Contributions

from the Museum of Paleontology, University of Michigan

VOL. 37, NO. 3, PP. 69–78 NOVEMBER 24, 2025

A NEW RAPTORIAL BIRD FROM THE LOWER EOCENE GREEN RIVER FORMATION OF NORTH AMERICA

BY

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Abstract — Despite thousands of well-preserved avian specimens from Eocene lacustrine deposits in China, Europe and North America, the Paleogene record of raptorial birds allied with Accipitriformes, Strigiformes, and Falconiformes remains scarce. Here, we identify a new species from two specimens from the Fossil Lake deposits (Ypresian, Green River Formation) of Wyoming. These specimens, one an isolated skull and the other comprising both a skull and postcranial remains alongside dark feather impressions, provide new evidence that contributes to our understanding of diversity in the Green River avifauna. The recovery of beak and pedal morphologies indicate a raptorial ecology, but this suite of traits is known to characterize a paraphyletic assemblage within higher landbirds. While skull shape in the new species appears similar to Old World Vultures (Gypaetinae and Aegypiinae), the mandible morphology, size, and position of the narial opening and the limb proportions are unlike those seen in extant Accipitriformes. The new species most closely resembles *Masillaraptor parvunguis*, a raptorial taxon described from the Eocene Messel and London Clay formations that has previously been allied with Falconiformes. We conducted a series of phylogenetic analyses to evaluate placement of the new species, *Masillaraptor parvunguis*, and other early Paleogene taxa employing a backbone constraint based on the Bird 10,000 Genomes Project (B10K) molecular phylogeny of extant birds. The analysis recovers the new species within a large polytomy containing Passeriformes, Psittaciformes, Falconiformes, Phorusrhacidae as well as *Masillaraptor parvunguis* and *Danielsraptor phorusrhacoides*. We also included the new species in a published matrix assessing the relationships of *Masillaraptor* and *Danielsraptor*. Results from this analysis place this species in a clade with *M. parvunguis* and *D. phorusrhacoides*. We find further support close affinities between *Masillaraptor* and *Danielsraptor* and extant Falconiformes while highlighting the likely underestimated diversity of extinct Falconiformes. The new fossils additionally expand our knowledge of the avifauna of North America and Europe during the Eocene and contribute to our understanding of both the ecological diversity of birds in the Green River Formation and the morphological evolution of birds of prey.

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INTRODUCTION

Traditionally, "Falconiformes" comprised several closely related clades that were grouped together based on morphological characters and included Falconidae, Accipitridae, Pandionidae, Sagittariidae and Cathartidae (Cracraft and Rich, 1972; Livezey and Zusi, 2007; Mayr and Clarke, 2003; Olson, 1985); however, multiple molecular datasets have recovered a clade containing only part of "Falconiformes," including Falconidae, Psittacidae, Passeriformes and often Cariamiformes (Braun and Kimball, 2021; Hackett et al., 2008; Stiller et al., 2024). Current evidence suggests that the remaining "Falconiformes" are monophyletic, namely Accipitriformes, with Strigiformes consistently being placed as their sister taxon (Jarvis et al., 2014). Furthermore, some analyses have recovered Accipitriformes and Strigiformes as sister taxa, but a number of recent analyses have instead recovered Accipitriformes as sister to the rest of Afroaves (Kimball et al., 2019; Kuhl et al., 2021; Prum et al., 2015). The lack of consistency across different hypotheses for the placement of traditional "Falconiformes" is likely due to convergent adaptations of a similar raptorial morphology and ecology across several avian lineages (Bright et al., 2016; Jollie, 1977; Mahmood et al., 2014).

Relatively complete Paleogene bird skeletons with proposed raptorial ecologies are mostly known from Europe and North and South America (Mayr, 2009a), including the Phorusrhacidae, Bathornithidae (*Bathornis grallator*; Wetmore, 1944), Messelasturidae (*Tynskya* and *Messelastur*; Mayr, 2000; Peters, 1994), and Masillaraptoridae (*Masillaraptor parvunguis*; Mayr, 2009a). Records of Paleogene raptorial birds are rare in Africa and Asia, with one reported occurrence of an Oligocene strigiform from Egypt and a mysterious middle Paleocene *Strigogyps*-like specimen from Paleogene of the Qianshan Basin in southern China (Mayr et al., 2013; Smith et al., 2020). Phorusrhacidae is represented by an abundance of fossil material from South America and is considered to be a close relative of extant Cariamidae as well as the extinct Bathornithidae of North America (Alvarenga and Höfling, 2003; Mayr, 2009a). Messelasturidae has been proposed to be closely related to Strigiformes as well as the Halcyornithidae, Psittaciformes, and a clade containing both Psittaciformes and Passeriformes across several different phylogenetic analyses (Ksepka and Clarke, 2012; Mayr, 2000, 2005, 2021). *M. parvunguis* was originally proposed to be either the sister taxon to a clade comprising Falconiformes, Accipitriformes and the extinct Horusornithidae or within an unresolved polytomy containing Falconiformes, Accipitriformes, Tytonidae, Strigidae, and Horusornithidae (Mayr, 2006, 2009b). The most recent phylogenetic study including *M. parvunguis* places it as the sister taxon to *Danielsraptor phorusrhacoides* (Mayr and Kitchener, 2021) with medium bootstrap support (73% in Mayr and Kitchener, 2021). However, the matrix used in this phylogenetic analysis only comprised nine ingroup taxa and one outgroup taxon, only three of which are extant. The partial similarities shared between *M. parvunguis* and Falconiformes, Accipitriformes, and Cariamiformes continue to make its phylogenetic placement difficult to robustly resolve.

