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SKELETON OF A NEW OWL FROM THE EARLY EOCENE OF NORTH AMERICA (AVES, STRIGIFORMES) WITH AN ACCIPITRID-LIKE FOOT MORPHOLOGY

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ABSTRACT—We describe a partial skeleton of a large-sized owl from Wasatchian strata of the Willwood Formation (Wyoming, U.S.A.). The holotype of *Primoptynx poliotauros*, gen. et sp. nov., includes all major postcranial bones and is one of the most substantial Paleogene records of the Strigiformes. The fossil shows that owls exhibited a considerable morphological diversity in the early Eocene of North America and occupied disparate ecological niches. As in the protostrigid taxon *Minerva* from the late early to early middle Eocene of North America, but unlike in extant owls, the ungual phalanges of the hallux and the second toe of the new species are distinctly larger than those of the other toes. *Primoptynx poliotauros* gen. et sp. nov., however, does not exhibit the derived tibiotarsus morphology of the Protostrigidae. Even though the new species may well be a stem group representative of protostrigid owls, current data do not allow an unambiguous phylogenetic placement. Concerning the size of the ungual phalanges, the feet of *P. poliotauros* correspond to those of extant hawks and allies (Accipitridae). We therefore hypothesize that it used its feet to dispatch prey items in a hawk-like manner, whereas extant owls kill prey with their beak. *Primoptynx* and protostrigid owls were possibly specialized in foraging on prey items that required an accipitrid-like killing strategy, such as larger-sized or more defensive mammals. The extinction of these peculiar owls may have been related to the radiation of accipitrid diurnal birds of prey, which appear to have diversified in the late Eocene and early Oligocene.

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INTRODUCTION

Owls (Strigiformes) have an extensive fossil record, beginning in the mid-Paleocene (Mayr, 2009, 2017; Kurochkin and Dyke, 2011; Göhlich and Ballmann, 2013). However, most early Cenozoic taxa are represented by only a few bones, and it remains elusive when and how owls acquired their characteristic skeletal morphology.

The earliest fossil species belong to the taxa *Ogygoptynx* and *Berruornis*. *Ogygoptynx wetmorei* Rich and Bohaska, 1976, from the mid-Tiffanian (60–59 Ma) of Colorado, U.S.A. (Rich and Bohaska, 1976, 1981), is the sole representative of the taxon Ogygoptyngidae and is only known from a single tarsometatarsus. *Berruornis* includes two species, *B. orbisantiqui* Mourer-Chauviré, 1994, from the upper Paleocene (late Thanetian; ~57.5 Ma) of France (Mourer-Chauviré, 1994), and *B. halbedeli* Mayr, 2002, from the middle Paleocene (~61 Ma; Mayr and Smith, 2019) of Germany (Mayr, 2002, 2007). *Berruornis* was assigned to the taxon Sophiornithidae, which was first established for *Sophiornis quercynus* Mourer-Chauviré, 1987, a species from an unknown stratigraphic interval in the middle Eocene to upper

Oligocene Quercy fissure fillings of France (Mourer-Chauviré, 1987, 1994).

Most Eocene owls are assigned to the Protostrigidae. This taxon was established by Wetmore (1933) for a tibiotarsus from the late early to early middle Eocene Bridger Formation (Wyoming, U.S.A.). At that time, the fossil was classified as ‘*Protostrix lydekkeri* Shufeldt, 1913.’ However, a subsequent revision by Mourer-Chauviré (1983) showed this species to be a junior synonym of *Minerva antiqua* Shufeldt, 1913, which is represented by fragmentary leg bones and pedal phalanges from the Bridger Formation. According to Mourer-Chauviré (1983), the taxon *Minerva* includes three further species, two of which, *M. leptosteus* (Marsh, 1871) and *M. saurodosis* Wetmore, 1921, likewise stem from the Bridger Formation. The published material of *M. leptosteus* consists of a distal tibiotarsus (Wetmore, 1937) and a tentatively referred distal tarsometatarsus (Rich, 1982); a previously undescribed and nearly complete tarsometatarsus of *M. cf. leptosteus* is reported in the present study. Of *M. saurodosis*, only the distal end of the humerus is known (Wetmore, 1921), and another species of *Minerva*, *M. californiensis* (Howard, 1965), from the upper Eocene of California, is likewise based on a humerus.

In addition to *Minerva*, the Protostrigidae currently also include the taxa *Eostrix* and *Oligostrix*. *Eostrix* comprises four species from lower Eocene localities in North America and Asia: *E. mimica* (Wetmore, 1938) (Willwood Formation,

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Wyoming, U.S.A.), *E. martinellii* Martin and Black, 1972 (Wind River Formation, Wyoming), *E. gulottai* Mayr, 2016 (Nanjemoy Formation, Virginia, U.S.A.), and *E. tsaganica* Kurochkin and Dyke, 2011 (Naranbulag Formation, Mongolia). All of these species are represented by distal tarsometatarsi, and for *E. mimica* and *E. tsaganica* the distal end of the tibiotarsus is also known. A proximal tarsometatarsus and a pedal phalanx from the lower Eocene London Clay were likewise assigned to *Eostrix* (*E. vincenti* Harrison, 1980). The taxon *Oligostrix* was originally erected for *O. rupelensis* Fischer, 1983, from the lower Oligocene of Germany, which is based on a distal tibiotarsus (Fischer, 1983). Another, tentatively referred species, ?*O. bergeri* De Pietri, Mourer-Chauviré, Menkveld-Gfeller, Meyer, and Costeur, 2013, is based on a tarsometatarsus from the upper Oligocene of Switzerland (De Pietri et al., 2013).

Most of the above strigiform taxa are known from fragmentary tarsometatarsi and tibiotarsi. The only Paleogene strigiform species that is represented by more than a few leg bones is a species from the uppermost lower Eocene of Messel in Germany, which was described as *Palaeoglaux artophoron* Peters, 1992. The taxon *Palaeoglaux* was initially established for *P. perrierensis* Mourer-Chauviré, 1987, from the upper Eocene of the Quercy fissure fillings in France, which is represented by fragmentary limb bones (Mourer-Chauviré, 1987). *P. artophoron* is known from postcranial skeletons of two individuals (Peters 1992; Mayr, 2009), but owing to the poor bone preservation, few osteological details can be discerned in these specimens.

Berruornis, *Ogygoptynx*, and the species assigned to the Protostrigidae are outside crown group Strigiformes, the clade including extant Tytonidae (barn owls) and Strigidae (true owls) (Mourer-Chauviré, 1987; Mayr, 2009, 2017), but the phylogenetic affinities of early Cenozoic Strigiformes are poorly resolved and have not yet been subjected to a formal phylogenetic analysis. Mourer-Chauviré (1994) hypothesized that in the evolution of owls, the tarsometatarsal trochleae for the second and fourth digits gradually became more plantarly deflected, with the trochlea metatarsi II decreasing in size. These progressive modifications of the tarsometatarsus were interpreted as a specialization toward improved grasping or perching capabilities. Otherwise, however, very little is known about the evolutionary history and paleobiology of early Cenozoic owls.

Here, we describe a partial skeleton of a new species of owl from the early Eocene Willwood Formation in North America, which includes all major postcranial bones. The specimen was discovered three decades ago, and even on a global scale it constitutes one of the most complete Paleogene fossils of a strigiform bird discovered so far. As detailed in the following, the fossil differs from extant owls in a number of skeletal features and exhibits a distinctive foot morphology, which documents unusual foraging strategies in some early Cenozoic Strigiformes.

MATERIALS AND METHODS

Osteological comparisons are based on skeletons of the following species of extant Strigiformes (all in the collection of the Senckenberg Research Institute Frankfurt): Tytonidae: *Phodilus badius*, *Tyto alba*, *Tyto novaehollandiae*; Strigidae: *Aegolius funereus*, *Asio flammeus*, *Asio otus*, *Athene cunicularia*, *Athene noctua*, *Bubo bubo*, *Bubo magellanicus*, *Bubo scandiacus*, *Bubo virginianus*, *Glaucidium brasilianum*, *Glaucidium passerinum*, *Ninox novaeseelandiae*, *Ninox scutulata*, *Otus asio*, *Otus lempiji*, *Otus scops*, *Ptilopsis leucotis*, *Pulsatrix perspicillata*, *Pseudoscops clamator*, *Surnia ulula*, *Strix aluco*, *Strix nebulosa*, *Strix rufipes*, and *Strix uralensis*.

Measurements refer to the maximum length of a bone along its longitudinal axis. Osteological terminology follows Baumel and Witmer (1993). Nomenclature of the extant species is based on

the International Ornithological Congress (IOC) World Bird List at www.worldbirdnames.org.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, New York, U.S.A.; SMF, Senckenberg Research Institute, Frankfurt, Germany; UMMP, University of Michigan, Museum of Paleontology, Ann Arbor, Michigan, U.S.A.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758

STRIGIFORMES Wagler, 1830

Family incertae sedis

PRIMOPTYNX, gen. nov.

Included Species—*Primoptynx poliotauros*, sp. nov.

Diagnosis—Distinguished from all other strigiform taxa by the combination of the following features: coracoid with deeply excavated fossa in sulcus supracoracoideus; carpometacarpus with wide spatium intermetacarpale and large proximal portion; tibiotarsus with mediolaterally narrow condylus medialis; and tarsometatarsus with broad trochlea metatarsi II, which bears a distal fossa and forms a shovel-shaped medial flange that terminates in a crest. The medial flange of the trochlea metatarsi II is here considered to be a diagnostic autapomorphy.

Etymology—The genus name is derived from ‘primus’ (Latin), first, and ‘ptynx’ (Greek), owl, and is feminine in gender.

PRIMOPTYNX POLIOTAUROS, sp. nov.

Holotype—UMMP 96195, a partial skeleton including a fragment of the mandibular symphysis, three thoracic vertebrae, both coracoids, the cranial portion of the right scapula, fragments of the sternum, both humeri, portions of both radii, the left ulna, the right os carpi ulnare, the right carpometacarpus, both legs, as well as unidentifiable bone fragments.

