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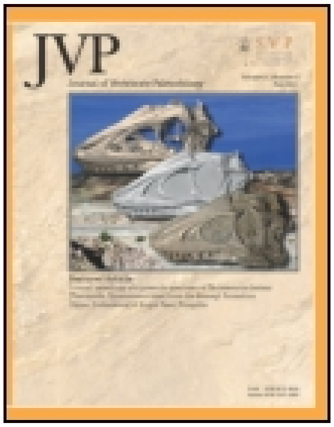

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A confuciusornithiform (Aves, Pygostylia)-like tarsometatarsus from the Early Cretaceous of Siberia and a discussion of the evolution of avian hind limb musculature

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ARTICLE

A CONFUCIUSORNITHIFORM (AVES, PYGOSTYLIA)-LIKE TARSOMETATARSUS FROM THE EARLY CRETACEOUS OF SIBERIA AND A DISCUSSION OF THE EVOLUTION OF AVIAN HIND LIMB MUSCULATURE

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ABSTRACT—We describe a new isolated tarsometatarsus from the Early Cretaceous (Barremian–Aptian) Ilek Formation Shestakovo-3 locality in western Siberia. The new specimen represents a new taxon, *Evgenavis nobilis*, gen. et sp. nov., significantly increasing the Mesozoic avifauna from Russia. The specimen shares morphologies with a number of basal ornithothoracine taxa, but shows most similarity to the basal pygostylian *Confuciusornis sanctus*, the oldest known beaked bird and most common taxon from the Yixian Formation. *Evgenavis* may represent the first record of Confuciusornithiformes outside of the Jehol Group and its equivalent deposits. However, this is not supported by cladistic analysis, which weakly resolves the new species and *Mystiornis* both within the diverse Enantiornithes, indicating that additional material is required to assess the systematic position of *Evgenavis nobilis* (Aves incertae sedis). The three-dimensional preservation of the specimen allows for a partial reconstruction of the pedal musculature, revealing a primitive stage in the evolution of the neornithine condition.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Mesozoic birds are rare in the fossil record; bird bones are small and delicate by nature, preventing their preservation in high-energy depositional environments. With the exception of the Early Cretaceous avifauna recovered from the Jehol Group in northeastern China, the record of Mesozoic birds in most countries is fragmentary. Russia, although regionally vast, is no exception; the record of Mesozoic birds is limited to an isolated Early Cretaceous metatarsus (*Mystiornis cyrili*), a Late Cretaceous cranial endocast (*Cerebavis*), and some fragmentary Late Cretaceous specimens representing the holotype of *Hesperornis rossicus* and a purported neognath taxon, *Volgavis marina* (Nessov and Jarkov, 1989, 1993; Kurochkin et al., 2006, 2011). Feathers have also been reported from several localities (Kurochkin, 1985; Nessov, 1992).

The isolated metatarsus PM TSU 16/5-45, the holotype of *Mystiornis cyrili*, was collected from the Early Cretaceous (Barremian) Ilek Formation Shestakovo-1 locality in western Siberia (Kurochkin et al., 2011). The small and gracile metatarsus is distinct from other known avians and possesses puzzling features (e.g., the presence of three rather than two cotyla forming the proximal articular surface), interpretations of which have led researchers to assign the taxon to a new order, Mystiornithiformes. With information from only a single bone, it is difficult to place the taxon in a phylogenetic context. Kurochkin et al. (2011) used cladistics to explore the relationship of *Mystiornis* with other Mesozoic birds; both TNT and WinClade resulted in a large polytomy, but PAUP resolved the taxon in a clade with the enantiornithine *Avisaurus*, which together form a clade with *Mei long* (a basal troodontid theropod dinosaur) and *Vorona berivotrensis*, a primitive ornithothoracine most commonly resolved as a basal ornithuromorph (Forster et al., 1996; Clarke, 2004; Z.-H. Zhou et al., 2008, 2009). This clade is positioned basal to all other birds, with the exception of *Archaeopteryx*. Given the homoplastic nature of paravian evolution and the fragmentary nature of *Mystiornis* (and *Avisaurus*), additional material is probably needed to clarify the systematic position of this taxon, which shares some features with avisaurid enantiornithines. With the exception of the questionable phylogenetic position of *Mystiornis*, all other Mesozoic bird specimens from Russia are regarded as falling within the derived clade, Ornithothoraces, which includes Enantiornithes and Ornithuromorpha, the latter clade including living birds.