Rich assemblages of arboreal fossil birds have been reported from the Ypresian-age Fossil Lake deposits of the Green River Formation, providing evidence for an early radiation of major modern avian families (Grande, 2013). Here, we describe a new raptorial bird from Wyoming's Fossil Basin and the Fossil Butte and Angelo members of the Green River Formation (Fig. 1). The two new specimens representing this new taxon significantly differ from any other known taxa and share cranial features with Falconiformes, Accipitriformes, Cariamiformes, and the Masillaraptoridae. We evaluate phylogenetic positions of the new taxon using a new dataset which includes relevant extinct taxa and most core extant taxa of higher land birds as well as the matrix of Mayr and Kitchener (2021). These specimens representing a new bird of prey species from the Green River Formation provide insight into the evolution and diversity of extinct Falconiformes, and illuminate a particular niche in the Paleogene sub-tropical ecosystem.

INSTITUTIONAL ABBREVIATIONS

FMNH — The Field Museum, Chicago, IL, U.S.A.
FOBU — Fossil Butte National Monument, Kemmerer, WY, U.S.A.

SYSTEMATIC PALEONTOLOGY

Aves, Linnaeus, 1758
Falconiformes Sharpe, 1874
Masillaraptoridae Mayr, 2009b
Masillaraptor Mayr, 2006
Masillaraptor buchheimi sp. nov.

Etymology.— The specific epithet honors Dr. H. Paul Buchheim, a longtime friend of Fossil Butte National Monument as a geologist who provided key insights into the Green River Formation. He was a professor in the Department of Earth and Biological Sciences at Loma Linda University, California, U.S.A., from 1979 to 2019.

Holotype.— The holotype specimen (FOBU 9510; Fossil Butte National Monument, Wyoming, U.S.A.) comprises a complete skull, a partial cervical series, and the partial bones of an articulated hind limb (a distal femur, broken tibiotarsus, and impressions of the tarsometatarsus and pedal phalanges; Fig. 2). Part of the skull was preserved as slab and counter slab (nasal to cranium region), and a few bony portions were missing (Fig. 3). Measurements of the holotype (FOBU 9510; Fig. 2): skull length, 54.2 mm; prenasal portion of the skull, 26.4 mm; mandible length, 43.8 mm; cranial tracheal ring diameter, 4.3 mm; tibiotarsus length, 47.2 mm.

Referred specimens.— The referred specimen (FMNH PA 777) primarily comprises the negative mold of the skull (Fig. 4), although additional data were acquired after it was impregnated with silica and prepared from the reverse side at

