) listed in the diagnosis, and in having the humerus stouter, hypotarsus with two strongly protruding cristae, and trochlea metatarsi IV with smaller trochlea accessoria.

MESSELASTUR Peters, 1994
MESSELASTUR GRATULATOR Peters, 1994
(Figs. 3, 4)

Referred Specimen—SMF-ME 11080, articulated skeleton on a slab lacking most of right wing and leg, as well as left foot and tip of left wing (Figs. 3, 4).

Locality and Horizon—Messel near Darmstadt (Hessen, Germany), middle Eocene (Schaal and Ziegler 1988, Mayr 2000b).

Measurements—Dimensions of the holotype of *Tynskya eocaena*, after Mayr 2000a, in brackets: skull, 44.7; mandible, 29.2; maximum height of ramus mandibulae, 7.0; coracoid, ~24.0 (right), ~24.0 (left); left humerus, 43.0 [36.6]; left ulna, ~47.5 [40.0/~39.4]; left carpometacarpus, 25.8 [20.1]; left femur, 29 (estimated); left tibiotarsus, 45.4 [42.0].

Description and Comparison—The skull of *Messelastur* has already been described by Peters (1994) and specimen SMF-ME 11080 offers only a few new details. The skull of *Messelastur* is large in relation to the overall size of the bird (note that the cranium of *Tynskya eocaena* is not preserved in the holotype and that the slab has been painted in this area). The beak is short, measuring about 1/4 the total length of the skull; its tip is deeply hooked. The os lacrimale bears a well-developed processus supraorbitalis (Fig. 1), which among modern falconiform birds occurs in Sagittariidae (secretary bird), Falconidae (falcons), and most Accipitridae (including presumably basal [Griffiths 1994, Holdaway 1994] taxa, such as *Elanus*). Within Strigiformes

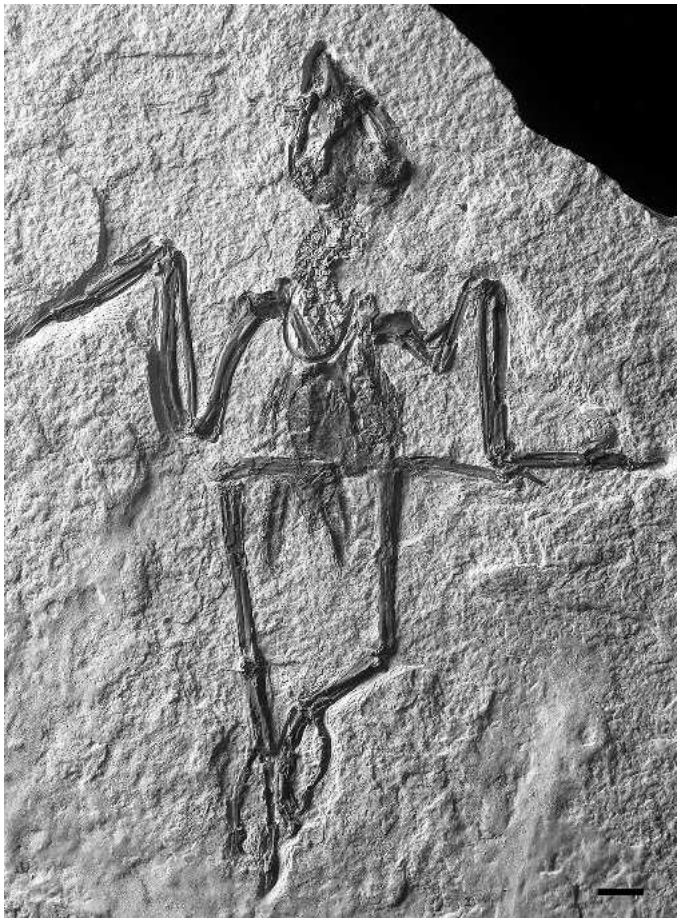

FIGURE 2. *Tynskya eocaena* Mayr, 2000a, holotype (BSP 1997 I 6). Scale bar equals 10 mm.

(owls), decidedly smaller processus supraorbitales are present in, e.g., *Aegolius*, *Athene*, and *Surnia*, but vestigial or absent in Tytonidae (barn owls), *Strix*, and some larger species. However, although adults of *Strix aluco*, for example, lack processus supraorbitales, they are present in pulli of this species (May 1962: 197), thus indicating that processus supraorbitales probably were present in the stem species of crown group Strigiformes. As noted by Peters (1994), the processus supraorbitalis of *Messelastur* lacks an os supraorbitalis that occurs in many Accipitridae (Jollie 1977b:211; Fig. 1D). The caudal part of the crista tomialis forms a 'nose'-like projection ventral to the caudal end of the unusually robust jugal bone (Fig. 1), which I did not find in any extant raptorial bird. Unfortunately, not many details of the palatal area can be identified. The two slender osseous bars between the rami mandibulae belong to the cornu branchiale of the hyoid apparatus. Part of the left pterygoid is visible next to the left ramus mandibulae but does not allow the recognition of informative details. Whether there were processus basipterygoidei as in the Strigiformes cannot be discerned. The caudal surface of the processus oticus of the right quadratum is visible next to the caudal end of the right mandibular ramus. It is similar to the processus oticus of some Accipitridae (e.g., *Circaetus*), whereas that of strigiform birds strongly differs in that the capitulum oticum is very slender and separated from the capitulum squamosum by a marked incisura intercapitularis. The rami mandibulae are much deeper than in any extant falconiform or strigiform bird (Fig. 1), almost approaching the condition in crown-group parrots (Psittacidae). The symphysis mandibulae also is fairly long compared to owls and birds of prey. The proximal end of the mandible exhibits a marked mediolateral ridge along its ventral surface as in, e.g., the Tytonidae.

Messelastur has 19 presacral vertebrae, as most Strigiformes, Accipitridae, and Falconidae (although most cervical vertebrae are hidden by overlying bones in specimen SMF-ME 11080, the distinctive 14th vertebra is visible, and the number of the presacral vertebrae can thus be counted by comparison with the holotype specimen, which lacks the caudal thoracic vertebrae). Contrary to owls and most modern birds of prey, the third cervical vertebra seems to lack an osseous bridge from the processus transversus to the processus articularis caudalis (Mayr and Clarke, 2003:fig. 6). The 14th vertebra exhibits a large pneumatic foramen on its corpus (Peters, 1994) that occurs in many birds, including Strigiformes, Accipitridae, and Psittaciformes (parrots), but is absent in the Falconidae. The 15th vertebra bears a well-developed processus ventralis and is strongly mediolaterally compressed, as is the 16th vertebra. Contrary to all Falconidae except *Herpetotheres* and *Micrastur*, the thoracic vertebrae are not fused to a notarium. Although Peters (1994) noted similarities between the vertebral column of *Messelastur* and Accipitridae, it is also very similar to that of the Strigiformes and many other taxa (e.g., Psittaciformes).