Differential Diagnosis—The new species was about the size of a female of the extant spectacled owl, *Pulsatrix perspicillata*. In addition to the autapomorphic shape of the trochlea metatarsi II (see genus diagnosis), it is distinguished from (1) *Minerva antiqua* (Shufeldt, 1913) in condylus medialis of tibiotarsus not mediolaterally widened; first phalanx of hallux proportionally longer (20.2 vs. 16.4–19.4 mm in *M. antiqua* [see Mourer-Chauviré, 1983]); the distal width of the tibiotarsus smaller (13.1 vs. 15.8–15.9 mm in *M. antiqua* [see Mourer-Chauviré, 1983]); tuberculum extensorium of ungual phalanx of hallux more dorsally directed and cotyla articularis less plantarly facing; and proximal (first) phalanx of second toe with symmetrical proximal end (forming medial projection in *M. antiqua*); (2) *Minerva leptosteus* (Marsh, 1871) in tibiotarsus without mediolaterally broad condylus medialis; and trochlea metatarsi III of tarsometatarsus proportionally narrower; (3) *Minerva saurodosis* (Wetmore, 1921) and *M. californiensis* Howard, 1965, in distal end of humerus forming well-defined tuberculum supracondylare dorsale (absent in *M. saurodosis* and *M. californiensis*); (4) all species of *Eostrix* Wetmore, 1938, in larger size (Table 1); and trochlea metatarsi II of tarsometatarsus proportionally larger, reaching farther distally, and without plantar flange; (5) *Ogygoptynx* Rich and Bohaska, 1976, in tarsometatarsus much stouter; tuberositas musculi tibialis cranialis shorter and more medially situated; trochlea metatarsi II mediolaterally wider and hardly plantarly deflected; and trochlea metatarsi III proportionally narrower; and (7) *Berruornis* Mourer-Chauviré, 1994, in tarsometatarsus with proportionally narrower shaft; trochlea metatarsi III about as deep as wide (dorsoplantarly deeper in *Berruornis*); and proximal end of tarsometatarsus with deep fossa infracotylaris dorsalis.

Type Locality and Horizon—McCullough Peaks locality MP-228 in the Willwood Formation of the northern Bighorn Basin,

TABLE 1. Measurements (in mm) of *Primoptynx poliotauros*, gen. et sp. nov., compared with those of other strigiform species from the Eocene of North America, Europe, and Asia.

Taxon	Tibiotarsus Distal width	Tarsometatarsus Distal width	Humerus Distal width	Humerus Length
<i>Primoptynx poliotauros</i>	13.1	~17	18.0	102.4
<i>Minerva antiqua</i>	15.8–15.9 ^a	—	—	—
<i>Minerva leptosteus</i>	13.5 ^b	14.3 ^b	—	—
<i>Minerva saurodosis</i>	—	—	18.7 ^d	—
<i>Minerva californiensis</i>	—	—	18.6 ^c	105 ^c
<i>Eostrix mimica</i>	11.5 ^b	13.2 ^b	—	—
<i>Eostrix martinellii</i>	—	9.8 ^b	—	—
<i>Eostrix tsaganica</i>	—	7.8 ^c	—	—
<i>Eostrix gulottai</i>	—	3.9	—	—

^aAfter Mourer-Chauviré (1983:table 3).

^bAfter Rich (1982:table 1).

^cAfter Kurochkin and Dyke (2011).

^dAfter Wetmore (1921).

^eAfter Howard (1965).

Park County, Wyoming, U.S.A. The general area of the locality is ‘Roan Wash’ on the U.S. Geological Survey’s Ralston 7.5-minute topographic quadrangle; the land survey description is SW¼, SW¼, Section 15, Township 54 North, Range 99 West. Stratigraphically, the locality is at the 360 m level (measured above the Paleocene-Eocene boundary) in the Lower Peerless local section and the McCullough Peaks Central composite section of Clyde (2001), with a substantial associated mammalian fauna of early middle Wasatchian age, biochron Wa-3 (early Graybullian), 54.5–55 Ma (Gingerich, 1983, 2010). The specimen was found by Xiaoyuan Zhou and collected by X. Zhou and P. Gingerich in 1990.

Measurements—(in mm; l: left, r: right): Coracoid, length, 42.5 (r). Humerus, length of assembled halves, ~102 (l), proximal width, 19.5 (r), distal width, 18.0 (r). Ulna, length, 105.7 (l). Carpometacarpus, length, 50.1 (r). Femur, length, 64.9 (l)/64.7 (r); proximal width, 15.7 (l)/14.3 (r); distal width, 13.7 (l)/17.2 (r). Tibiotarsus, length >109 (l)/>108 (r); distal width, 13.1 (r). Tarsometatarsus, length, ~55–65; width of shaft proximal near breakage of distal end, 9.0 (r); mediolateral width of trochlea metatarsi II, 10.1 (l)/8.6 (r); mediolateral width of trochlea metatarsi III, 5.0 (r); preserved distal width, 14.3 (r); estimated distal width, ~17 (r). Pedal phalanges, length: I1, 20.3 (r); I2, ~26 (>23.8) (r); III1, 13.3 (r); II2, 27.2 (r); II3, ~27 (>24.5) (r); III1, 11.5 (l)/12.5 (r); III2, 13.5 (l); III3, 19.7 (l); III4, ~19 (>17.5) (l); IV1, 8.5 (r); IV2, 6.1 (r); IV3, 5.9 (r); IV4, 15.4 (l); IV5, ~19 (>14.0) (l).

Etymology—The species epithet is coined from ‘polios’ (Greek), gray, and ‘tauros’ (Greek), bull, in reference to the fact that the fossil stems from the Graybullian substage of the Wasatchian.

Taphonomic Remarks—The fossil was together with a skeleton of the artiodactyl mammal *Diacodexis* Cope, 1882. All of the long hind limb bones are broken, and this postmortem breakage seems to have occurred before the fossil was embedded in the sediment. The right femur, for example, is broken into two parts, which are preserved in situ. Both ends are slightly displaced relative to each other but show a concordant morphology, with a flat caudal surface and a convex cranial surface. The two portions of the left femur, however, have contrasting morphologies: whereas the distal half has a convex cranial and a flat caudal surface, the proximal half has a convex caudal and a flat cranial surface. We hypothesize that this morphology is due to the fact that the left femur was already broken into two pieces when it was embedded in the sediment, and that the bone fragments were oriented in different positions when they experienced compression from the overlying sediment. Fossilization in a fractured state was also assumed for the holotype of *Calcardea junnei* Gingerich, 1987, another avian species from the Willwood Formation

(Mayr et al., 2019). Unambiguous predation marks are, however, not visible on the bones of either *C. junnei* or the new strigiform species, so that the reason for this unusual taphonomy remains elusive.

Description and Comparisons—The only cranial bone associated with the holotype of *Primoptynx poliotauros*, gen. et sp. nov., is the mandibular symphysis (Fig. 1A, B), the immediate tip of which is broken. This bone is narrower than the mandibular symphysis of the Strigidae (Fig. 1D) and more similar to that of *Tyto alba* (Tytonidae; Fig. 1C) in its proportions.

The fossil includes three diagenetically flattened thoracic vertebrae, which are preserved in articulation (Fig. 1E, F). The lateral sides of the vertebral corpora of at least two of these vertebrae exhibit large pneumatic foramina, which are absent in crown group Strigiformes. The lack of processus ventrales suggests that the vertebrae represent the caudal-most thoracics.

The left coracoid is nearly complete, whereas the right one lacks the midsection (Fig. 2A–F). The bone agrees with the coracoid of crown group Strigiformes in overall shape but differs in osteological details. As in extant owls, a foramen nervi supracoracoidei is present. The processus procoracoideus is broken in both coracoids, so that its length is unknown. The tip of the processus acroracoideus is more rounded than in crown group Strigiformes (Fig. 3C, E), and, unlike extant owls, the medial surface of the facies articularis clavicularis bears a distinct sulcus that extends in a sterno-omal direction (Fig. 2B). The cotyla scapularis is more deeply excavated than in crown group Strigiformes. However, the most distinctive feature of the bone is a marked fossa in the sulcus supracoracoideus (Fig. 2B, E). This morphology is not present in crown group Strigiformes (in which the sulcus supracoracoideus may exhibit pneumatic foramina), but an equally deep fossa in the sulcus supracoracoideus was reported for the taxon *Palaeoglaux* (Mourer-Chauviré, 1987; Peters, 1992). The dorsal surface of the sternal extremity exhibits distinct muscle striae (Fig. 2F); the angulus medialis is less prominent than in crown group Strigiformes.

UMMP 96195 includes the proximal end of the right scapula, which lacks the acromion (Fig. 2G). The preserved portion of the shaft of the bone is craniocaudally curved. Remains of the furcula could not be identified. A fragment of the cranial-most portion of the sternum is still embedded in a piece of matrix (Fig. 1G). In addition, a fragment of the right(?) costal margin of the sternum with three processus costales is situated next to the left ulna and humerus (Fig. 2Q).

The left humerus (Figs. 2L, M, N, R, 3A) is distorted by dorso-ventral compression, whereas the right humerus (Fig. 2H–K) is craniocaudally flattened. Both humeri are broken into two pieces, and at least the shorter right one lacks a section of the