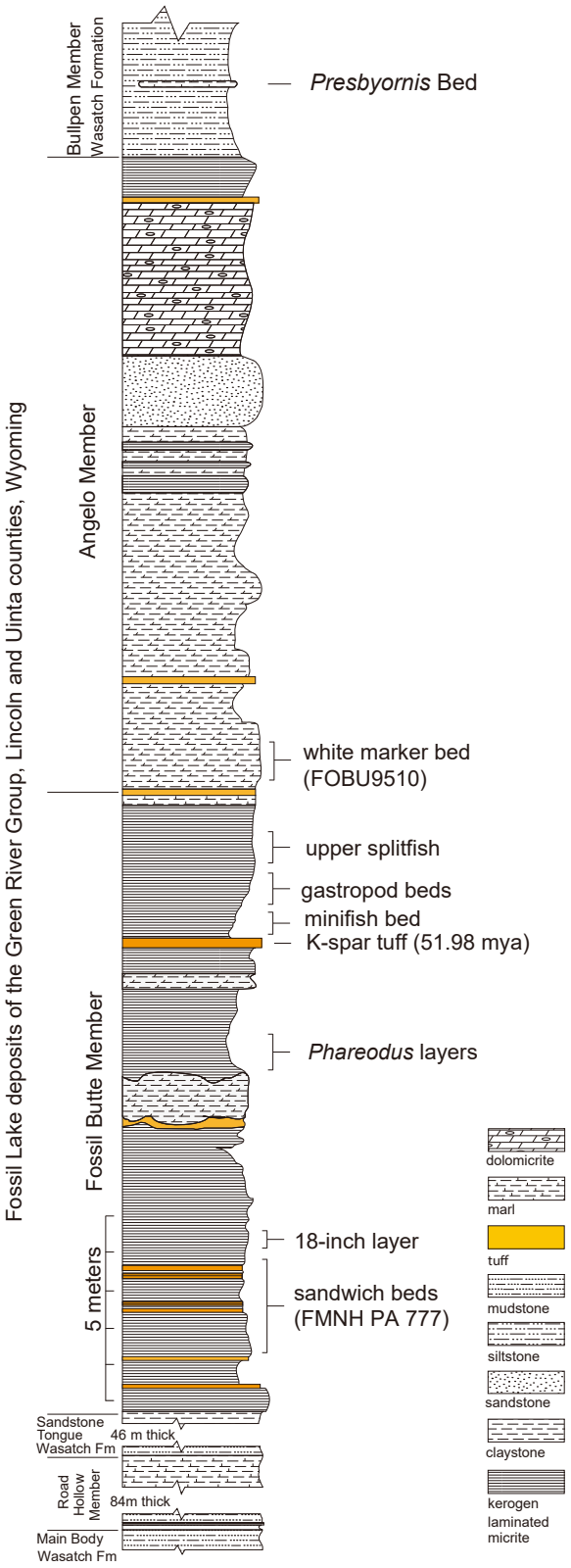


FIGURE 1 — Stratigraphic section of the Fossil Lake deposits indicating the units from which the holotype and referred specimen of Masillaraptor buchheimi were recovered relative to other key marker units. This composite section of Fossil Lake deposits (one of three lake deposits in the Green River Group) incorporates maximum thickness for the three members modified from (Buchheim et al. 2011). The *M. buchheimi* holotype specimen was recovered in a 15-cm-thick laminated micrite layer within the informally named "white marker bed" near the base of the Angelo Member. All other bird fossils are from other informal units within the Fossil Butte Member (Grande, 2013), except the "*Phareodus* layers." The "sandwich beds," from which the referred specimen was recovered, have produced the greatest number of fossil birds; this is attributed to more rock being excavated from these beds than all other units combined. This figure and caption are by Arvid Aase, a U.S. Government federal employee, and were completed as part of his official duties, and as such are considered a U.S. Government publication. Under provisions of the Copyright Act (17 USC Section 8), "No copyright shall subsist…in any publication of the U.S. Government, or any report in whole or in part thereof.," furthermore 44 USC Section 58 states that "…no government publication shall be copyrighted." Therefore, copyright protection cannot be directly indicated with affixing a copyright notice, or through inference of any kind for those contributions.

FMNH. Measurements for the referred specimen (FMNH PA 777; Fig. 4): skull length, 59.7 mm; prenasal portion of the skull, 28.6 mm; mandible length, 48.4 mm.

Locality.— The holotype specimen was collected under research permit on land managed by the Bureau of Land Management from the informal "white marker bed" within the Angelo Member of Fossil Lake deposits of the Green River Group, west of Kemmerer, Wyoming (Rendon, 2017). The specific location may be obtained for research purposes by contacting the Superintendent at Fossil Butte National Monument (Fig. 1). The referred specimen was collected from locality H of Grande and Buchheim (Grande and Buchheim, 1994) from the F-2 facies (nearshore Sandwich Beds) of the Fossil Butte Member of the Green River Formation (Grande, 2013). The different stratigraphic positions of these specimens indicate a potential range for the new species of about two million years (Grande, 2013).

Diagnosis and Differentia.— The new species is assigned to *Masillaraptor* based on the following features: a "raptorial-like" curved, massive beak with a straight culmen; a deeply hooked tip; a slightly dorsally deflected narrow symphysis of the mandible; a well-developed, straight and club shaped supraorbital process of the lacrimal (sup, Fig. 3) and tibiotarsus slightly shorter than skull length with a low cnemial crest. The new species is distinguished from *Danielsraptor phorusrhacoides* by its significantly smaller size, its further recurved, hook-like tip of the premaxilla, its recurved orbital process of the lacrimal that tapers to a wider terminus and meets the descending process of the lacrimal at an acute angle,

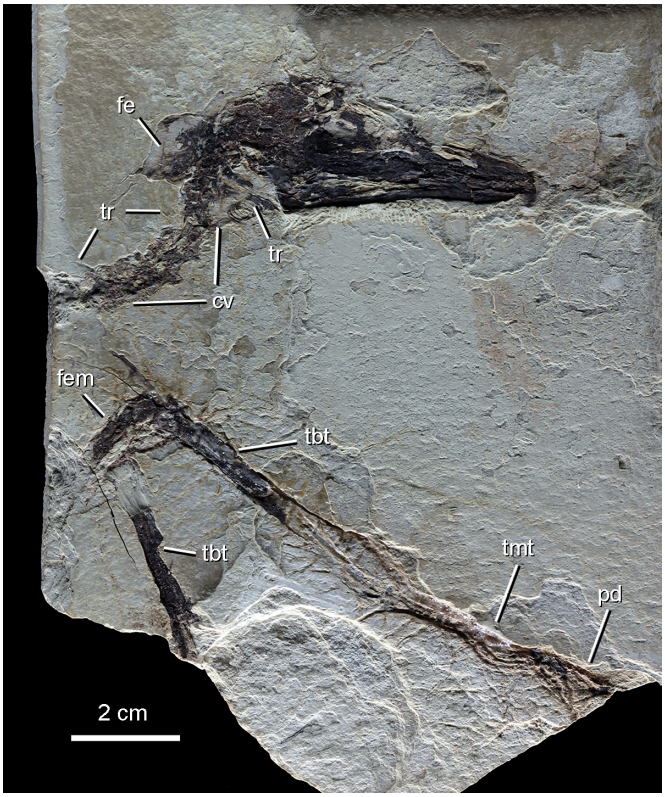


FIGURE 2 — Holotype specimen of *Masillaraptor buchheimi* (FOBU 9510). Anatomical abbreviations: *cv*, cervical vertebrae; *fe*, feather; *fem*, femur; *pd*, pedal digits; *tbt*, tibiotarsus; *tmt*, tarsometatarsus; *tr*, tracheal ring.