The coracoid is relatively slender and similar to the corresponding bone of Strigiformes and Falconidae in its proportions (the coracoid of *Tynskya eocaena* is unknown). The processus procoracoideus that is visible through the reverse of the slab appears to have been short as in Accipitridae and Sagittariidae, whereas it is very long in Strigiformes and Falconidae. There further appears to have been no articulation facet for the furcula on the extremitas omalis. Such a facet (Fig. 5B–D) is a derived characteristic of Strigidae (true owls), Accipitridae, and Falconidae but absent in the Tytonidae. The facies articularis scapularis of the coracoid of *Messelastur* is shallow as in Strigiformes, Falconidae, and *Pandion*, whereas it is cup-like in most other Accipitridae, Sagittariidae, and the fossil Horusornithidae (Mourer-Chauviré, 1991). A foramen nervi supracoracoidei is visible through the reverse of the transparent slab (Fig. 5A). The exact shape of the sternal end cannot be discerned.

The furcula is widely U-shaped as in *Tynskya eocaena*, Falconidae, and Accipitridae, whereas it is more V-shaped in strigiform birds. The extremitas omalis is, however, slender and not as greatly widened as in most Accipitridae and Falconidae (Fig. 5G). The extremitas sternalis is narrow; an apophysis furculae cannot be discerned. In Strigidae, Falconidae, and Accipitridae the extremitas omalis of the furcula bears a strongly developed, laterally protruding facies articularis acrocoracoidea that articulates with a distinct ovoid facies articularis clavicularis of the coracoid. This articulation facet appears to be absent in the fossil, which in this respect agrees with the Tytonidae (and most other birds).

The extremitas cranialis of the scapula is visible through the reverse of the transparent slab. It lacks a tuberculum coracoideum, which is in concordance with the presence of a shallow facies articularis scapularis on the coracoid. The acromion is short as in *Tynskya eocaena* and Tytonidae. Details of the sternum cannot be discerned.

The humerus has similar proportions to that of *Tynskya eocaena*, which it also closely resembles in all osteological details that are discernible in the fossil specimens. Compared with extant raptorial birds it comes closest in its proportions to the humerus of the Falconidae, whereas the humerus of Strigiformes and most Accipitridae is more elongated. As in the Tytonidae but in contrast to Strigidae, Falconidae, and most Accipitridae, there is a deep sulcus transversus. Most notably, and as in *Tynskya eocaena* (Mayr, 2000a), the proximal end of the bone lacks a foramen pneumaticum, which is present in all Strigiformes and Falconiformes. As in the Cathartidae (New World vultures) and

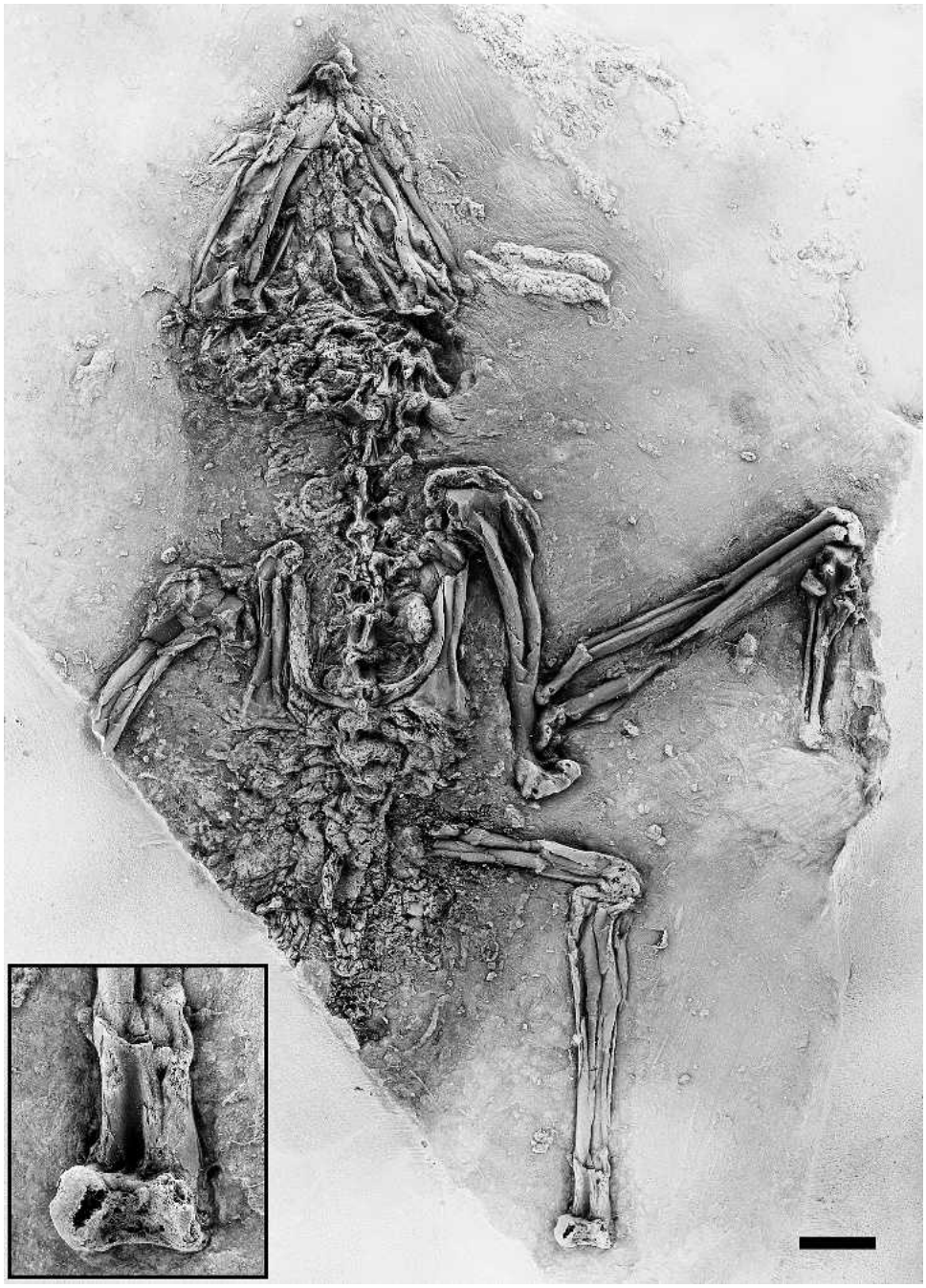

FIGURE 3. *Messelastur gratulator* Peters, 1994, referred specimen SMF-ME 11080 with detail of distal end of left tibiotarsus inserted. Coated with ammonium chloride to enhance contrast. Scale bar equals 10 mm.