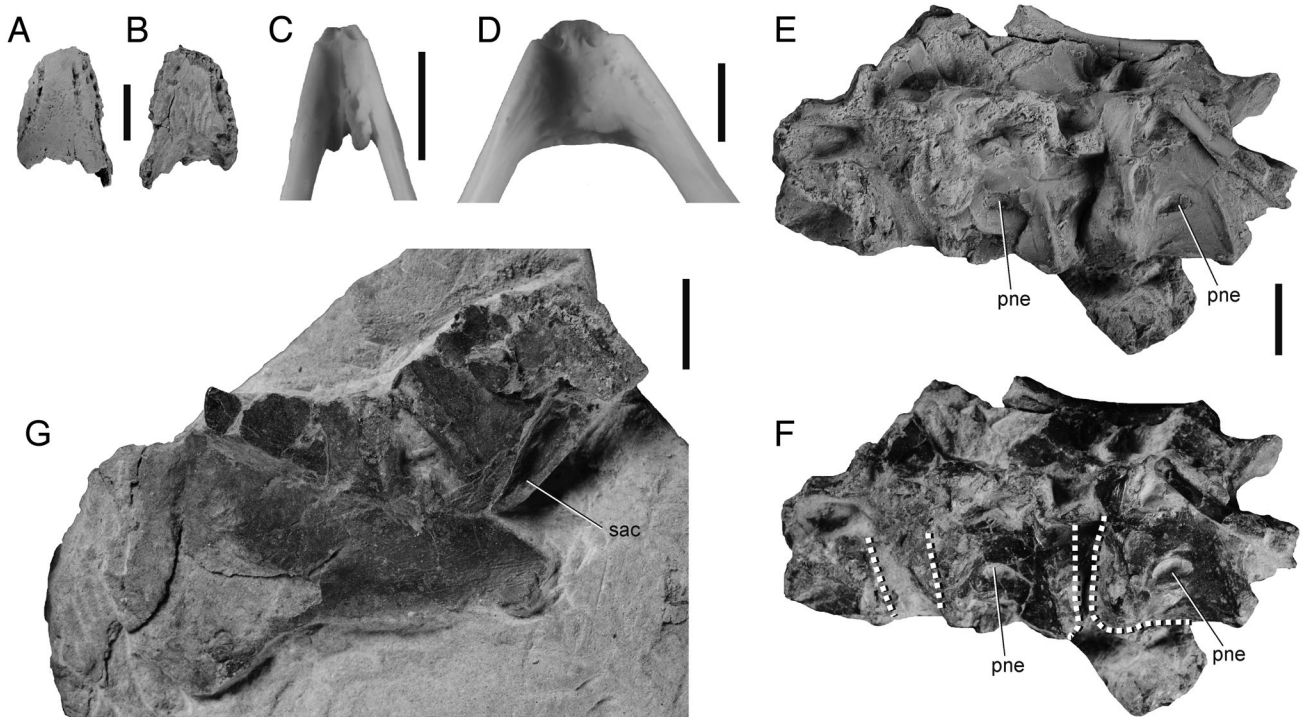


FIGURE 1. **A, B**, *Primoptynx poliotauros*, gen. et sp. nov., UMMP 96195, holotype, fragment of mandibular symphysis in **A**, ventral and **B**, dorsal views. For comparison, mandibular symphyses of **C**, *Tyto alba* (Tytonidae) and **D**, *Bubo scandiacus* (Strigidae). **E, F**, *Primoptynx poliotauros*, gen. et sp. nov., UMMP 96195, holotype, three thoracic vertebrae in articulation; the dotted lines in **F** delimit individual vertebral bodies; **G**, fragment of sternum. Specimens in **A, B**, and **E** were coated with ammonium chloride. **Abbreviations:** **pne**, pneumatic openings in vertebral corpus; **sac**, sulcus articularis coracoideus. Scale bars equal 5 mm.

shaft. However, because the humeri of owls and other representatives of Telluraves never exceed the ulna in length, the completely preserved left ulna provides a maximum length constraint of about 105 mm for the humerus of *P. poliotauros*. From this length estimate, it can be concluded that the humerus of *Primoptynx* was proportionally shorter and stouter than the elongate humerus of crown group Strigiformes. The proximal end of the right humerus appears to be only slightly distorted by diagenetic compression, even though the tuberculum ventrale is broken and missing. The proximal portion with the caput humeri is proportionally longer than in crown group Strigiformes, and the crista bicipitalis is less developed and shorter. The crista deltopectoralis is of similar length to that of extant Strigiformes. Unlike in extant owls, the impressio coracobrachialis in the dorsal portion of the cranial surface appears to have been shallow and did not define a deep depression (Fig. 3B). The fossa pneumotricipitalis is proportionally larger than in crown group Strigiformes. As in extant owls, the tuberculum dorsale is small and situated on the proximodorsal margin of the humerus. On the distal end of the bone, there is a well-defined tuberculum supracondylare dorsale, which also occurs in crown group Strigiformes but is absent in the humeri of *Minerva saurodosis* and *M. californiensis*. Owing to the crushing of the bones, the exact extent of the fossa musculi brachialis cannot be determined. The tuberculum supracondylare ventrale appears to be larger than in crown group Strigiformes. The condylus dorsalis has similar proportions to that of crown group Strigiformes, in which it is small and forms an angle of about 45° with the distal margin of the humerus. The condylus ventralis likewise is of similar shape to that of extant owls, whereas it is more globose in *Palaeoglaux perrierensis* from the upper Eocene of the Quercy fissure fillings in France. The morphologies of the

processus flexorius and the tuberculum supracondylare ventrale correspond with crown group Strigiformes. As in extant Strigiformes, the sulcus scapulotricipitalis is short and well defined.

The left ulna is represented by two pieces that fit together seamlessly, so that the original length of the bone can be reliably assessed (Fig. 2N). The proximal end of the bone differs from that in crown group Strigiformes in the proportionally longer cotyla dorsalis, which is about as long as the cotyla ventralis (Fig. 2P). Unlike in *Palaeoglaux perrierensis*, the proximal end of the ulna is not dorsoventrally compressed. The shape of the distal end of the bone (Fig. 2Q) is similar to that in extant Strigiformes, except that the tuberculum carpale is situated farther dorsally, which may be a result of the diagenetic deformation of the fossil. As in extant owls, the condylus dorsalis is long in proximo-distal direction.

UMMP 96195 includes the proximal and distal sections of both radii (Fig. 2S–V). The preserved portions of the shaft do not show any traces of an osseous arch, the presence of which is a characteristic derived feature of extant owls (Bock and McEvey, 1969). The proximal end exhibits a distinct and elongate tuberculum bicipitale radii; in proximal view, the facies articularis ulnaris has a more circular outline than in extant Strigiformes.

The right carpometacarpus (Figs. 2W, X, 3G) is largely complete except for the os metacarpale minus; the left carpometacarpus is not preserved. The remaining sections of the os metacarpale minus indicate that the latter was bowed and delimited a wide spatium intermetacarpale. In crown group Strigiformes, the width of the spatium intermetacarpale shows much variation (e.g., Kessler, 2017:pl. 11), and whereas it is narrow in, e.g., *Tyto alba*, a wide spatium intermetacarpale of similar proportion to that of *P. poliotauros* occurs in, e.g., *Pulsatrix perspicillata* (Fig. 3O). The extremitas proximalis is proportionally