and approximate midpoint of the mandibular rami is slightly projected dorsally. The symphysis of mandible is shorter than that of *D. phorusrhacoides*. *Masillaraptor buchheimi* differs from *M. parvunguis* in the combination of following characters: a longer rostrum which is approximately half the length of the skull; a wide supraorbital process (sup, Fig. 3) of the lacrimal that is slightly recurved with a slightly tapered, rounded terminus; a slit-like, small external narial opening without an internarial septum present; a nearly straight mandible; a robust mandibular angle; dorsal deflection of the short symphysis of the mandible; a truncate, dorsally projecting hook-like accessory projection present caudolateral to the cotyla caudalis (Musser and Clarke, 2020: character 238); and a tibiotarsus that is slightly shorter than the skull in length and possesses a weakly proximally projected crista cnemialis cranialis.

ZooBank.— This work and the nomenclatural acts it contains have been registered in ZooBank, and the Life Science Identifiers (LSID) for the new species are registered with ZooBank (http://zoobank.org) with the identifiers urn:lsid:zoobank.org:pub:B9B747D8-C4AA-4920-B74D-AF66F3468C7D.

ANATOMICAL DESCRIPTION

The skull is flattened in both specimens (Figs. 2–4). The general cranial shape and rostrum proportions are superficially similar to those of accipitrid vultures (Accipitriformes) but the narial opening is much smaller in *Masillaraptor buchheimi*. The rostrum of *M. buchheimi* is about half length of the skull (see measurements) and is longer than those of most Accipitriformes and Falconiformes as well as that of *M. parvunguis*. The skull of *M. buchheimi* is significantly smaller than that of *D. phorusrhacoides*, and the hook at the tip of the premaxilla is more strongly recurved in *M. buchheimi* than in *D. phorusrhacoides*. The bony, anterior-most portion of the rostrum is broken in the holotype, with the strongly curved rhamphotheca identified (rha, Fig. 3) in black colored keratinized tissue altered during diagenesis, via processes such as carbonization, however, the rhamphotheca appears to be much less robust and curved than that of *D. phorusrhacoides*. In comparison to *D. phorusrhacoides*, the maxillae of *M. buchheimi* are narrower in the dorsoventral dimension. The external narial openings are elongate, ovoid and slit-shaped, and make up about one third the length of the rostrum. No nasal septum can be discerned. The supraorbital process of the lacrimal is elongate, slightly recurved and unfused to the cranium, whereas those of Accipitriformes and Falconiformes tend to either be fused to the cranium or further recurved (Jollie, 1977). The supraorbital process (sup, Fig. 3) of the lacrimal has a slightly tapered, rounded terminus (Fig. 3). Although the terminus of the supraorbital process of the lacrimal is tapered in many Accipitriformes it often tapers into a finer, more rounded point, and the orbital processes of Falconiformes often have with a more robust, spatulate terminus present. This process is straight and tapers to a finer point in *D. phorusrhacoides*. Additionally, the supraorbital process of the lacrimal meets the descending process of the lacrimal at approximately a right angle in *D. phorusrhacoides*, whereas this angle is less than 90 degrees in *M. buchheimi*. The jugal is more robust in *D. phorusrhacoides* than in *M. buchheimi*. A partial quadrate is present in *M. buchheimi* with large otic and orbital process present. Due to crushing it cannot be differentiated from that of *D. phorusrhacoides*. A curved outline delineates the caudal margin of the quadrate (Fig. 3) between the caudal condyle and the otic process.

The mandible is almost straight, with a robust mandibular angle present around the midpoint of the mandibular rami. This is in contrast to the mandibular angle of Accipitriformes, Falconiformes and *D. phorusrhacoides*, which is located near the condylar area of the mandible. Falconiformes additionally exhibit a significant ventral deflection of their mandibular symphysis, resulting in dramatic inferior curvature when viewed in lateral aspect (Fig. 5). This may be due to an adaptation caused by a heavy reliance on forceful bites for feeding rather than on specialized grasping feet as in Accipitriformes (Hertel, 1994). The similar downward deflection on the cranial portion of the mandible is less distinct in accipitrids. The symphysis of *M. buchheimi* is shorter than that of *D. phorusrhacoides*. A truncate, dorsally projecting hook-like accessory projection is present caudolateral to the cotyla caudalis