most other birds, the small tuberculum dorsale is located on the caudal surface of the proximal humerus, whereas it is shifted onto the proximo-dorsal margin of the humerus in the Strigiformes and Falconiformes. The crista bicipitalis is further less developed than in all Strigiformes and Falconiformes. The crista deltopectoralis is fairly short and situated farther proximally than in Accipitridae. The condylus ventralis on the distal end is more elongated than in Falconidae and Accipitridae. The tuberculum supracondylare ventrale is small, as is the condylus dorsalis. As in *Tynskya eocaena*, the processus flexorius is short and bears two adjacent pits; the sulcus scapulotricipitalis is shallow.

The ulna is the longest limb element and distinctly exceeds the humerus in length. Unfortunately, except for the small tuberculum carpale, no osteological details of its articulation surfaces are recognizable.

The carpometacarpus closely resembles the corresponding bone of *Tynskya eocaena*. This bone is very similar in owls and diurnal bones of prey and it is not possible to discern derived carpometacarpal features that show *Messelastur* to be more closely related to any of those taxa. There is a deep fovea carpalis cranialis, and the processus pisiformis is situated in the center of the extremitas proximalis. The spatium intermetacarpale is narrow.

In concordance with *Tynskya eocaena*, the phalanx digiti alu-

FIGURE 4. *Messelastur gratulator* Peters, 1994, X-ray picture of referred specimen SMF-ME 11080. Scale bar equals 10 mm.

lae of *Messelastur* bears a very thin and fairly long claw. This digit also bears a claw in some modern owls and diurnal birds of prey (Stephan, 1992). The os carpi radiale is similar to that of *Elanus* (Accipitridae), whereas this bone appears to be somewhat narrower dorsoventrally in strigiform birds. The distal elements of the hand are not preserved in the specimen. There is no os prominens, which occurs in many Strigiformes and Accipitridae (Bock and McEvey, 1969).

Phylogenetically informative details of the pelvis and femur are not visible in the specimen.

The tibiotarsus is fairly short and stout, with low cristae cnemiales; it is proportionally slightly shorter than the corresponding bone of *Tynskya eocaena* and more robust than that of owls. In the single known specimen of *Tynskya eocaena* the cranial side of the bone is not visible, whereas in *Messelastur* the trochlea cartilaginis tibialis (visible through the reverse of the slab) is broken, although of similar proportions to that of *T. eocaena*. The condyli are proximo-distally low and widely separated; the condylus lateralis is smaller than the condylus medialis. Two scars mark the attachment site of the retinaculum extensorium tibiotarsi (Fig. 5I), the medial one is located much farther proximally than the lateral one; the sulcus extensorius is wide and shallow as in owls. Also as in the Strigiformes but contrary to most other neornithine (crown group) birds, there is no ossified pons supratendineus (Figs. 3, 5). The specimen unquestionably is from an adult bird and no signs of breakage of this bridge are visible. An ossified pons supratendineus is also absent in the Horusornithidae (Mourer-Chauviré, 1991), from which the tibiotarsus of *Messelastur*, however, differs in the much lower condyli. Contrary to the condition in most Strigiformes, Accipitridae, and Falconidae, the fibula appears to have been rather short, although this bone may not be completely preserved.

Feather remains are not preserved.

RESULTS OF PHYLOGENETIC ANALYSIS

Analysis of the character matrix in Appendix 2 results in a sister-group relationship between *Messelastur* and *Tynskya*. Both taxa, the Messelasturidae, are shown to be the sister group of the Strigiformes, and the clade (Messelasturidae + Strigiformes) is shown to be the sister group of the clade (Falconidae + Accipitridae) (Fig. 6). None of these clades was, however, retained in the bootstrap analysis.

The following two characters are unambiguously optimized as synapomorphies of the clade (*Messelastur* + *Tynskya*), i.e., found with both the delayed transformation (DELTRAN) and accelerated transformation (ACCTRAN) mode (Fig. 6, node 15; numbers refer to characters in Appendix 1): (52) humerus with-