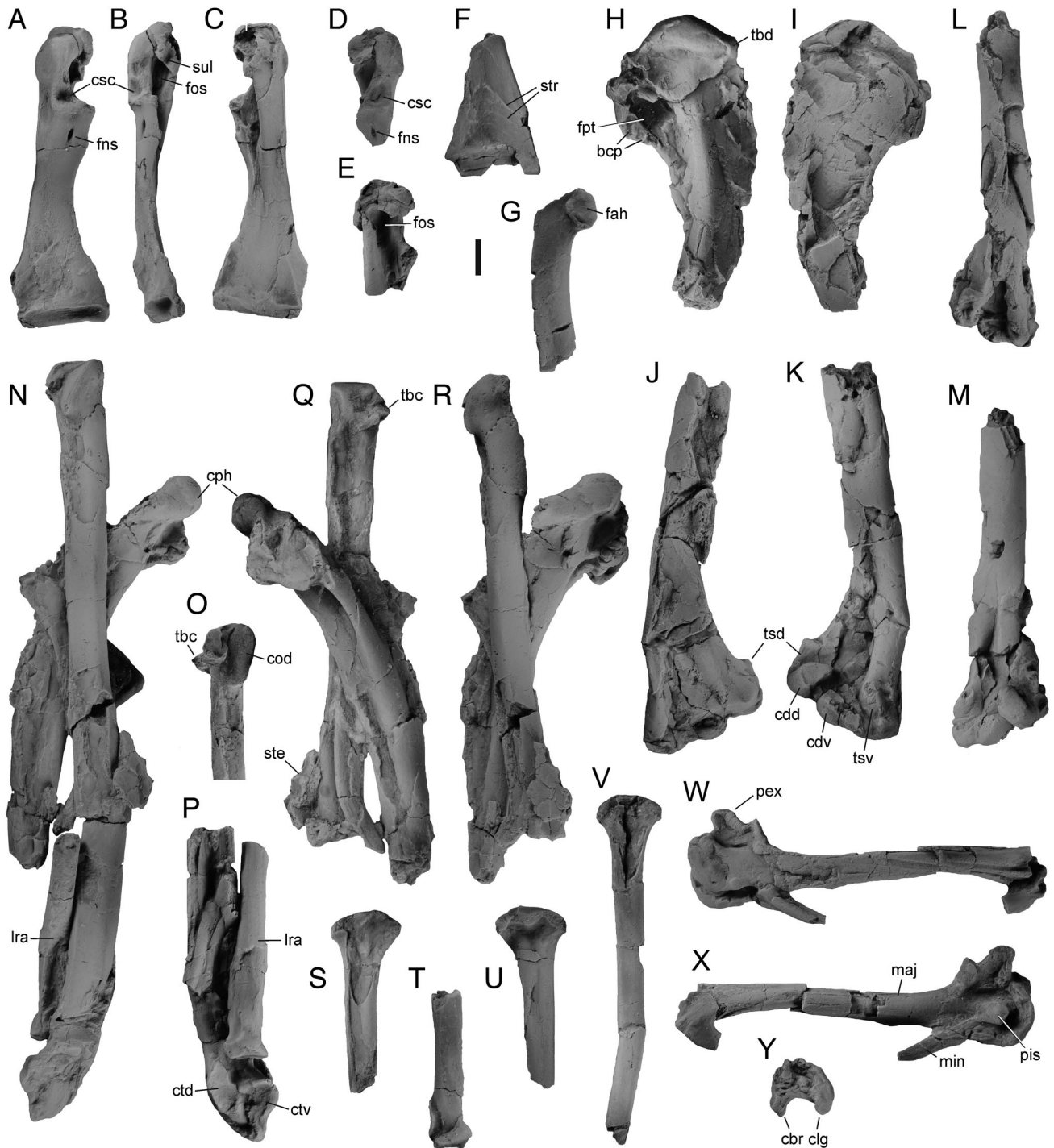


FIGURE 2. *Primoptynx poliotaurus*, gen. et sp. nov., UMMP 96195, holotype, pectoral girdle and wing bones. **A–C**, left coracoid in **A**, dorsal, **B**, medial, and **C**, ventral views. **D, E**, extremitas omalis of right coracoid in **D**, dorsal and **E**, medial views. **F**, extremitas sternalis of right coracoid in dorsal view. **G**, cranial portion of right scapula in lateral view. **H, I**, proximal portion of right humerus in **H**, caudal and **I**, cranial views. **J, K**, distal portion of right humerus in **J**, caudal and **K**, cranial views. **L, M**, distal portion of left humerus in **L**, caudal and **M**, cranial views. **N**, left ulna (the two fragments of the bone were assembled for the picture) and proximal portion of left humerus. **O**, distal portion of left ulna in ventral view. **P**, proximal portion of left ulna (cranial view) with associated proximal portion of left radius. **Q, R**, distal portion of left ulna and proximal portion of left humerus in association in two different views. **S, U**, distal end of left radius in **S**, cranial and **U**, caudal views. **T**, proximal portion of right radius in ventral view. **V**, distal portion of right radius in cranial view. **W, X**, right carpometacarpus in **W**, dorsal and **X**, ventral views. **Y**, right os carpi ulnare. All bones were coated with ammonium chloride. **Abbreviations:** **bcp**, crista bicipitalis; **cbr**, crus breve; **cdd**, condylus dorsalis (humerus); **cdv**, condylus ventralis; **clg**, crus longum; **cod**, condylus dorsalis (ulna); **cph**, caput humeri; **csc**, cotyla scapularis; **ctd**, cotyla dorsalis; **ctv**, cotyla ventralis; **fah**, facies articularis humeralis; **fns**, foramen nervi supracoracoidei; **fos**, fossa in sulcus supracoracoideus; **fpt**, fossa pneumotricipitalis; **ira**, left radius; **maj**, os metacarpale majus; **min**, os metacarpale minus; **pex**, processus extensorius; **pis**, processus pisiformis; **ste**, fragment of margo costalis of sternum; **str**, muscle striae; **sul**, sulcus in medial surface of facies articularis claviculae; **tbc**, tuberculum carpalae; **tbd**, tuberculum, dorsale; **tsd**, tuberculum supracondylare dorsale; **tsv**, tuberculum supracondylare ventrale. Scale bar equals 5 mm.

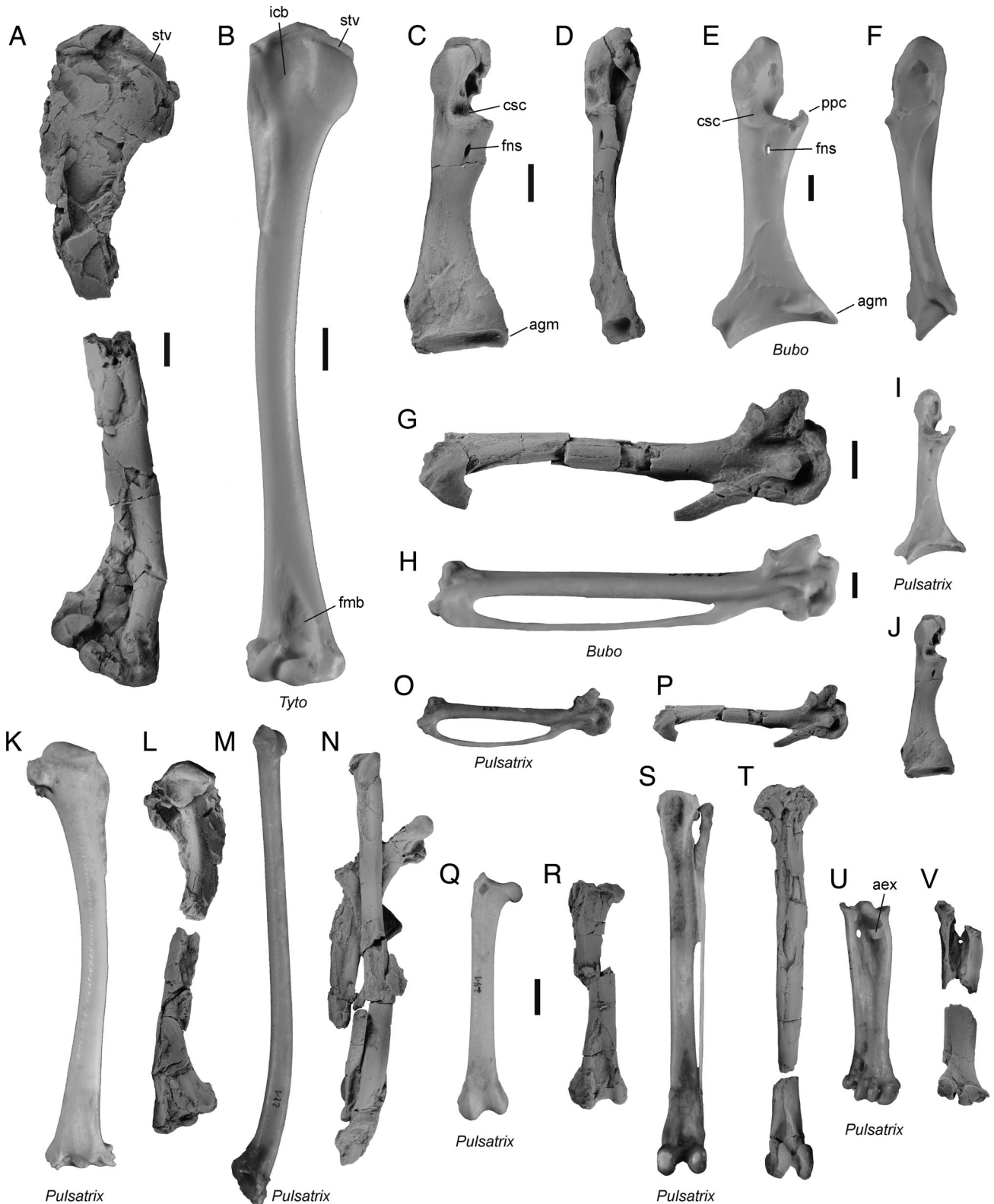


FIGURE 3. *Primoptynx poliotauros*, gen. et sp. nov., UMMMP 96195, holotype, major postcranial bones in comparison with extant Strigiformes. **A, B**, right humerus (cranial view) of **A**, *P. poliotauros* and **B**, *Tyto alba* (Tytonidae). **C, D**, left coracoid of *P. poliotauros* in **C**, dorsal and **D**, medial views. **E, F**, left coracoid of *Bubo scandiacus* (Strigidae) in **E**, dorsal and **F**, medial views. **G, H**, ventral views of right carpometacarpi of **G**, *P. poliotauros* and **H**, *B. scandiacus*. **I–V**, to-scale comparison of the major postcranial bones of *P. poliotauros* and *Pulsatrix perspicillata* (Strigidae): **I, J**, dorsal views of right coracoids of **I**, *Pu. perspicillata* and **J**, *P. poliotauros*; **K, L**, caudal views of right humeri of **K**, *Pu. perspicillata* and **L**, *P. poliotauros*; **M, N**, ventral views of left ulna of **M**, *Pu. perspicillata* and **N**, *P. poliotauros*; **O, P**, ventral views of right carpometacarpi of **O**, *Pu. perspicillata* and **P**, *P. poliotauros*; **Q, R**, cranial views of right femur of **Q**, *Pu. perspicillata* and **R**, *P. poliotauros*; **S, T**, cranial views of left tibiotarsi of **S**, *Pu. perspicillata* (image mirrored) and **T**, *P. poliotauros*; **U, V**, dorsal views of right tarsometatarsi of **U**, *Pu. perspicillata* (image mirrored) and **V**, *P. poliotauros*. The bones of *P. poliotauros* were coated with ammonium chloride. **Abbreviations:** **aex**, arcus extensorius; **agm**, angulus medialis; **csc**, cotyla scapularis; **fmb**, fossa musculi brachialis; **fns**, foramen nervi supracoracoidei; **icb**, impressio coracobrachialis; **ppc**, processus procoracoideus; **stv**, sulcus transversus. Scale bars equal 5 mm (**A–H**) and 10 mm (**I–V**).

larger than in crown group Strigiformes, and the distally adjacent section of the carpometacarpus does not form a craniocaudally narrow neck. Furthermore, unlike in extant owls, the os metacarpale minus joins the os metacarpale majus at the level of the distal end of the facies articularis alularis, whereas the contact between the os metacarpale minus and the os metacarpale majus is situated farther distally in crown group Strigiformes. The processus extensorius is more prominent than in crown group Strigiformes, and unlike in the latter it is oriented perpendicular to the longitudinal axis of the bone (in extant owls, the tip of the processus extensorius is somewhat proximally deflected). The processus pisiformis is not continuous with a distal ridge, and the synostosis metacarpalis proximalis is proportionally shorter than in all crown group Strigiformes (including *P. perspicillata*). Of other owls from the Paleogene of North America, only the proximal end of the carpometacarpus of *Minerva antiqua* is known; judging from the published figure (Shufeldt, 1915:fig. 154b) and the description of Mourer-Chauviré (1983), the bone has a proportionally shorter processus extensorius than the carpometacarpus of *P. poliotaurus*.

The right os carpi ulnare (Fig. 2Y) resembles the corresponding bone of the Strigidae in its shape. As in the latter, the tip of the crus longum is slightly inflected. In *Tyto alba* (Tytonidae), by contrast, the crus longum is proportionally longer.

Both femora are craniocaudally flattened (Fig. 4A–F). As far as comparisons are possible based on the published figures (Mourer-Chauviré, 1983:fig. 1), the morphology of the proximal and distal ends of the bone correspond well with those of the femur of *Minerva antiqua*, and as in the latter species the proximal end of the bone has a very low crista trochanteris. Along the plantar surface of the distal end of the shaft is a marked crista supracondylaris medialis, which also occurs in extant owls. Unlike in crown group Strigiformes, the distal margin of the fossa poplitea is straight and there is no notch between the condylus medialis and the condylus lateralis. The shape of the condyli themselves agrees with that in extant owls.

The tibiotarsi are broken into two (left side) and three (right side) pieces, respectively, which are kept separated (Fig. 4G–O). Owing to abrasion of the broken ends, they do not show proper fits. However, if the pieces from each side are assembled, both tibiotarsi are of similar length, which probably represents the original length of the bone. The crista cnemialis cranialis of both tibiotarsi is broken and missing. The crista cnemialis lateralis is of similar shape to that of extant owls. The medial tuberositas retinaculi extensoris is a low embossment that is situated in a proximal position (Fig. 4I). The distal ends of the bones show different morphologies, with the distal end of the left tibiotarsus being distorted by mediolateral compression and therefore appearing narrower than it originally was. As in all other Strigiformes, a pons supratendineus is lacking; the medial portion of the sulcus extensorius bears a shallow fossa. Unlike in *Minerva* and *Oligostrix*, the condylus medialis is not mediolaterally broad, and the distal end corresponds with that of *Berruornis* in that the condyles are of equal size and mediolaterally narrow. In caudal view, the rims of both condyles are likewise narrow and separated by a wide sulcus.