Here we report on a new isolated tarsometatarsus (Figs. 1–2) from the Early Cretaceous Ilek Formation, Shestakovo-3 locality, in western Siberia, approximately 5 km west of the Shestakovo-1 locality that yielded *Mystiornis*. The new specimen (ZIN PH 1/154) is 30% larger than *Mystiornis* and exhibits a number of unique morphologies that indicate that it represents a new taxon. This new discovery augments the current record of Mesozoic birds from Russia as well as overall known diversity. We make broad comparisons with other known Mesozoic birds and discuss the implications of the observed morphological differences.

Institutional Abbreviations—IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **NHMW**, Naturhistorisches Museum Wien, Vienna, Austria; **PM TSU**, Paleontological Museum of Tomsk State University, Tomsk, Russia; **ZIN PH**, Paleoherpetological Collection, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

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Anatomical Abbreviations—**adII**, origin site of the m. adductor digiti II; **adIV**, sulcus for the m. abductor digiti IV; **ct**, caudal tubercle; **df**, dorsal depression; **f**, unusual foramen on the plantar surface of the metatarsal IV; **fcl**, fovea for the collateral ligament; **fdl**, sulcus for the distal tendon of the m. flexor digitorum longus; **mc**, medial condyle; **mtc**, attachment of the m. tibialis cranialis; **mtII**, metatarsal II; **mtIII**, metatarsal III; **mtIV**, metatarsal IV; **mtV**, metatarsal V; **p/g**, pit and distally extending groove; **pw**, plantarly projecting wing of the metatarsal II trochlea (medial condyle); **tg**, tendinal groove; **vf**, vascular foramen; **vk**, ventral keel.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758
EVGENAVIS NOBILIS, gen. et sp. nov.
(FIGS. 1, 2)

Holotype—ZIN PH 1/154, an isolated right tarsometatarsus missing only the proximal half of metatarsal IV.

Locality and Horizon—Early Cretaceous (Barremian) Ilek Formation, Shestakovo-3 locality, in western Siberia, Russia.

Etymology—The name is in honor of the late Russian paleornithologist Evgeny Kurochkin, as much for his incredible contributions to science as for his kind and noble spirit.

Diagnosis—A medium-sized bird with the unique combination of the following features: metatarsal V present; metatarsals fused only proximally; tarsometatarsus plantarly excavated; tubercle on the proximal dorsal surface of metatarsal III, with another just distal to it on metatarsal II; metatarsal II trochlea wide and angled so that lateral condyle extends farther than the medial condyle; medial condyle of metatarsal II trochlea strongly projected plantarly; dorsal and plantar depressions of the metatarsal II trochlea well developed; plantar surface of metatarsal III strongly medially excavated proximal to the trochlea; distal vascular foramen closed by medial projection of metatarsal IV; metatarsal IV with small, non-perforating, plantar foramina; and metatarsal IV trochlea non-ginglymous.