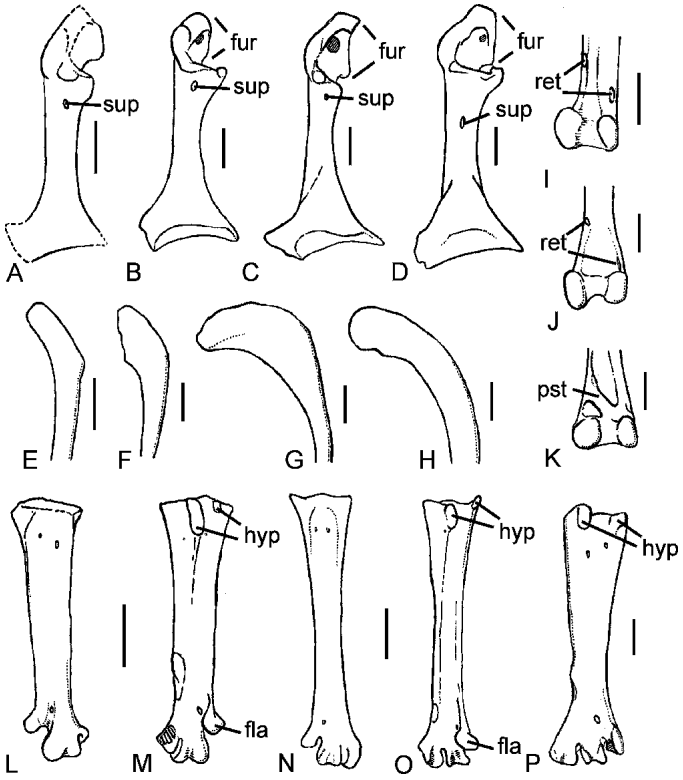

FIGURE 5. Selected skeletal elements of the Messelasturidae, fam. nov., in comparison with modern Strigiformes and Falconiformes. Left coracoid (**A**–**D**) of **A**, *Messelastur gratulator* (Messelasturidae; after SMF-ME 11080); **B**, *Asio otus* (Strigidae, Strigiformes); **C**, *Elanus leucurus* (Accipitridae, Falconiformes); **D**, *Milvago chimango* (Falconidae, Falconiformes). Left extremitas omalis of furcula (**E**–**H**) of **E**, *Messelastur gratulator* (Messelasturidae; after SMF-ME 11080); **F**, *Asio otus* (Strigidae, Strigiformes); **G**, *Elanus leucurus* (Accipitridae, Falconiformes); **H**, *Milvago chimango* (Falconidae, Falconiformes). Distal end of left tibiotarsus (**I**–**K**) of **I**, *Messelastur gratulator* (Messelasturidae; after SMF-ME 11080); **J**, *Asio otus* (Strigidae, Strigiformes); **K**, *Elanus leucurus* (Accipitridae, Falconiformes). Right tarsometatarsus in dorsal (**L**, **N**) and plantar (**M**, **O**, **P**) view of **L**, **M**, *Tynskya eocaena* (Messelasturidae; after Mayr 2000a:text-fig. 6); **N**, **O**, *Otus scops* (Strigidae, Strigiformes); **P**, *Elanus leucurus* (Accipitridae, Falconiformes). **Abbreviations**: **fla**, wing-like flange on trochlea metatarsi IV; **fur**, facet for articulation with furcula; **hyp**, cristae hypotarsi; **ret**, retinaculum extensorium tibiotarsi; **pst**, pons supratendineus; **sup**, foramen nervi supracoracoidei. Scale bars equal 5 mm.

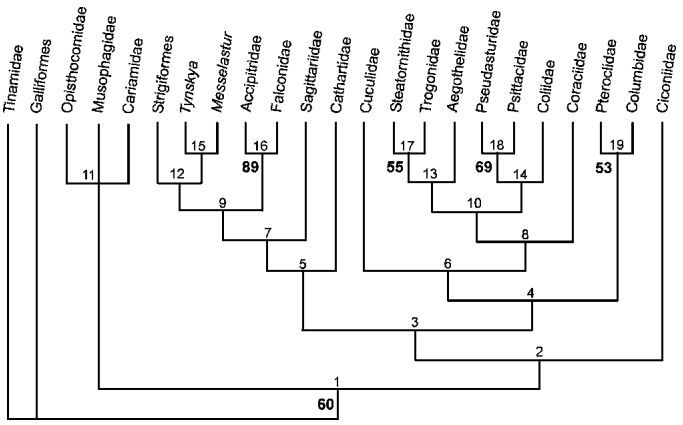

FIGURE 6. The strict-consensus cladogram of two most-parsimonious trees resulting from analysis of the character matrix in Appendix 2, with four characters (64, 74, 75, and 79) ordered (Length = 343, CI = 0.36, RI = 0.47, RC = 0.17). Bootstrap support values of more than 50% are indicated in boldface next to the corresponding node. Unambiguously optimized synapomorphies of the recovered nodes in both most parsimonious trees (numbers reference characters and states listed in Appendix 1; asterisked characters have a CI = 1.0; character transformation is 0→1, if not indicated otherwise): **1** – 22*, 38*, 48, 54 (1→0), 66, 77. **2** – 8, 11, 58, 90, 105 (1→0). **3** – 23 (1→0), 30 (1→0), 50 (1→0). **4** – 40, 65 (1→0), 85. **5 –** 1, 43 (1→0), 52, 91, 102, 106. **6 –** 3, 4, 16, 47, 64 (2→1), 69 (1→0), 98. **7** – 3, 6, 100. **8** – 39, 76, 94, 101 (1→5). **9 –** 73* (0→2), 83*, 87, 88*, 98. **10 –** 8 (1→0), 21, 103*. **11 –** 19, 61, 62*, 68. **12** – 72 (1→0), 79. **13 –** 16 (1→0), 34 (1→0). **14** – 71*, 84, 85 (1→0), 96*, 100, 104, 107 (1→0). **15 –** 52 (1→0), 53**. 16 –** 11 (1→0), 16, 41, 50, 60, 86. **17 –** 2, 9 (1→0), 10, 25*, 56. **18** – 60, 75, 78*, 79 (0→2), 80*. **19 –** 8 (1→0), 37, 51, 54, 61, 90 (1→0).

out well developed crista bicipitalis (reversal into primitive condition), and (53) humerus without foramen pneumaticum. The latter character is absent in all other raptorial birds (owls and diurnal birds of prey). As far as the specimens are comparable owing to their preservation, *Messelastur* and *Tynskya* are also very similar in overall osteology.

Sister-group relationship between Messelasturidae and Strigiformes (Fig. 6, node 12) is supported by: (72) distal end of tibiotarsus without ossified pons supratendineus (Fig. 5I), and (79) trochlea metatarsi IV of tarsometatarsus with plantarly projecting wing-like flange indicating a semi-zygodactyl foot (Fig. 6, only known from *Tynskya eocaena*). The combination of these two character states otherwise only occurs in some crown-group Psittacidae (see Appendix 2), from which messelasturids and owls are distinguished by several shared derived characters that were optimized as synapomorphies of higher hierarchical levels, as follows.

The clade including Strigiformes, Messelasturidae, Accipitridae, and Falconidae (Fig. 6, node 9) shares: (73) tarsometatarsus, hypotarsus without bony canals, crista lateralis separated from crista medialis by a wide sulcus, and (83) osseous claws, pair of canals lateral and medial to tuberculum flexorium (both characters are only known from *Tynskya eocaena*). In addition, Messelasturidae, Accipitridae, Falconidae, and Sagittariidae (Fig. 6, node 7) exhibit well-developed, caudally projecting processus supraorbitales on the os lacrimale. Reduction of these processes in owls (see above) may be due to the unusually large sclerotic rings and nocturnal way of living of strigiform birds. Other synapomorphies of nodes 7 and 9 in Figure 6 are unknown for the Messelasturidae.

DISCUSSION

The phylogenetic relationships between owls (Strigiformes) and diurnal birds of prey (Falconiformes) are among the problems of longest standing in ornithology. Many early authors considered these taxa to be closely related, but mainly due to the work of Fürbringer (1888) and Gadow (1893), the Strigiformes are currently widely separated from the Falconiformes and the shared similarities attributed to convergent evolution (see Sibley and Ahlquist, 1990, for a review of the history of avian classification). Although some recent cladistic analyses resulted in monophyly of a clade including Strigiformes, Accipitridae, and Falconidae (McKitrick 1991; Mindell et al., 1997:fig. 8.9; Mayr et al., 2003; Mayr and Clarke, 2003; see also Cracraft, 1981, 1988), many others did not (e.g., Kemp and Crowe, 1990; Griffiths, 1994; Livezey and Zusi, 2001; Sorenson et al., 2003; Mayr et al., 2003:fig. 5).