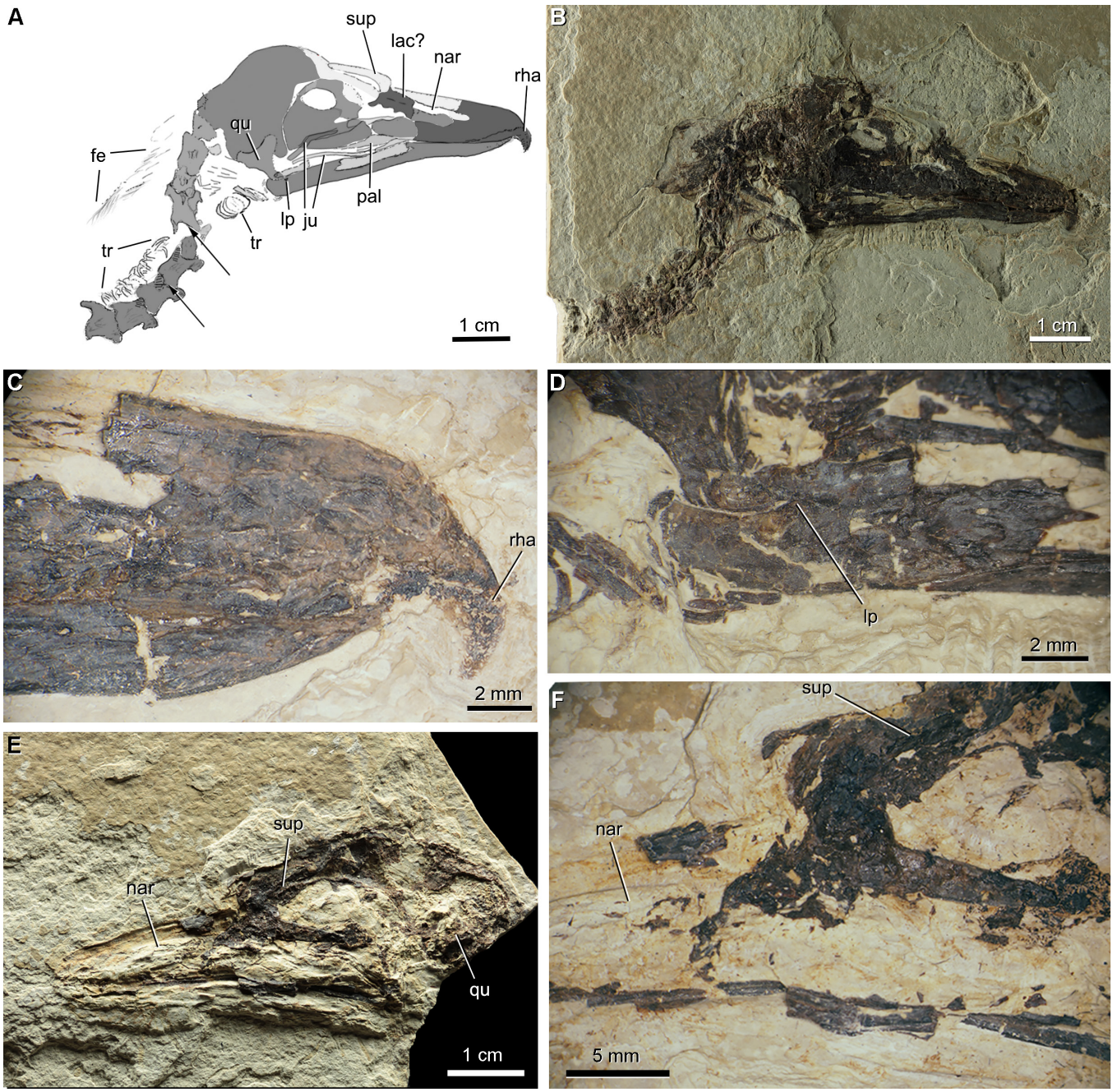


FIGURE 3 — Skull of the holotype specimen main part (**A–D**) and counterpart slab (**E–F**). **A**, line drawing; **B**, photograph of main slab. Arrows in **A** point to the facet of the zygapophysis oriented at different angles in the anterior and posterior cervical vertebrae. **C**, detail view of the rostral portion and post mandibular portion (**D**) of the holotype specimen. Photograph of the counterpart slab of the holotype skull (**E**) with enlarged view of the narial region (**F**). Anatomical abbreviations: *fe*, feather; *ju*, jugal; *lac*, lacrimal; *lp*, lateral process; *nar*, naris; *pal*, palatine; *qu*, quadrate; *rha*, rhamphotheca; *sup*, supraorbital process of the lacrimal; *tr*, tracheal rings.

(Musser and Clarke, 2020, character 238; lp, Fig. 3). This feature is present in extant Falconiformes and *Masillaraptor*, but is smaller and less distinct in *M. buchheimi*.

There are at least 10 cervical vertebrae preserved in the holotype specimen FOBU 9510. The individual length of each cervical vertebra appears to be relatively short compared to extant Accipitriformes, but similar to that of falconiform species. The middle series of the cervical vertebrae are distinguished by the presence of a rounded acute angle formed by the left and right side of the zygopophyses, i.e., lacuna interzygapophysialis (Baumel and Witmer, 1993) as seen in many accipitrids (e.g., *Neophron*). The posterior cervical