DESCRIPTION

Anatomical nomenclature primarily follows Baumel and Witmer (1993) using the English equivalents of most skeletal terms while retaining Latin for muscles. The new tarsometatarsus is 48.7 mm in length (see Table 1 for a complete list of measurements); it is nearly complete, missing the lateral cotyla of the proximal articular surface and the proximal half of metatarsal IV (Fig. 1). A metatarsal V is present (as in *Archaeopteryx*, *Jeholornis*, *Sapeornis*, *Confuciusornis*, and *Vorona*), reduced to a thin splint of bone with the complete distal extent unknown; it is preserved extending for one-third of the length of the tarsometatarsus. Proximally, metatarsal IV is not preserved but it appears that metatarsal V would have been plantolaterally located with respect to this metatarsal. Metatarsal V appears to be mediolaterally compressed, with an oval cross-section. As in other birds, the proximal articular surface of the tarsometatarsus is expanded relative to the metatarsals, so that just distal to the proximal articular surface the tarsometatarsus narrows dorsoventrally and mediolaterally (e.g., *Apsaravis*, *Avisaurus*, *Vorona*, *Yixianornis*). The tarsometatarsus continues to taper slightly distally, reaching its narrowest point one-third of the distance from the distal end; at this point the tarsometatarsus begins to increase in width distally so that the medial and lateral margins of the tarsometatarsus are concave (absent in *Avisaurus* and *Vorona*; more defined in ornithuromorphs such as *Gansus* and *Apsaravis*; comparable in confuciusornithiforms). Proximally, the medial cotyla is nearly complete; it is concave and ovoid, with a mediolaterally oriented long axis. The plantar margin of the medial cotyla slightly projects proximally and is most prominent near its lateral margin, where it forms a proximoplantarly projecting tubercle. A shallow but distinct groove is present on the plantar surface of the bone just medial to this tubercle—this groove is visible in proximal view as a notch in the ventral margin of the medial cotyla (Fig. 1E). In plantar view, the lip of the cotyla enlarges distally, and is thickest distal to the tubercle; a similar morphology is observed in some enantiornithines (*Avisaurus*, *Qiliania*, *Yungavolucris*), whereas in *Mystiornis* the plantar labrum appears to be a constant thickness. Members of Ornithuromorpha have a much more developed plantar projection, the hypotarsus; the enantiornithine *Lectavis* and basal ornithothoracine *Vorona* have proximocaudal expansions of the tarsometatarsus, but these are much more distinct than the projection observed in the new specimen (Chiappe, 1993; Forster et al., 2002).

TABLE 1. Select measurements from ZIN PH 1/154.

Element and dimension	Measurements, mm
Tarsometatarsus length (metatarsal III)	48.68
Metatarsal II	41.14
Metatarsal V	(12.44)
Metatarsal II, trochlea	4.77
Metatarsal III, trochlea	3.77
Metatarsal IV, trochlea	2.4
Metatarsus, maximum proximal width	(8.6)
Metatarsus, maximum distal width	10.78

Incomplete measurements are given in parentheses.

Metatarsals II and III are fused along their proximal quarter but are unfused along their remaining lengths. Metatarsal III is the longest, followed by metatarsal IV—which reaches the proximal margin of the metatarsal III trochlea, and then metatarsal II—which almost reaches the proximal margin of the metatarsal IV trochlea. Metatarsal III is the widest; metatarsals II and IV are subequal in width. The dorsal surface of metatarsal III is not strongly convex, unlike in *Mystiornis* and avisaurid enantiornithines (Chiappe, 1992; Kurochkin et al., 2011). Metatarsals II–IV are coplanar throughout their lengths, as in most basal birds, enantiornithines, and *Vorona*. There are two tubercles present on the dorsal surface of the metatarsus, one just distal to the other (Fig. 1A): the larger tubercle is located on metatarsal II, close to the contact with metatarsal III; the smaller, more proximally located tubercle is located on the dorsal surface of metatarsal III (nearly centered but slightly displaced medially). Some specimens of *Confuciusornis* possess two tubercles in similar arrangement and *Vorona* possesses a scar in place of the second tubercle (Chiappe et al., 1999; Forster et al., 2002); two tubercles are also present in the ornithurine *Ichthyornis* (Clarke, 2004). The larger tubercle on metatarsal II is similar in morphology and position to the attachment site of the m. tibialis cranialis in basal birds (Enantiornithes, Confuciusornithiformes). The attachment site moves laterally and is smaller and much more proximally located in ornithurines (e.g., *Ichthyornis*). *Mystiornis* bears a slight tubercle on the cranial surface of metatarsal III, most similar to the ornithurine condition. Where two tubercles are present (e.g., some specimens of *Confuciusornis*, *Ichthyornis,* and some neornithines), both are inferred to be for the attachment of the m. tibialis cranialis (Chiappe et al., 1999). The presence of a proximal vascular foramen, like that in *Mystiornis*, avisaurid enantiornithines, and ornithuromorphs (e.g., *Apsaravis*, *Vorona*, *Hongshanornis*, *Ichthyornis*), cannot be determined because the proximal half of metatarsal IV is not preserved.