The present phylogenetic analysis supports inclusion of owls in the Falconiformes, as does the analysis of Mayr & Clarke (2003) on which the character matrix is based. The osteology of the Messelasturidae lends further support to this hypothesis, as messelasturids provide a morphological link between strigiform and falconiform birds in combining the derived tibiotarsus and tarsometatarsus characters of owls (absence of pons supratendineus, presence of well-developed trochlea accessoria) with a more plesiomorphic, 'falcon-' or 'hawk-like' skull morphology. Unfortunately, both sister group relationship between Messelasturidae and Strigiformes and inclusion of Strigiformes in the Falconiformes received no bootstrap support, and more data are needed to draw definitive conclusions. Clearly, however, the analysis shows that *Messelastur* is not a member of the Accipitridae, as tentatively assumed in the original description (Peters 1994).

In an earlier study (Mayr, 1998) and at a time when only the skull of this taxon was known, I considered the possibility that *Messelastur* is a member of the early Eocene psittaciform Pseudasturidae (Mayr, 2002); I also compared *Tynskya eocaena* with the Pseudasturidae in the original description (Mayr, 2000a). Presumably derived characters shared by Messelasturidae and Pseudasturidae include well-developed processus supraorbitales, the absence of a foramen pneumaticum on the proximal humerus, and the presence of an at least semi-zygodactyl foot (fully zygodactyl in Pseudasturidae). Also in overall morphology, i.e., bone shape and proportions, Messelasturidae and Pseudasturidae are very similar; this is especially notable as many earlier authors indeed assumed a close relationship between Psittaciformes, Strigiformes, and/or Falconiformes (see Sibley and Ahlquist, 1972, 1990). However, a clade including these taxa has not been supported by any cladistic analysis, and the present study results in a sister-group relationship between Psittaciformes (Pseudasturidae + Psittacidae) and Coliiformes (mousebirds). This grouping was initially proposed by Berman and Raikow (1982) and is also supported by some other analyses of morphological and molecular data (McKitrick, 1991; Mayr and Clarke, 2003; Chubb, 2004; contra, e.g., Sibley and Ahlquist, 1990; Espinosa de los Monteros, 2000; Livezey and Zusi, 2001).

Little can still be said about the way of living of the Messelasturidae. Judging from their short feet they were arboreal birds that probably were not adapted to nocturnal foraging, as the skull lacks many of the derived features of the otic and orbital region of owls. Messelasturids are fairly small and may have been hunting insects and other small birds. However, the very deep mandibular rami indicate a specialized feeding technique on hard food items. Whether the beak was used to crack hard-shelled insects (e.g., large beetles), bones, or even plant material remains unknown, owing to the absence of direct evidence in form of stomach content.

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APPENDIX 1

Character descriptions (see Mayr and Clarke 2003 for a more detailed discussion).

1. Upper beak, praemaxilla with sharply hooked tip: no (0), yes (1).
2. Skull, distinct naso-frontal hinge, i.e. caudal part of beak markedly set off by furrow against rostral part of cranium: absent (0), present (1).
3. Septum internasale largely ossified: no (0), yes (1).
4. Palate, processus maxillopalatini of ossa maxillaria fused along their midline: no (0), yes (1).
5. Os lacrimale, well developed descending process which touches or nearly touches jugal bar: yes (0), no (1).
6. Os lacrimale, caudally projecting processus supraorbitales: absent or vestigial (0), present and well developed (1).
7. Os ectethmoidale, greatly expanded and more or less inflated, plate-like, with dorsal margin largely fused with os frontale: no (0), yes (1).
8. Os palatinum, well-developed crista ventralis: absent (0), present (1).
9. Os palatinum, pars lateralis: absent or very small (0), present and well developed (1).
10. Ossa palatina completely fused along midline: no (0), yes (1).
11. Vomers: present, variably developed (0), vestigial or absent (1).
12. Vomers, caudal ends not fused, more or less deeply cleft: yes (0), no (1).
13. Vomers mediolaterally wide: yes (0), no (1).
14. Vomers forming a midline, narrow, and dorsoventrally high lamella: no (0), yes (1).