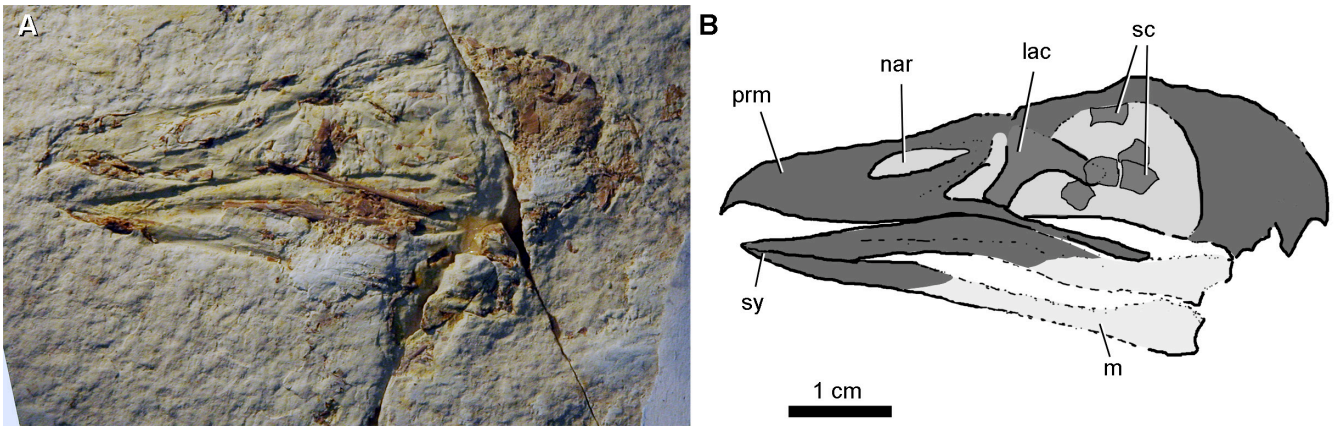


FIGURE 4 — Referred specimen of *Masillaraptor buchheimi* (FMNH PA 777). **A**, photograph and **B**, line drawing. Anatomical abbreviations: *lac*, lacrimal; *m*, mandible; *nar*, naris; *prm*, premaxilla; *sc*, sclerotic ossicles; *sy*, symphysis.

vertebrae are characterized by having relatively larger zygopophyses and a decreased angle where the two zygopophyses meet (arrow, Fig. 3). These discrete cervical features are consistent with those present in Accipitriformes rather than those of Falconiformes, which have an obtuse angle between their cervical zygopophyses and rather tight contact between these cervical vertebrae, especially for the articulation of anterior ones. In *D. phorusrhacoides*, one of several cranial thoracic vertebrae has larger prezygopophyses than the posterior vertebrae, which is present in Accipitriformes but not in Phorusrhacidae (Degrange et al., 2015). The hind limbs are partially preserved in the new holotype specimen. The crista cnemialis cranialis is well projected and projects more than that of *D. phorusrhacoides*. The length of the tibiotarsus is slightly shorter than the skull length, which is similar to the condition in *M. parvunguis* (Mayr, 2006).

PHYLOGENETIC ANALYSIS

We examined extant and extinct raptorial birds to evaluate the potential phylogenetic affinities of *Masillaraptor buchheimi* and built a small new dataset including 15 osteological characters preserved in the new species (Appendix 1). Two representatives of Charadriiformes and Gruiformes (Burhinidae and Psophiidae, respectively) were chosen as outgroup taxa based on previously proposed higher-level avian phylogeny (Hackett et al., 2008). Ingroup taxa (*Acanthisitta*, *Agapornis*, *Athene*, *Andalgalornis*, *Aquila*, *Cathartes*, *Chunga*, *Dendrocopos*, *Falco*, *Leptosomus* and *Urocolius*) were selected and coded at the family level to represent major character variation. We also scored *M. buchheimi* into the phylogenetic matrix of Mayr and Kitchener (2021). We performed unconstrained heuristic parsimony analyses of each dataset in PAUP∗ (Swofford, 2002; Version 4.0a169) using 10,000 random taxon addition replicates per run. Tree bisection-reconnection branch swapping was employed and minimum branch lengths valued at zero were collapsed, following Mayr and Clarke (2003) and Musser and Cracraft (2019). No character weighting was applied. Bootstrap analyses were performed for both matrices using 500 bootstrap replicates each with 1,000 random taxon addition replicates following the methodology of Mayr and Clarke (2003). We used a backbone constraint based on the well-supported B10K molecular phylogeny of extant birds during analysis of our newly constructed matrix (Stiller et al., 2024). Extinct taxa were unconstrained in all analyses.

Phylogenetic analyses yield consistent results that differ in their resolution. The analysis of the dataset in Appendix 1 recovers 50 most parsimonious trees (best tree score = 51, consistency index [CI] = 0.4118, homoplasy index [HI] = 0.5882, retention index [RI] = 0.5313, rescaled consistency index [RC] = 0.2188). *M. buchheimi* is recovered in a strict consensus cladogram within a polytomy containing *M. parvunguis*, *D. phorusrhacoides*, Falconiformes, Phorusrhacidae, Passeriformes and Psittaciformes (Fig. 5A). Cariamidae is recovered as the closest outgroup to this more inclusive clade. Results across trees recover two unambiguous (6, 1→0; 11, 0→1) characters that are shared by *M. buchheimi* and Falconiformes: having a small external narial opening (6: 0) and having an elongate and straight orbital process of the lacrimal (11: 1).