The right tarsometatarsus is represented by major sections of the proximal (Fig. 4P–R) and distal (Fig. 4V–X) ends of the bone as well as a fragment of the proximal end including the cotyla medialis and surrounding bone (Fig. 4S). Of the left tarsometatarsus, only the partial distal portion is preserved, which is distorted by dorsoplantar flattening (Fig. 4T, U, Y). The following description is largely based on the more complete right tarsometatarsus, which appears to be unaltered by diagenetic compression. The major fragment of the proximal end exhibits a deep fossa infracotyleris dorsalis, which reaches to the distal broken edge of the bone. Because there is no indication of a fossa on the preserved distal portion of the right tarsometatarsus,

an intermediate shaft section of unknown length must be missing. Even though the exact tarsometatarsus proportions therefore remain unknown, it seems that only a short part is lacking, so that the bone probably had a similar shape to the tarsometatarsus of *Minerva leptosteus* (Fig. 5D, E, I, J) and the extant *Pulsatrix perspicillata* (Fig. 3U). The species of *Berruornis* likewise have a stout tarsometatarsus (Mourer-Chauviré, 1994:pl. 1), whereas the bone is much more elongate and slender in *Ogygoptynx wetmorei* (Fig. 5K–M) and *?Oligostrix bergeri* (see De Pietri et al., 2013:fig. 3). The eminentia intercotylaris, on the proximal end of the bone, is low. As in other strigiform birds, the hypotarsus apparently consisted of two widely separated crests, of which only the lateral crest is preserved and forms a small projection. The lateral margin of the lateral foramen vasculare proximale is present and shows that the foramen must have been fairly large. The medial foramen vasculare proximale cannot be discerned within the deep fossa infracotyleris dorsalis and appears to have been in a missing section of the bone. On the medial surface of the bone, the distal-most section of the fossa parahypotarsalis medialis is visible. The tuberositas musculi tibialis cranialis is situated in the medial section of the fossa infracotyleris dorsalis. The right tarsometatarsus exhibits the medial margin of the foramen vasculare distale, which shows the dorsal opening of the foramen to have been comparatively large; proximal to the foramen vasculare distale, a shallow but distinct sulcus extensorius is visible on the dorsal surface of the bone. The plantar surface is essentially flat in its proximal portion but forms a moderately deep sulcus flexorius in the distal section of the shaft. On the distal end of the bone, the fossa metatarsi I is very shallow and situated in a proximal position at the medial margin of the bone (Fig. 4W). The trochlea metatarsi II is twice as wide as the trochlea metatarsi III and hardly plantarly deflected; in the right tarsometatarsus, it projects distally beyond the trochlea metatarsi III, whereas the trochlea metatarsi II of the left tarsometatarsus is shorter than the trochlea metatarsi III. Because the left tarsometatarsus is altered by diagenetic compression, we hypothesize that the right tarsometatarsus more closely reflects the original morphology of the bone. Regarding the wide and hardly deflected trochlea metatarsi II, the distal end of the tarsometatarsus of *P. poliotaurus* resembles that of *Berruornis orbisantiqvi* and *?Oligostrix bergeri*. However, unlike in the latter two species, the trochlea metatarsi II of *P. poliotaurus* forms a marked, medially directed, and shovel-shaped flange that terminates in a sharp crest. The distal surface of the trochlea bears a lateral bulge that is situated next to a distinct fossa in the medial portion of the trochlea, and the dorsal surface is elevated relative to the shaft, from which it is offset by a distinct step. As in *Minerva antiqua*, the medial portion of the trochlea metatarsi II is separated from the lateral portion of the trochlea by a concave incision in its plantar surface. Unlike in crown group Strigiformes, the trochlea metatarsi II does not exhibit a plantarly directed flange. In both tarsometatarsi, the trochlea metatarsi III is worn and its plantar surface is damaged; the trochlea is dorsally bulging and does not exhibit a distinct trochlear furrow. In distal view, the trochleae metatarsorum II and III are aligned. Both trochleae metatarsorum IV are broken and missing, but the breakage areas of the tarsometatarsus shafts indicate that this trochlea was very narrow mediolaterally.

Altogether, 24 phalanges or fragments thereof are preserved, including portions of all but one of the unguis phalanges (Fig. 6A, B). The only phalanges that are missing are the first three phalanges of the left fourth toe and the unguis phalanx of the right third toe. With regard to their position in the digits, identification of most phalanges is quite straightforward, but assignment to a particular side (left or right) is tentative for the distal and unguis phalanges.

The first phalanx of the hallux is much more elongated than the unusually short phalanx that was identified as the first phalanx of



FIGURE 4. *Primoptynx poliotauros*, gen. et sp. nov., UMMP 96195, holotype, from the Willwood Formation of the northern Bighorn Basin, Wyoming, U.S.A., leg bones. **A, B**, right femur in **A**, caudal and **B**, cranial views. **C, D**, proximal portion of left femur in **C**, caudal and **D**, cranial views. **E, F**, distal portion of left femur in **E**, caudal and **F**, cranial views. **G, H**, proximal portions of right tibiotarsus in **G**, cranial and **H**, caudal views. **I, J**, distal portion of right tibiotarsus in **I**, cranial and **J**, caudal views. **K, L**, proximal portion of left tibiotarsus in **K**, craniomedial and **L**, lateral views. **M–O**, distal portion of left tibiotarsus in **M**, cranial, **N**, caudal, and **O**, distal views. **P, Q**, proximal end of right tarsometatarsus in **P**, dorsal and **Q**, plantar views. **V, W**, distal end of right tarsometatarsus in **V**, dorsal and **W**, plantar views. **R, S**, proximal end of right tarsometatarsus in proximal view, with fragment of cotyla medialis digitally brought into its original position in **S, T, U**, distal end of left tarsometatarsus in **T**, dorsal and **U**, plantar views. **X, Y**, distal ends of **X**, right and **Y**, left tarsometatarsi in distal view. In **U, W, X**, and **Y**, the trochleae metatarsorum are numbered. All bones were coated with ammonium chloride. **Abbreviations:** **ccl**, crista cnemialis lateralis; **cdl**, condylus lateralis; **cdm**, condylus medialis; **cfi**, crista fibularis; **chl**, crista lateralis hypotarsi; **ctl**, cotyla lateralis; **ctm**, cotyla medialis; **eic**, eminentia intercotylaris; **fid**, fossa infracotylaris dorsalis; **fig**, medial flange formed by trochlea metatarsi II; **fos**, distal fossa on trochlea metatarsi II; **fvd**, foramen vasculare distale; **mds**, fossa in medial portion of sulcus extensorius; **mtl**, fossa metatarsi I; **tre**, medial tuberositas retinaculi extensoris; **ttc**, tuberositas musculi tibialis cranialis. Scale bar equals 5 mm.