15. Os palatinum and os pterygoideum fused: yes (0), no (1).
16. Basipterygoid articulation in adulthood: present (0), absent (1).
17. Tubae auditivae: paired and lateral (0), paired and close to/adjacent on cranial midline or single anterior opening (tuba auditiva communis) (1).
18. Marked processus parasphenoidales mediales: absent (0), present (1).
19. Os opisthoticum/prooticum, pila otica with cluster of small pneumatic openings: no (0), yes (1).
20. Fronto-parietal suture: open (0), closed (1).
21. Processus zygomaticus: present, variably developed (0), absent or vestigial (1).
22. Quadratum, processus oticus, two well-separated heads for articulation with os squamosum and os prooticum: absent (0), present (1).
23. Quadratum, processus oticus, pneumatic foramina on dorsal end of caudal surface: absent (0), present (1).
24. Quadratum, condylus medialis, marked, rostrally projecting, concave articular surface: absent (0), present (1).
25. Columella with large, hollow, bulbous basal and footplate area exhibiting large fenestra on one side: no (0), yes (1).
26. Mandible, long and strongly mediolaterally compressed processus retroarticularis: absent (0), present (1).
27. Mandible, processus medialis, long, narrow, and dorsally-oriented: no (0), yes (1).
28. Atlas, well-developed, narrow processus ventralis: absent (0), present (1).
29. Atlas, foramina transversaria: absent (0), present (1).
30. Axis, corpus with pneumatic foramina on lateral sides: no (0), yes (1).
31. Axis, foramina transversaria: present (0), absent (1).
32. Axis, processus costales: present (0), absent (1).
33. Axis, osseous bridge from processus transversus to processus articularis caudalis: absent (0), present (1).
34. Third cervical vertebra, osseous bridge from processus transversus to processus articularis caudalis: absent (0), present (1).
35. At least 7th and 8th cervical vertebra, osseous bridge from processus costalis to midsection of corpus vertebrae: no (0), yes (1).
36. Number of praesacral vertebrae (all vertebrae cranial to synsacrum): 18–19 (0), 20–22 (1).
37. Several thoracic vertebrae fused to a notarium: no (0), yes (1).
38. Posterior caudal vertebrae with well-developed processus haemales: no (0), yes (1).
39. Pygostyle, discus pygostyli: absent (0), present (1).
40. Pygostyle, corpus perforated at caudoventral end: yes (0), no (1).
41. Furcula, extremitas omalis with strongly developed, laterally protruding facies articularis acrocoracoidea: no (0), yes (1).
42. Furcula, apophysis furculae: not as follows (0), abutting with an articular facet at apex carinae of carina sterni (1).
43. Coracoid, foramen nervi supracoracoidei: present (0), absent (1).
44. Coracoid, ?pneumatic foramen directly below facies articularis scapularis that does not penetrate shaft: absent (0), present (1).
45. Coracoid, impressio musculi sternocoracoidei on dorsal surface of extremitas sternalis with pneumatic foramina: no (0), yes (1).
46. Sternum, sulci coracoidei crossed: absent (0), present (1).
47. Sternum, well-developed, blade-like spina externa rostri: absent (0), present (1).
48. Sternum, number of processus costales: 3–4 (0), 5–6 (1).
49. Sternum, facies visceralis with numerous pneumatic foramina along midline and lateral margins: no (0), yes (1).
50. Sternum, caudal margin: with four notches/fenestrae (0), with two notches/fenestrae (1), or without notches/fenestrae (2).
51. Humerus short and stocky with crista deltopectoralis strongly protruding and triangular: no (0), yes (1).
52. Humerus, crista bicipitalis well developed: no (0), yes (1).
53. Humerus, foramen pneumaticum: present (0), absent (1). Note that this character has been incorrectly coded for Coliidae in Mayr and Clarke (2003).
54. Humerus, tuberculum dorsale greatly elongated proximodistally: no (0), yes (1).
55. Humerus, fossa musculi brachialis not present or very indistinct: yes (0), no (1).
56. Humerus, fossa musculi brachialis very deep and sharply delimited: no (0), yes (1).
57. Humerus, well-developed sulcus scapulotricipitalis: absent (0), present (1).
58. Ulna, distinctly exceeding humerus in length: no (0), yes (1).
59. Ulna, proximal end dorsoventrally compressed and craniocaudally inflected: yes (0), no (1).
60. Ulna, distal end with marked depressio radialis: no (0), yes (1).
61. Carpometacarpus, os metacarpale minus strongly bowed, delimiting large spatium intermetacarpale: no (0), yes (1). Note that this character has been incorrectly coded for Opisthocomidae in Mayr and Clarke (2003).
62. Carpometacarpus, proximal end of os metacarpale minus dorsoventrally wide and strongly deflected ventrally: no (0), yes (1).
63. Os carpi ulnare with crus longum greatly abbreviated: no (0), yes (1).
64. Pelvis, number of vertebrae ankylosed in synsacrum: 9–10 (0), 11–12 (1), 13–14 (2), 15–16 (3), 17–18 (4). This character was coded as ordered.
65. Pelvis, cristae iliacae dorsales largely or completely fused cranially with crista spinosa of synsacrum, thus forming closed canalis iliosynsacralis: no (0), yes (1).
66. Pelvis, tubercula praeacetabularia: large (0), absent or vestigial (1).
67. Pelvis, foramen ilioischiadicum caudally closed: no (0), yes (1).
68. Pelvis, deeply excavated recessus caudalis fossae: absent (0), present (1).
69. Femur, crista trochanteris markedly projected cranially: no (0), yes (1).
70. Femur, pneumatic foramen at cranio-lateral side of proximal end: absent (0), present (1).
71. Tibiotarsus, proximal end with ridge along medial side, opposite to crista fibularis: no (0), yes (1).
72. Tibiotarsus, distal end, ossified pons supratendineus: absent (0), present (1).
73. Tarsometatarsus, hypotarsus: not as follows (0), without bony canals, crista lateralis separated from crista medialis by wide sulcus (1), as before with crista medialis being much longer than crista lateralis (2).
74. Tarsometatarsus, hypotarsus, tendon of musculus flexor digitorum longus: not as follows (0), situated in marked furrow (1), enclosed in bony canal (2). This character was coded as ordered.
75. Tarsometatarsus, hypotarsus, tendon of musculus flexor hallucis longus: not as follows (0), situated in marked furrow (1), enclosed in bony canal (2). This character was coded as ordered.
76. Tarsometatarsus, canalis interosseus distalis: present (0), absent (1).

77. Tarsometatarsus, trochlea metatarsi II plantarly deflected and distal end reaching much less far distally than distal end of trochlea metatarsi IV: yes (0), no (1).
78. Trochlea metatarsi III much wider in mediolateral than in dorsoplantar direction, with distinct groove between rims; its dorsal surface not being significantly raised above dorsal surface of shaft: no (0), yes (1).
79. Trochlea metatarsi IV: not as follows (0), with plantarly projecting wing-like flange (typical of semi-zygodactyl feet) (1), with large trochlea accessoria (typical of fully zygodactyl feet) (2). This character was coded as ordered.
80. Tarsometatarsus, distal end, furrow between dorsal side of trochlea metatarsi IV and incisura intertrochlearis lateralis (Mayr, 2002:fig. 7): no (0), yes (1).
81. Hallux: not as follows (0), greatly reduced or completely absent (1).
82. Second and third phalanx of fourth toe: not as follows (0), greatly abbreviated, measuring less than half length of fourth phalanx (1), as before but with first phalanx also greatly abbreviated (2).
83. Osseous claws, pair of canals lateral and medial to tuberculum flexorium: absent (0), present (1).
84. Musculus iliotibialis lateralis, pars acetabularis: present (0), absent (1).
85. Musculus iliofemoralis externus: present (0), absent (1).
86. Musculus femorotibialis externus, distal head: present (0), absent (1).
87. Musculus flexor cruris lateralis, pars accessoria: present (0), absent (1).
88. Musculus flexor cruris lateralis, pars pelvica: present (0), absent (1).
89. Musculus caudofemoralis, pars caudalis: present (0), absent or poorly developed (1).
90. Musculus caudofemoralis, pars pelvica: present (0), absent (1).
91. Musculi obturatorii medialis et lateralis fused distally: yes (0), no (1).
92. Musculus iliofemoralis internus: present (0), absent (1).
93. Musculus iliotrochantericus medius: present (0), absent (1).
94. Musculus ambiens: present (0), absent (1). Modified from Mayr and Clarke (2003) according to George and Berger (1966:421).
95. Musculus ambiens, extent of origin: limited to tuberculum praeacetabulare (0), extending from tuberculum praeacetabulare to pubis (1).
96. Tendon of musculus extensor digitorum longus sending branch to hallux: no (0), yes (1).
97. Musculus fibularis longus, branch to flexor perforatus digiti III: present (0), absent (1).
98. Musculus flexor perforans et perforatus digiti III, vinculum: present: (0), absent (1).
99. Musculus flexor perforans et perforatus digiti II, origin from ansa iliofibularis: no (0), yes (1).
100. Musculus plantaris: present (0), absent (1).
101. Musculus flexor hallucis longus and musculus flexor digitorum longus, type of arrangement.
102. Musculus flexor hallucis longus, number of heads: one (0), two (1).
103. Musculus popliteus: present (0), absent (1).
104. Accessory musculus hallucis longus: present (1), absent (0).
105. Wing: diastataxic (0), eutaxic (1).
106. Beak with well-defined cere surrounding narial openings (feathered in some Psittacidae): absent (0), present (1).
107. Oil gland: tufted (0), minutely tufted (only vestigial feather remains present)/naked (1).
108. Medulla spinalis, cornu dorsale of substantia grisea: 'leiocerate', i.e., smooth and rounded (0), 'schizocerate', i.e. markedly inflected, 'split-horned' (1).
109. Syrinx, complete double A elements on bronchi caudal to tracheo-bronchial junction: absent (0), present (1); (after Griffiths 1994).
110. Syrinx, tympanum, fusion of A elements cranial to tracheobronchial junction: absent (0), present (1); (after Griffiths 1994).