In plantar view, the tarsometatarsus is excavated; the plantar surface of metatarsal III is flat, but this surface in metatarsals II and IV is keeled (crista plantaris medialis and lateralis, respectively), particularly along the middle third of their lengths (Fig. 1B). A similar morphology is observed in several enantiornithines (*Avisaurus archibaldi*, *Lectavis*, *Soroavisaurus*, *Sinornis*)

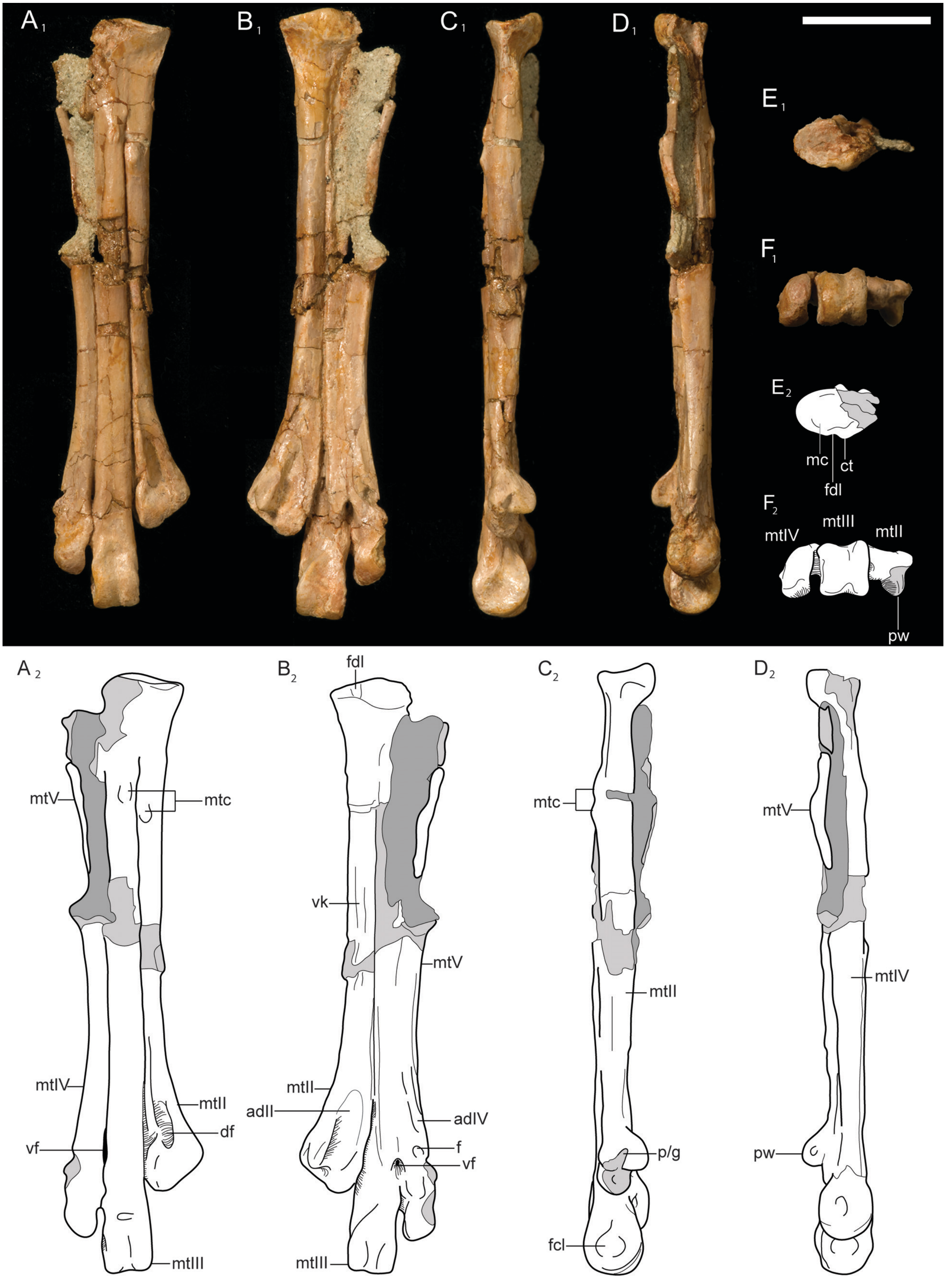

FIGURE 1. Photograph (top) and interpretive drawing (bottom) of the right tarsometatarsus (ZIN