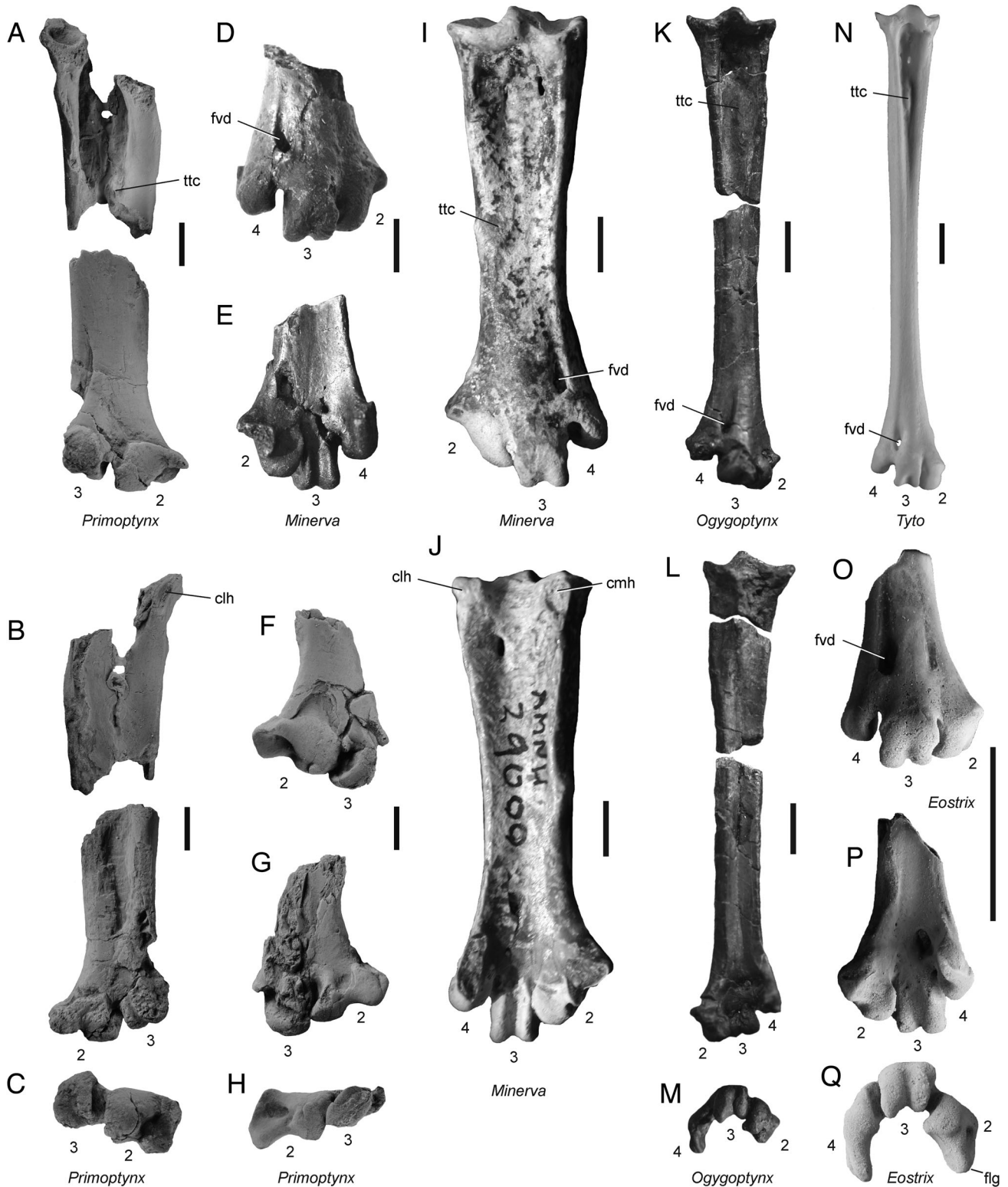


FIGURE 5. *Primoptynx poliotauros*, gen. et sp. nov., UMMP 96195, holotype, from the Willwood Formation of the northern Bighorn Basin, Wyoming, U.S.A., right tarsometatarsus in comparison with the tarsometatarsi of other early Cenozoic and extant owls. **A–C**, *P. poliotauros*, right tarsometatarsus in **A**, dorsal, **B**, plantar, and **C**, distal views. **D, E**, *Minerva* cf. *leptosteus*, right tarsometatarsus from the uppermost lower to lower middle Eocene Bridger Formation in Wyoming, U.S.A. (AMNH 2629, holotype) in **D**, dorsal and **E**, plantar views. **F–H**, *P. poliotauros*, left tarsometatarsus in **F**, dorsal, **G**, plantar, and **H**, distal views. **I, J**, *M.* cf. *leptosteus*, left tarsometatarsus from the upper lower to lower middle Eocene Bridger Formation in Wyoming, U.S.A. (AMNH 29000) in **I**, dorsal and **J**, plantar views. **K–M**, *Ogygoptynx wetmorei*, right tarsometatarsus from the upper Paleocene of Colorado, U.S.A. (holotype, AMNH 2653) in **K**, dorsal, **L**, plantar, and **M**, distal views. **N**, extant *Tyto alba* (Tytonidae), right tarsometatarsus in dorsal view. **O–Q**, *Eostrix gulottai*, distal end of right tarsometatarsus from the early Eocene Nanjemoy Formation in Virginia, U.S.A. (SMF Av 627) in **O**, dorsal, **P**, plantar, and **Q**, distal views. The tarsometatarsal trochleae are numbered. The bones of *P. poliotauros* and *E. gulottai* were coated with ammonium chloride. **Abbreviations:** **chl**, crista lateralis hypotarsi; **cmh**, crista medialis hypotarsi; **fig**, flange formed by trochlea metatarsi II; **fvd**, foramen vasculare distale; **ttc**, tuberositas musculi tibialis cranialis. Scale bars equal 5 mm.

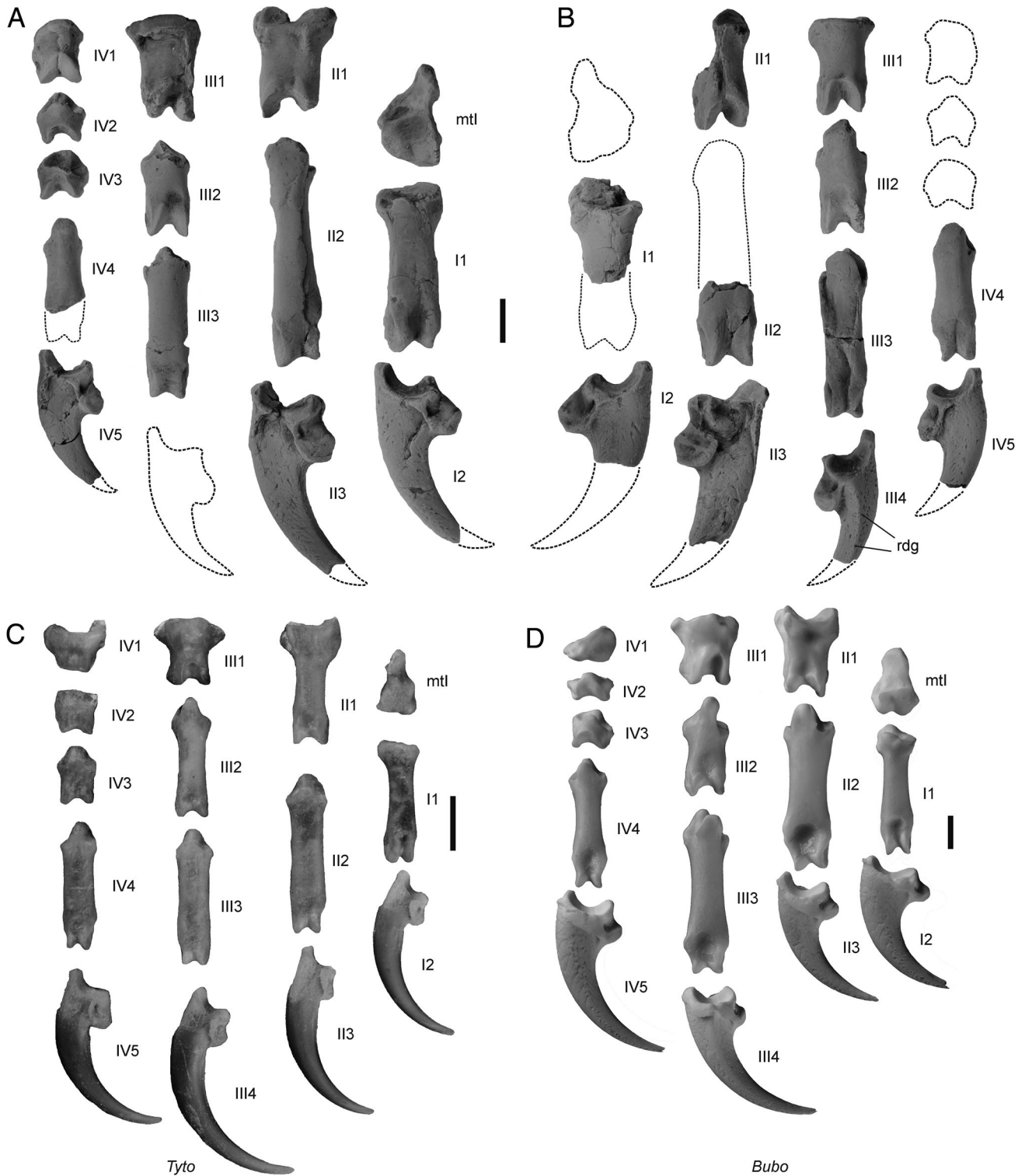


FIGURE 6. *Primoptynx poliotauros*, gen. et sp. nov., UMMP 96195, holotype, from the Willwood Formation of the northern Bighorn Basin, Wyoming, U.S.A., pedal phalanges in comparison with those of extant owls. Note the large unguinal phalanges of the first and second toes of the fossil species. **A, B**, *P. poliotauros*, **A**, right and **B**, left feet. **C, D**, pedal phalanges of the right foot of **C**, *Tyto alba* (Tytonidae) and **D**, *Bubo scandiacus* (Strigidae); in **C**, the unguinal phalanges bear the keratinous sheaths. The phalanges are numbered; the dotted lines indicate missing phalanges or parts thereof. All fossil bones were coated with ammonium chloride. **Abbreviations:** **mtl**, os metatarsale I; **rdg**, ridge on medial surface of unguinal phalanx of third toe. Scale bars equal 5 mm.

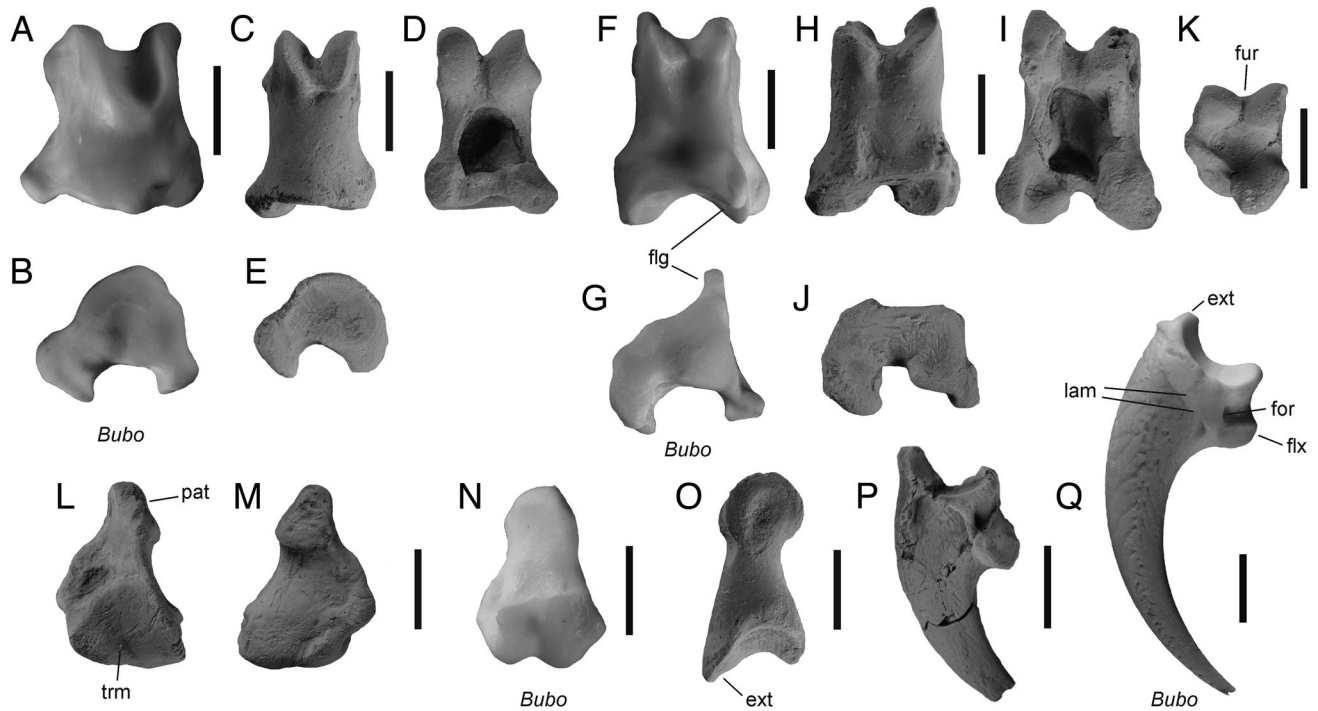


FIGURE 7. *Primoptynx poliotauros*, gen. et sp. nov., UMMP 96195, holotype, from the Willwood Formation of the northern Bighorn Basin, Wyoming, U.S.A., details of selected pedal phalanges in comparison with the extant *Bubo scandiacus* (Strigidae). **A, B**, *B. scandiacus*, first phalanx of third toe (right side, mirrored) in **A**, dorsal and **B**, proximal views. **C–E**, *P. poliotauros*, first phalanx of third toe (left side) in **C**, dorsal, **D**, plantar, and **E**, proximal views. **F, G**, *B. scandiacus*, first phalanx of second toe (right side) in **F**, dorsal and **G**, proximal views. **H–J**, *P. poliotauros*, first phalanx of second toe (right side) in **H**, dorsal, **I**, plantar, and **J**, proximal views. **K**, *P. poliotauros*, first phalanx of fourth toe (right side) in plantar view. **L, M**, *P. poliotauros*, os metatarsale I (right side) in **L**, plantar and **M**, dorsal views. **N**, *B. scandiacus*, os metatarsale I (right side) in plantar view. **O**, *P. poliotauros*, second phalanx of third digit (left side) in medial view. **P**, *P. poliotauros*, unguis phalanx of fourth digit (right side) in medial view. **Q**, *B. scandiacus*, unguis phalanx of fourth digit (right side) in medial view. All fossil bones were coated with ammonium chloride. **Abbreviations:** **ext**, tuberculum extensorium; **fig**, dorsal flange; **flx**, tuberculum flexorium; **for**, foramen of sulcus neurovascularis; **fur**, trochlear furrow; **lam**, bony lamella encompassing the base of the keratinous sheath of the unguis phalanx; **pat**, processus articularis tarsometatarsalis; **trm**, trochlea metatarsi I. Scale bars equal 5 mm.