Analysis of the Mayr and Kitchener (2021) matrix yielded six most parsimonious trees (best tree score = 64, CI = 0.6721, HI = 0.3279, RI = 0.7619, RC = 0.5238; Fig. 5B) and in a strict consensus cladogram places *M. parvunguis* as the sister taxon to *D. phorusrhacoides* with 80% bootstrap support. The *M. parvunguis*+*D. phorusrhacoides* sister group is recovered within a polytomy containing Falconidae and *M. buchheimi* with 63% bootstrap support (Fig. 5B). M. buchheimi shares with Falconidae four unambiguous characters (5, 1→0; 8, 0→1; 9, 0→1, CI = 1.0; 13, 0→1, CI = 1.0): having a

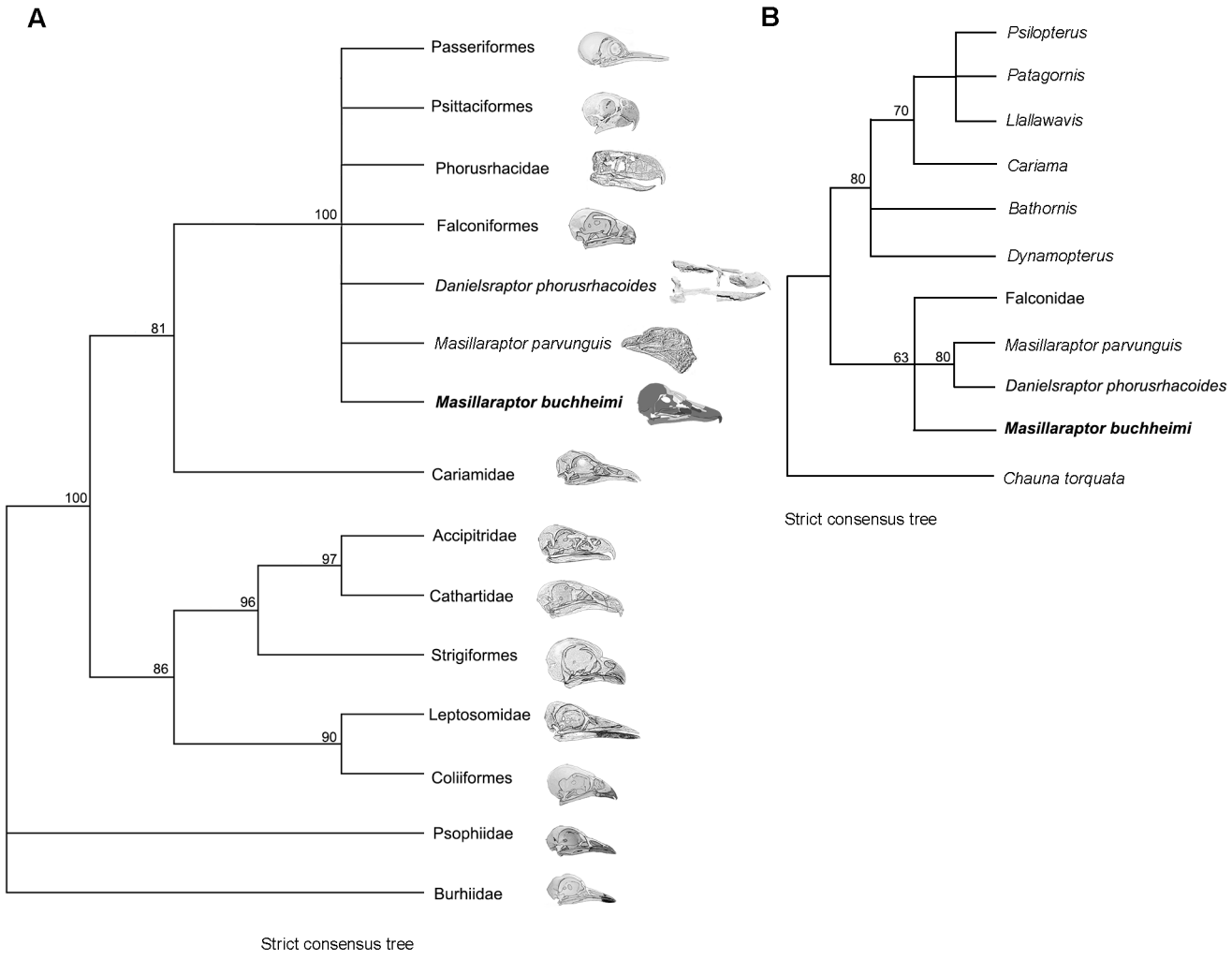


FIGURE 5 — Results of the phylogenetic analyses. **A**, Strict consensus of 50 trees from analysis of the dataset in Appendix I (TL=51, CI = 0.4118, RI = 0.5313, RC = 0.218); **B**, the strict consensus of six most parsimonious trees (TL=64, CI = 0.6875, RI = 0.7619, RC = 0.5238) derived from analysis of the new species in the matrix of Mayr and Kitchener (2021). Bootstrap support values are labeled next to the corresponding nodes.

processus postorbitalis slender and mainly ventrally projected (5: 0), having an upper beak with a sharply hooked tip (8: 1), tomial grooves (9: 1), and having a dorsal projection at the caudal articular end of the mandible which rostrally borders the cotyla lateralis:(13: 1; lp, Fig. 3D).