PH 1/154, holotype) of *Evgenavis nobilis*, gen. et sp. nov. **A$_1$**, **A$_2$**, dorsal view; **B$_1$**, **B$_2$**, plantar view; **C$_1$**, **C$_2$**, medial view; **D$_1$**, **D$_2$**, lateral view; **E$_1$**, **E$_2$**, proximal view; **F$_1$**, **F$_2$**, distal view. See text for abbreviations. Scale bar equals 10 mm.

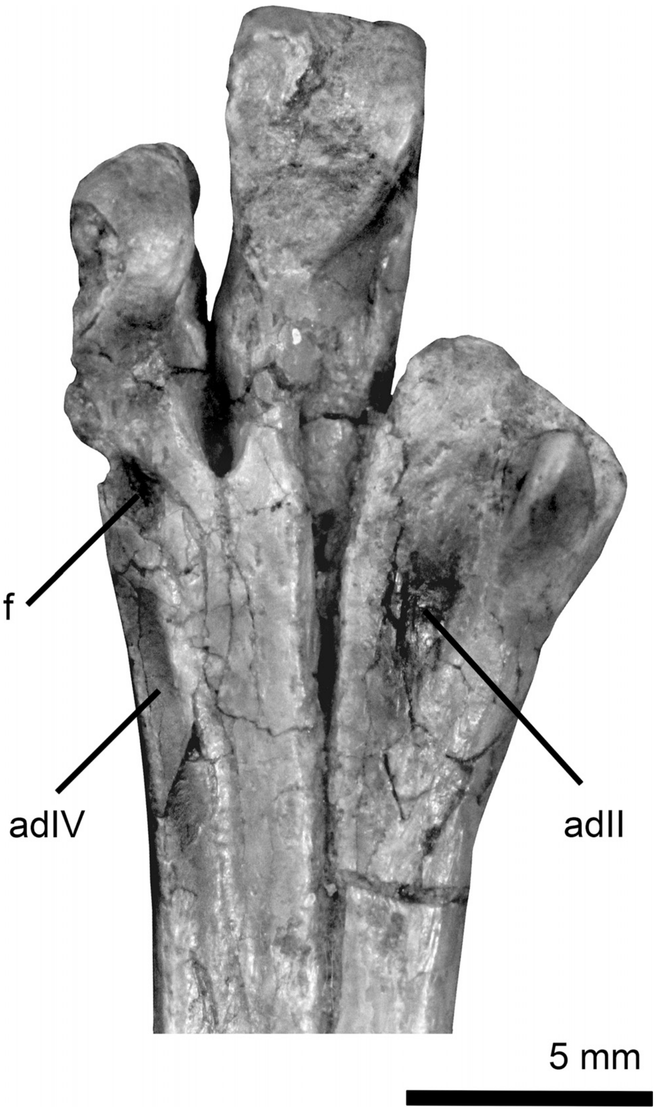

FIGURE 2. Close up of the distal end of the right tarsometatarsus (ZIN PH1/154) of *Evgenavis nobilis*, gen. et sp. nov., in plantar view. See text for abbreviations.