the hallux of *M. antiqua* by Mourer-Chauviré (1983). As in *M. antiqua*, the unguis phalanx of the hallux of *P. poliotauros* exhibits a strongly concave articulation facet, which has a semicircular shape in lateral view. Unlike in *M. antiqua*, however, the cotyla articularis is not facing plantarly but proximally. As in *M. antiqua*, the tuberculum extensorium projects strongly proximally, even though it is more dorsally directed in *P. poliotauros*. The sulcus neurovascularis of the unguis phalanx of the hallux and the other toes is laterally closed and opens with a foramen next to the tuberculum flexorium; this condition is characteristic of strigiform birds and also occurs in many diurnal birds of prey. Unlike in extant owls, however, the plantar surfaces of the unguis phalanges are slightly flattened rather than convex, and unlike in some Strigidae the bases of the unguis phalanges do not form a bony lamella that in extant true owls encompasses the base of the keratinous sheath (Fig. 7Q).

The stocky and wide first phalanx of the second toe (Fig. 7H–J) articulates well with the broad trochlea metatarsi II. The phalanx differs from the corresponding phalanx of *M. antiqua* (Mourer-Chauviré, 1983:fig. 3e) in that the proximal end has a symmetrical shape, whereas it forms a prominent medial projection in *M. antiqua*; these differences correspond with the different shapes of the trochlea metatarsi II in *Primoptynx* and *Minerva*. The cotyla articularis exhibits a concavity in its right portion, whereas the left portion is convex. This morphology reflects the shape of the trochlea metatarsi II, with which the phalanx articulates well. The broad proximal end of the phalanx bears two plantar flanges, which in proximal view are separated by a deep

sulcus (Fig. 7J). The distal end of the phalanx exhibits a markedly concave trochlear furrow. Compared with crown group Strigiformes (Fig. 6C, D), the first phalanx of the second toe corresponds with that of the Strigidae in its proportions, whereas this phalanx is more elongated in the Tytonidae. Unlike in all crown group Strigiformes (Fig. 7F, G), however, there is no dorsally directed flange on the medial side of the proximal end. As in crown group Strigiformes, the second phalanx of the second toe is the longest of all pedal phalanges and distinctly exceeds the first phalanx in length. Except for a mediolaterally broader tuberculum extensorium, this phalanx resembles the corresponding one of extant owls. The large unguis phalanx of the second toe corresponds with that of the hallux in size and morphology, whereas the unguis phalanges of the third and fourth toes are much smaller, a condition also noted by Mourer-Chauviré (1983) for *Minerva antiqua*.

The proximal end of the first phalanx of the third toe (Fig. 7C–E) bears an ovate cotyla, which, unlike in extant owls, is not subdivided into two facets; this unusual morphology corresponds with the fact that the articular surface of the trochlea metatarsi III appears to lack a well-developed sulcus. As in crown group Strigiformes, the distal end of the phalanx, however, exhibits a marked trochlear sulcus, which is particularly pronounced on the dorsal surface of the bone where it encompassed the proximally projected tuberculum extensorium of the second phalanx of this toe. The strongly proximodorsally projected tuberculum extensorium of the second phalanx of the third toe is here identified as a previously unrecognized apomorphy of strigiform birds.

The third phalanx of the third toe resembles that of extant Strigiformes in its proportions. The unguis phalanx of the third toe is identified by a distinct longitudinal ridge on its medial surface, which is a characteristic derived feature of owls (Mourer-Chauviré, 1983).

Identification of the phalanges of the fourth toe is straightforward, because the proximal three phalanges of this toe are strongly abbreviated and all phalanges are smaller than those of the other digits. The first phalanx is proportionally longer than in the Strigidae (Fig. 6D) and more closely resembles the corresponding phalanx of the Tytonidae (Fig. 6C) in its proportions. As in crown group Strigiformes, its proximal end is markedly asymmetrical and forms a medial projection. Unlike in all extant owls, however, the distal trochlea is well developed and bears a distinct trochlear furrow (Fig. 7K). In concordance with crown group Strigiformes, the two central phalanges of the fourth toe are greatly shortened, with the third one being somewhat shorter than the second. The fourth phalanx does not exhibit notable differences from the corresponding phalanx of extant owls. The small unguis phalanx of the fourth toe is of similar size to that of the third toe.

The pedal proportions of *P. poliotaurus* are different from those of ‘*Palaeoglaux*’ *artophoron* from Messel (Peters, 1992) in that the first phalanx of the second toe is stouter in *P. poliotaurus* and the central phalanges of the fourth toe are more strongly abbreviated. In ‘*Palaeoglaux*’ *artophoron*, the unguis phalanges of the hallux and the second toe are furthermore not much larger than those of the third and fourth toes.

The os metatarsale I (Fig. 7L, M) is distinguished from the corresponding bone of *M. antiqua* in having a somewhat longer and more pointed processus articularis tarsometatarsalis (compare Fig. 7L, M with Mourer-Chauviré 1983:fig. 1h). The short and dorso-plantarily compressed processus articularis tarsometatarsalis of *P. poliotaurus* also differs from that of crown group Strigiformes (Fig. 7N), in which it is more compressed mediolaterally. As in crown group Strigiformes, the medial margin of the bone is straight, but the lateral margin forms a distinct bulge, which is absent in extant owls. Furthermore, unlike in extant owls, the trochlea metatarsale I does not bear a distinct longitudinal sulcus.

DISCUSSION

Primoptynx poliotaurus gen. et sp. nov., comes from strata that are 54.5–55 million years old and is the earliest temporally well-constrained record of the Strigiformes from the Eocene of North America. The only previously described owl from the Wasatchian of the Willwood Formation is *Eostrix mimica*, which was collected on the south side of Ten Mile Creek, 12 miles northwest of Worland, Wyoming (Wetmore, 1938). The precise locality of *E. mimica* is unknown, but the biochron is almost certainly Wa-4 and the age middle Graybullian (54–54.5 Ma; Bown et al., 1994; Gingerich, 2010). *Eostrix martinellii* from the Lysite Member of the Wind River Formation in Wyoming (Martin and Black, 1972) has an age of about 53–53.5 Ma, with the Lysitean substage of the Wasatchian being equivalent to biochron Wa-6 (Gingerich, 1983; Clyde et al., 1997). *Eostrix gulottai* from the Nanjemoy Formation of Virginia is about coeval in age and stems from strata that are 53.6–52.8 million years old (Mayr, 2016). The species of *Minerva* are from Bridgerian (50.5 to 45–46 Ma; Clyde et al., 1997) or younger strata.

Primoptynx poliotaurus, gen. et sp. nov., is identified as a strigiform bird by a number of diagnostic apomorphies, including (1) the absence of a supratendinal bridge on the distal tibiotarsus; (2) the widely separated hypotarsal crests (as shown by the far lateral position of the crista lateralis hypotarsi); (3) the mediolaterally wide trochlea metatarsi II; (4) the greatly abbreviated proximal phalanges of the fourth pedal digit (Fig. 6A); (5) the strongly proximally projecting tuberculum extensorium of the second

phalanx of the third toe (Fig. 7O); and (6) the longitudinal ridge on the medial surface of the unguis phalanx of the third toe (Fig. 6B). Several features indicate that *P. poliotaurus* is a taxon located in the stem of the Strigiformes. Among the most conspicuous of these characteristics are the proportionally stouter humerus, the hardly deflected trochlea metatarsi II that lacks a plantarly directed flange, the absence of a dorsal flange on the first phalanx of the second toe, and the presence of a well-developed distal trochlea on the first phalanx of the fourth toe. However, it is difficult to further constrain the affinities of *P. poliotaurus*, because most Paleogene taxa of the Strigiformes are based on tarsometatarsi, with this bone being fragmentary in the holotype of *P. poliotaurus*.

All strigiform birds from the Eocene of North America are currently assigned to the Protostrigidae (Mourer-Chauviré, 1983; Mayr, 2009). *Minerva* (‘*Protostrix*’), the type genus of this taxon, is well characterized by a mediolaterally broad condylus medialis of the tibiotarsus. A broad condylus medialis also occurs in *Oligostrix rupelensis* from the early Oligocene of Germany (Fischer, 1983), and this feature—which is not known from any other avian taxon—constitutes robust evidence for a clade including *Minerva* and *Oligostrix* (the tibiotarsus of ?*Oligostrix bergeri* is unknown, and this species was only tentatively referred to the taxon *Oligostrix* by De Pietri et al., 2013).

Protostrigid affinities of *Eostrix*, by contrast, have not yet been convincingly shown, and at least in *E. mimica* and *E. tsaganica* the condylus medialis of the tibiotarsus is not mediolaterally broad (Wetmore, 1938; Kurochkin and Dyke, 2011; the distal tibiotarsus of *E. martinellii* and *E. gulottai* is unknown). The trochlea metatarsi II (tarsometatarsus) is damaged in the holotypes of *Eostrix mimica* and *E. martinellii*, but in *E. gulottai* and *E. tsaganica* it forms a distinct, plantarly directed flange (Fig. 5O–Q). This derived feature is shared by *Eostrix* and crown group Strigiformes but is absent in *Berruornis* (Fig. 8A), *Primoptynx* (Fig. 8B), and ?*Oligostrix bergeri* (Fig. 8C). Judging from the published illustrations, the trochlea metatarsi II of *M. antiqua* appears to be similar to that of *P. poliotaurus* (compare Fig. 4T with Mourer-Chauviré 1983:fig. 1g), whereas this trochlea is damaged in all tarsometatarsi assigned to *M. leptosteus* and the tarsometatarsus of *O. rupelensis* is altogether unknown.