DISCUSSION

Masillaraptor buchheimi shares several features with other "raptorial birds" including the well-developed orbital process of the lacrimal known to be present in Falconiformes, some Accipitriformes, Phorusrhacidae, Cariamidae, *Masillaraptor parvunguis*, and *Danielsraptor phorusrhacoides*. This process in the new specimen is distinct in that it is straight with a club-shaped, slightly tapered terminus (sup, Fig. 3), which is most similar to that of *M. parvunguis* (Mayr, 2009b). The strongly curved beak shape of the new specimen indicates a raptorial ecology; but its straight, elongate culmen is most similar to those in some Accipitriformes (e.g., Old World vultures). The body size of the specimen is comparable to that of a small kestrel (e.g., *Falco sparverius*). It is also slightly smaller than another proposed carnivorous bird without a hooked rostral tip from the Green River Formation, the stem cuckoo roller *Pleisiocathartes* (Weidig, 2006).

Phylogenetic analyses suggest that *M. buchheimi* is likely most closely related to extant Falconiformes. No character support for close alignment of *M. buchheimi* with other included extinct taxa was found despite each fossil preserving the necessary elements for comparison. Ultimately, the relationships of early Eocene "raptorial-like" birds like *M. buchheimi* remain poorly resolved. A long, massive beak with a straight culmen that characterizes Masillaraptoridae may represent a trait that is convergent in Accipitridae, particularly in their overall rostrum shape. This contrasts with the vaulted or raised culmen observed in the dorsal culmen region of Cariamiformes and Falconiformes. These key differences in derived beak morphology may represent distinct adaptations for "raptorial" functions that differ from those present in Phorusrhacidae and Falconidae. Convergent evolution may additionally be obscuring the relationships of these extinct taxa.

Early raptorial birds from European and North American Eocene localities are extremely rare and their ecology remains enigmatic. Species of the Masillaraptoridae are now reported from the early Eocene Green River Formation as well as the Eocene Messel Formation in Germany and the earliest Eocene London Clay Formation in England. The expanded geographic distribution of *Masillaraptor* to include North America suggests that this taxon was critical to the ecology of paratropical forests across the Northern Hemisphere. They are widely spread through the early and middle Eocene Messel Formation in Germany and the earliest Eocene London Clay Formation in England, representing successful dispersal across two large continents. Extinct "raptorial birds" in North America and Europe appear to have inhabited larger regions within pantropical forests. Additional discoveries are needed to better understand this important ecological role and the phylogenetic placement of the Masillaraptoridae.

ACKNOWLEDGMENTS

We thank Lance Grande for starting our journey working with Green River birds. We further thank him for their support as a collaborator and mentor over many years and for their tireless passion for gaining a full picture of the diversity of Fossil Lake and its depositional environments. William Simpson has also been an important ally in supporting our work and provided assistance over many years. Additionally, we thank Angella Thompson for photographic assistance as well as Matthew Brown and Sebastian Egberts for preparation of the holotype specimen. Two anonymous referees provided valuable suggestions for improving earlier version of the manuscript. This work was supported early on grant NSF EAR 0938199 (0719758) "Collaborative Research: Integrated study of an exceptional avifauna from the Eocene Green River Formation: new data on avian evolution and taphonomy" to JAC, a collaborative grant with Lance Grande. Support from the Jackson School of Geosciences, Field Museum of Natural History, and Fossil Butte National Monument were key to making this work possible. Finally, support from the National Key Research and Development Project of China (2024YFF0807603) to ZL made completion of this project possible.

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APPENDIX 1 — Descriptions of characters used in the phylogenetic analysis. Dataset available online via OSF (DOI 10.17605/OSF.IO/G3XYB).

1. Dorsal outline of culmen: straight (0); dorsally vaulted (1).
2. Rostrum, upper beak shape: pointed (1); curved (1).
3. Rostrum, upper beak, dorsoventral width: narrow (0); medium (1); massive or wide (2).
4. Rostrum, tominal margin of the upper beak: smooth (0); notched (1); teethed notched (2). (Modified from Mayr 2009b).
5. Bony nares, shape: round (0); ovid (1); silt (2).
6. Bony nares, size: small (0); large (1).
7. Bony nares, relative position in rostrum: anterior (0); posterior (1).
8. Rostrum, length: around one-half skull length (0); approximately one-third total skull length (1); extremely short (2).
9. Internarial septum: absent (0); present (1).
10. Mandible, rostral tip: straight (0); ventrally deflected (1); slightly dorsally (upward) deflected (2).
11. Lacrimal, superorbital process: absent (0); long and straight (1); triangular shape (2).
12. Tibiotarsus, length relative to skull length: shorter or about the same (0); longer (1).
13. Zygomatic process: absent 0; present but small (1); well development (2). (Modified from Mayr, 2009b).
14. Pedal digit, proximal phalanx length (pedal digit II-1): shortened (0); long (1). (Adopted from Mayr, 2009b).
15. Fourth toe, central phalanges length (pedal digit IV-2, and 3): shortened (0); long (1). (Adopted from Mayr, 2009b).

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Contributions from the Museum of Paleontology, University of Michigan, is a medium for publication of reports based chiefly on museum collections and field research sponsored by the museum.

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Print (ISSN 0097-3556), Online (ISSN 2771-2192)