APPENDIX 2

Character matrix of 110 morphological characters for the 22 taxa included in this study (see Appendix 1 for character definitions). Polymorphic characters are coded as such, unknown character states are indicated by "?".

	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	1	0	0
Galliformes	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0
Opisthocomidae	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	1	1	0	1	1	0	0
Cariamidae	0	0	0	1	1	1	0	0	1	0	0	1	1	1	1	1	1	0	1	1	0	1	1	0	0
Strigiformes	1	1	1	0	0	0	0	1	1	0	1	?	?	?	1	0	1	0	0	1	0	1	0	0	0
Messelastur	1	?	?	?	0	1	?	?	?	?	?	?	?	?	1	?	?	?	?	1	0	1	0	?	?	
Tynskya	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Accipitridae	1	0	1	0	0	01	0	1	1	0	0	1	1	1	1	1	1	0	0	1	0	1	0	0	0
Falconidae	1	0	1	0	0	1	0	1	1	0	0	0	1	0	1	1	1	0	0	1	0	1	0	01	0
Sagittariidae	1	0	1	01	0	1	0	0	1	0	1	?	?	?	1	0	1	0	0	1	1	1	1	0	0
Cuculidae	0	0	1	1	0	0	1	1	1	0	1	?	?	?	1	1	1	0	01	1	0	1	01	0	0
Musophagidae	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	1	1	1	0	0	0
Cathartidae	1	0	0	0	0	0	0	1	1	0	1	?	?	?	1	0	1	1	0	1	0	1	0	1	0
Ciconiidae	0	0	0	1	1	0	?	1	1	0	1	?	?	?	1	1	1	1	0	1	0	1	1	1	0
Pteroclidae	0	0	0	0	0	0	1	0	0	0	1	?	?	?	1	0	1	0	0	1	0	1	0	0	0
Columbidae	0	0	0	0	0	0	1	0	1	0	1	?	?	?	1	0	1	0	1	1	1	1	0	0	0
Steatornithidae	1	1	1	1	1	0	0	0	0	1	1	?	?	?	1	0	1	0	0	1	1	1	0	0	1
Pseudasturidae	0	?	?	?	?	1	?	?	?	?	?	?	?	?	1	?	?	?	?	1	1	1	?	0	?
Psittacidae	1	1	1	1	0	0	0	0	1	0	1	?	?	?	1	1	1	0	0	1	1	1	0	0	0
Coliidae	0	0	1	1	1	0	1	0	1	0	1	?	?	?	1	1	1	0	1	1	1	1	1	0	0
Trogonidae	0	1	1	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	1	1	0	0	1
Aegothelidae	1	0	0	0	?	?	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0
Coraciidae	0	0	1	1	0	0	0	1	1	1	0	1	1	0	1	1	1	0	0	1	0	1	0	0	0

APPENDIX 2
Continued.

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Tinamidae	0	0	0	0	1	0	0	01	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1
Galliformes	1	1	0	0	0	01	1	0	1	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	0
Opisthocomidae	0	0	0	1	1	0	1	1	1	0	1	1	1	0	0	1	0	1	1	1	?	?	1	1	1
Cariamidae	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	1
Strigiformes	0	1	0	0	0	1	1	0	1	0	0	0	1	0	0	01	0	0	0	0	01	0	1	0	0
Messelastur	0	?	?	?	?	?	?	?	0	0	0	0	?	?	?	0	0	0	0	0	?	?	1	?	?
Tynskya	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Accipitridae	0	1	0	0	0	1	0	0	01	0	01	0	1	0	0	1	0	0	0	0	01	01	1	0	1
Falconidae	0	1	0	0	0	1	1	0	1	0	01	1	1	0	0	1	0	0	0	0	1	1	1	0	1
Sagittariidae	0	1	1	1	0	0	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	2
Cuculidae	0	1	0	0	0	01	0	0	1	01	0	0	1	0	1	0	0	1	01	0	0	1	0	0	01
Musophagidae	0	0	0	0	0	01	1	0	1	1	0	0	1	1	0	1	0	0	0	0	1	1	01	0	0
Cathartidae	0	1	0	0	0	01	1	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	1	0	0
Ciconiidae	0	0	0	01	1	0	0	0	1	0	1	0	1	0	0	0	1	01	0	0	01	0	1	1	1
Pteroclidae	1	1	0	0	0	1	1	0	1	0	1	1	1	0	1	0	0	1	0	0	0	0	1	0	0
Columbidae	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	0	0	1	0	0	0	01	0	0	01
Steatornithidae	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1
Pseudasturidae	0	?	?	?	?	?	?	?	?	0	0	0	?	?	?	0	0	0	0	0	?	?	0	?	0
Psittacidae	0	0	1	0	0	1	1	0	01	01	0	0	1	0	1	0	0	1	0	0	1	1	1	0	1
Coliidae	0	0	1	0	0	1	1	0	1	1	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0
Trogonidae	0	1	0	0	0	1	1	0	0	0	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0
Aegothelidae	0	0	1	0	0	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
Coraciidae	0	0	0	0	01	1	01	1	1	1	0	0	1	1	1	0	0	1	0	0	0	1	1	0	0