Primoptynx poliotaurus gen. et sp. nov., and *M. antiqua* share a distinctive morphology of their feet, in which the unguis phalanges of the first and second toes are greatly enlarged. The pedal phalanges are unknown for *Berruornis*, *Ogygoptynx*, and the species of *Eostrix*, but in *Palaeoglaux artophoron* from Messel the unguis phalanges of the hallux and the second toe are not larger than those of the other toes. Enlargement of the unguis phalanges of the first and second digits may therefore be a derived feature that is shared by *Primoptynx* and *Minerva*. However, the tibiotarsus of *P. poliotaurus* lacks a mediolaterally broad condylus medialis, and the new taxon is therefore clearly outside the clade including *Minerva* and *Oligostrix*. The new species may well be a stem group representative of protostrigid owls, but current data do not allow an unambiguous phylogenetic placement.

The large *Primoptynx poliotaurus* gen. et sp. nov., and the tiny *Eostrix gulottai*, which is the smallest known owl (Mayr, 2016), belong to vastly different size classes. These two species document that owls underwent a considerable radiation early in their evolutionary history and that taxa with very different foot morphologies coexisted in the early Eocene. Apart from the proportionally shorter trochlea metatarsi II (which is likely to be a plesiomorphic feature of the Strigiformes), the distal tarsometatarsus of *Eostrix* resembles that of crown group Strigiformes, and the species of this taxon may have preyed predominantly on rodents and other small vertebrates. *Primoptynx*, by contrast, is likely to have caught much larger prey items, and its distinctive foot morphology suggests a feeding ecology that was different from that of extant owls.

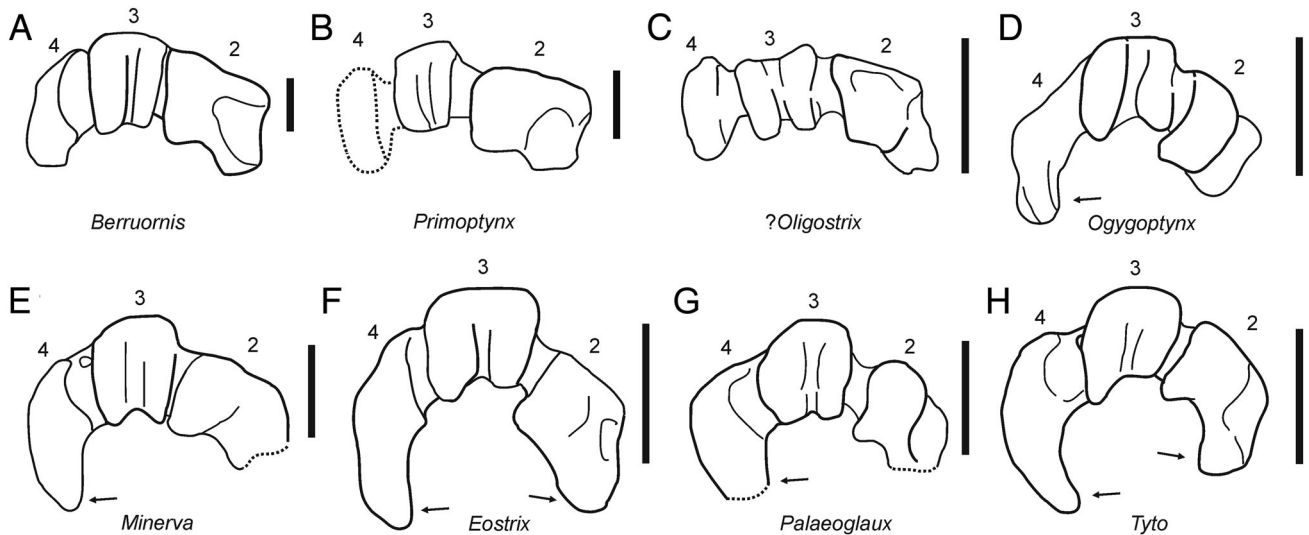


FIGURE 8. Schematic drawings of right tarsometatarsi of fossil and extant Strigiformes (distal view) to illustrate differences in the size and plantar extent of the trochleae metatarsorum II and IV. **A**, *Berruornis orbisantiqvi* (after Mourer-Chauviré, 1994). **B**, *Primioptynx poliotauros* gen. et sp. nov., (the shape of the trochlea metatarsi IV is hypothetical and based on that of *?Oligostrix bergeri*). **C**, *?Oligostrix bergeri* (after De Pietri et al., 2013). **D**, *Ogygoptynx wetmorei*. **E**, *Minerva* cf. *leptosteus* (after Rich, 1982). **F**, *Eostrix gulottai* (holotype). **G**, *Palaeoglaux perrierensis* (after Mourer-Chauviré, 1994). **H**, *Tyto alba*. The trochleae are numbered; the arrows denote the plantar flanges of the trochleae metatarsorum II et IV. Scale bars equal 5 mm (**A–E**, **G**, **H**) and 2 mm (**F**).

Extant raptorial birds exhibit various strategies to kill prey. Owls and falcons (Falconidae) immobilize quarry by severing the skull or the neck vertebrae with the beak (Johnsgard, 1988; Csermely et al., 1998). Hawks and allies (Accipitridae), by contrast, use their feet and body weight to pin down prey, which are punctured by the talons (Sustaita and Hertel, 2010). Functionally correlated with these different behaviors, owls and falcons have pedal claws of equal size, whereas in accipitrids the claws of the first and second digits are hypertrophied (Fowler et al., 2009). *Primioptynx poliotauros* gen. et sp. nov., and *M. antiqua* differ from crown group Strigiformes and agree with species of the Accipitridae in that the ungual phalanges of the first and second toes are greatly enlarged. Accordingly, these stem group Strigiformes probably employed different killing behaviors than extant owls and, like accipitrids, dispatched prey items with their feet. This foraging technique may have been functionally correlated with the wide trochlea metatarsi II. The flat articular surface of the trochlea metatarsi II of *Primioptynx* indicates that the basal phalanx of the second toe was not capable of much rotary movement and may have constituted a safety device to prevent injuries caused by struggling prey. Enlargement of the condylus medialis of the tibiotarsus in protostrigid owls (*Minerva* and *Oligostrix*) may constitute another adaptation related to this foraging strategy, in which the second (i.e., medial) toe was exposed to high strain.

The holotype of *Primioptynx poliotauros* provides further insights into the skeletal morphology of early Cenozoic Strigiformes, and a notable characteristic that distinguishes the new species from the crown group representatives is the deeply excavated sulcus supracoracoideus of the coracoid. This unusual feature is not found in any extant representative of the land bird clade (Telluraves) to which owls belong. However, a deeply excavated sulcus supracoracoideus also occurs in *Palaeoglaux perrierensis* from the upper Eocene of the Quercy fissure fillings in France (Mourer-Chauviré, 1987), and Peters (1992) noted its presence in *P. artophoron* from Messel. *Palaeoglaux* was assigned to the Tytonidae by Mourer-Chauviré (1987), whereas Peters (1992) moved it to its own family-level

taxon, Palaeoglaucidae. Although the exact affinities of *Palaeoglaux* remain to be established, the plantarily deflected trochlea metatarsi II suggests that the taxon is more closely related to crown group Strigiformes than *Primioptynx*. Occurrence of a deeply excavated sulcus supracoracoideus in *Primioptynx* therefore indicates that this feature is plesiomorphic for strigiform birds and challenges assignment of the Messel owl to the taxon *Palaeoglaux*, which was mainly based on this very feature (Peters, 1992).

Compared with extant owls, *P. poliotauros* also has a proportionally more abbreviated humerus and ulna. The femur and tibiotarsus are of similar length to the corresponding elements of the extant *Pulsatrix perspicillata*, but the humerus and the ulna are distinctly shorter (Fig. 3I–V). A proportionally short humerus is likewise found in *Palaeoglaux artophoron* from Messel and seems to be another plesiomorphic feature of early Cenozoic Strigiformes. The functional significance of wing lengthening in the evolutionary history of owls remains elusive but is likely to be correlated with differences in flight performance. Fossils from the London Clay (Mayr, 2017) and the Bridger Formation (Fowler et al., 2018) show that the skulls of early and middle Eocene owls possessed well-developed supraorbital processes. As discussed by Mayr (2017), these processes are likely to be plesiomorphic for strigiform birds and suggest that early Cenozoic owl were less nocturnal than their living relatives. It is possible that some of the postcranial differences between early Paleogene and extant owls outlined here were correlated with the evolution of a crepuscular or nocturnal way of living, but the evolutionary history of early Cenozoic owls is still too insufficiently known for well-founded conclusions.




In any case, the two late Paleocene strigiform taxa, European *Berruornis* and North American *Ogygoptynx*, already exhibit markedly different tarsometatarsus morphologies and document a considerable radiation of owls in the early Cenozoic (Mayr, 2009). *Primioptynx poliotauros* gen. et sp. nov., adds a distinctive new taxon to the known diversity of early Eocene owls and shows that by this time North American owls occupied disparate ecological niches. This early radiation of strigiform birds is likely to have been correlated with the rapid diversification of small

mammals after the K/Pg boundary (e.g., Chen et al., 2019), and judging from the morphologies of their tarsometatarsi early Cenozoic owls pursued divergent foraging techniques to subdue their prey. *Primoptynx* and protostrigid owls appear to have been specialized in foraging on prey items that required an accipitrid-like killing strategy, such as larger-sized or more defensive mammals. Extinction of these peculiar owls could have been related to the radiation of accipitrid diurnal birds of prey, which commenced toward the late Eocene and early Oligocene (Mayr, 2009). At present, critical aspects of the paleobiology of *Primoptynx* and the Protostrigidae remain unknown, but future studies that correlate their stratigraphic occurrence with that of potential mammalian prey taxa and avian competitors may yield further insights into the rise and demise of these stem group owls.

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