	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
Tinamidae	0	0	0	1	0	0	0	0	0	0	0	0	0	4	0	0	0	0	1	0	0	1	0	0	0
Galliformes	0	0	0	1	1	0	1	0	0	0	0	0	0	3	1	0	1	1	1	01	0	1	0	2	0
Opisthocomidae	0	0	0	0	1	1	1	0	1	0	1	1	0	3	1	1	1	1	0	0	0	0	0	2	0
Cariamidae	0	0	0	0	1	0	1	0	0	0	1	1	0	2	1	1	1	1	1	0	0	1	0	0	0
Strigiformes	0	1	0	0	1	0	1	1	1	0	0	0	0	2	1	1	1	1	0	0	0	0	2	?	?
Messelastur	0	0	1	0	1	0	1	1	?	?	0	0	0	?	?	?	1	?	?	?	?	0	?	?	?
Tynskya	0	0	1	0	?	?	1	1	?	?	0	0	?	?	?	?	?	?	?	?	?	?	2	?	?
Accipitridae	0	1	0	0	1	0	1	1	1	1	0	0	0	2	1	1	1	0	0	1	0	1	1	?	?
Falconidae	0	1	0	0	1	0	1	1	1	1	0	0	0	12	1	1	1	0	1	1	0	1	2	?	?
Sagittariidae	0	1	0	0	1	1	1	0	1	0	0	0	0	2	1	1	1	1	1	1	0	1	0	0	0
Cuculidae	0	0	0	0	1	0	1	0	1	0	01	01	1	1	01	01	1	01	0	0	0	1	0	2	2
Musophagidae	0	0	0	0	1	0	1	0	1	0	1	1	1	2	0	0	1	1	0	1	0	1	0	2	0
Cathartidae	0	1	0	0	1	1	1	1	1	0	0	0	0	2	1	1	1	0	1	1	0	1	0	0	0
Ciconiidae	0	0	0	0	1	0	1	1	1	01	0	0	0	3	1	1	1	0	1	1	0	1	0	?	0
Pteroclidae	1	0	0	1	1	0	1	1	1	0	1	0	0	2	0	1	1	0	1	0	0	1	0	2	0
Columbidae	1	0	0	1	1	0	1	1	1	0	1	0	0	2	0	1	1	0	1	0	0	1	0	2	0
Steatornithidae	0	0	0	0	1	1	1	1	1	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0
Pseudasturidae	0	0	1	0	1	0	1	1	1	1	0	0	0	?	0	1	1	?	0	0	1	1	0	1	1
Psittacidae	1	0	0	1	1	0	1	1	1	1	0	0	0	2	1	1	1	0	0	0	1	01	0	2	2
Coliidae	0	0	1	0	1	0	1	01	1	0	1	0	0	1	0	1	1	0	0	0	1	1	0	2	0
Trogonidae	0	0	0	0	1	1	1	1	1	0	1	0	0	1	0	1	1	0	0	0	0	1	0	2	2
Aegothelidae	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	2	0
Coraciidae	0	0	0	0	1	0	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	1	0	2	0

	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	00
Tinamidae	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galliformes	0	0	0	0	0	0	0	01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Opisthocomidae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0
Cariamidae	0	1	0	0	0	1	0	0	?	?	?	?	?	1	?	?	?	?	0	?	?	?	?	?	?
Strigiformes	0	1	0	1	0	0	2	1	0	0	0	1	1	0	1	0	0	0	1	?	0	0	1	0	1
Messelastur	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tynskya	1	1	1	1	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Accipitridae	0	1	0	0	0	0	1	1	0	0	1	1	1	0	1	1	0	0	0	0	0	0	1	0	1
Falconidae	0	1	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	0	0	0	0	0	1	0	0
Sagittariidae	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1
Cuculidae	0	1	0	2	0	0	0	0	0	1	1	0	0	01	1	0	1	1	0	1	0	0	1	1	0
Musophagidae	0	1	0	0	0	0	0	0	?	0	?	0	0	?	0	?	1	1	0	1	?	?	0	?	?
Cathartidae	0	1	0	0	0	0	0	0	0	0	1	0	0	01	1	1	0	0	0	0	0	0	0	1	0
Ciconiidae	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	01	0	0	0	0	0	0
Pteroclidae	0	0	0	0	0	1	0	0	?	?	?	?	?	?	0	?	?	?	0	?	?	?	0	?	1
Columbidae	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	01	0	0	0	0	0	0
Steatornithidae	0	1	0	0	0	0	1	0	0	1	0	0	0	1	1	?	0	0	1	?	?	?	0	0	0
Pseudasturidae	1	1	1	2	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Psittacidae	1	1	1	2	1	0	0	01	1	0	0	0	0	0	1	1	0	0	01	?	1	1	1	1	1
Coliidae	0	1	0	0	0	0	2	0	1	0	0	0	0	0	1	1	0	0	1	?	1	1	1	0	1
Trogonidae	1	1	0	0	0	0	0	0	1	1	?	1	?	?	?	?	?	0	1	?	0	0	?	?	0
Aegothelidae	1	1	0	0	0	0	0	0	0	1	0	?	?	0	1	?	0	0	1	?	?	?	1	0	0
Coraciidae	1	1	0	0	0	0	0	0	01	1	0	0	0	0	1	0	0	0	1	?	0	1	1	0	0

APPENDIX 2
Continued.

	01	02	03	04	05	06	07	08	09	10
Tinamidae	1	0	0	0	1	0	0	0	?	?
Galliformes	1	0	0	0	1	0	0	1	?	?
Opisthocomidae	1	0	0	0	1	0	0	1	?	?
Cariamidae	?	?	?	?	1	0	1	?	?	?
Strigiformes	1	1	0	0	0	1	1	1	0	0
Messelastur	?	?	?	?	?	?	?	?	?	?
Tynskya	?	?	?	?	?	?	?	?	?	?
Accipitridae	3	1	0	0	0	1	0	?	1	1
Falconidae	3	1	0	0	0	1	0	1	1	1
Sagittariidae	3	1	0	0	0	1	0	?	1	1
Cuculidae	1	0	0	0	1	0	1	0	?	?
Musophagidae	?	?	?	?	1	0	0	1	?	?
Cathartidae	5	1	0	0	0	1	1	1	1	0
Ciconiidae	1	0	0	0	0	0	0	?	0	0
Pteroclidae	?	?	?	?	0	0	1	1	?	?
Columbidae	1	0	0	1	01	1	1	0	?	?
Steatornithidae	?	0	1	0	0	0	1	1	?	?
Pseudasturidae	?	?	?	?	?	?	?	?	?	?
Psittacidae	9	0	1	1	0	1	0	1	?	?
Coliidae	5	1	1	1	1	0	0	1	?	?
Trogonidae	8	?	1	?	1	0	1	1	?	?
Aegothelidae	?	0	1	0	0	0	1	1	?	?
Coraciidae	5	1	0	?	0	0	1	1	?	?