and also *Mystiornis*, *Vorona*, and some ornithuromorphs (e.g., *Yixianornis, Hongshanornis*). In the new specimen, the excavation is closed proximally by the thickened plantar labrum of the proximal articular surface. The medial crest is located on the plantar surface of metatarsal II, whereas the lateral crest is located on the plantolateral surface of metatarsal IV so that the excavation is laterally displaced on the plantar surface. The excavation diminishes past the midpoint; the plantar surfaces of metatarsals II–IV are flat proximal to the trochlea. Proximal to the trochlea in plantar view, the edges of the metatarsals do not contact, although they do contact on the dorsal surface, so that the intertrochlear incisures between metatarsals II and III and III and IV are deeper (more proximally extensive) on the plantar surface than on the dorsal surface (Fig. 1B). Neither the medial nor plantar surface of metatarsal II show any indication of a scar or facet for metatarsal I (present in *Mystiornis*; Kurochkin et al., 2011).

The distal end of metatarsal II expands into the trochlea, which is the widest in the foot, as in confuciusornithiforms, most enantiornithines (e.g., *Avisaurus*, *Gobipteryx*, *Neuquenornis*, *Pengornis*, *Yungavolucris*), *Mystiornis*, and some neornithines (e.g., Accipitridae). The metatarsal II trochlea appears be non-ginglymoid—a well-defined ginglymous groove does not divide the trochlear condyles on the dorsodistal surface. A non-ginglymous metatarsal II is also present in *Confuciusornis* (Chiappe et al., 1999); *Mystiornis* is described as weakly ginglymous (Kurochkin et al., 2011). The dorsal surface of the trochlea of metatarsal II is deeply excavated centrally by a triangular depression that is sharply defined medially but shallows out laterally, proximally, and distally (depressio dorsalis trochlea II; Fig. 1A). A trochlea II dorsal depression is also present in *Mystiornis*, although it is not as well developed as in *Evgenavis* (Kurochkin et al., 2011); this feature is absent in *Confuciusornis*. The distal margin of the metatarsal II trochlea is angled with respect to the long axis of the tarsometatarsus, with the lateral half projecting farther than the medial half; this may be exaggerated in the new specimen by damage to the medial condyle of the metatarsal II trochlea. The distal end of metatarsal II is also angled in *Mystiornis*, *Confuciusornis*, and some enantiornithines (e.g., *Vescornis*). In plantar view, the medial condyle projects much farther caudally than the lateral trochlear condyle, forming a plantar wing-like flange (as in *Mystiornis*, *Apsaravis*, *Confuciusornis*, and many neornithines); the shallow intercondylar groove is continuous with a proximally extending shallow excavation (depressio plantaris trochlea II), also present in *Mystiornis* and *Confuciusornis* (NHMW1997z/0000). The medial and lateral surfaces of the metatarsal II trochlea appear to be flat; however, there is a small, deep pit on the mediodistal margin of the medial condyle of the trochlea; this pit is connected by a groove to another small pit located in the intercondylar incisure of the trochlea in distal view (Fig. 1B). The groove and latter pit may be the result of abrasion and breakage—however, we interpret these morphologies as actual features; the pit on the medial surface may possibly be for a collateral ligament.

The trochlea of metatarsal III is slightly narrower than that of metatarsal II and ginglymous. The two condyles of the trochlea are equal in plantar and distal extent and weakly separated by a groove, which may have been reduced by abrasion. On the dorsal surface, the intercondylar groove is continuous with a small, shallow circular depression (depressio dorsalis trochlea III), as in *Mystiornis*. Just proximal to this depression on the lateral side, a small groove runs diagonally from the dorsolateral surface distally on to the lateral surface. The medial edge of this groove is defined by a slight ridge that forms the lateral and proximal margins to the shallow trochlea III dorsal depression. Both the medial and lateral surfaces of the metatarsal III trochlea are excavated by a pit for the collateral ligament (only present on the medial surface in *Mystiornis*). In plantar view, the medial condyle of the trochlea is more defined than the lateral condyle. The medial edge of the medial condyle of the metatarsal III trochlea forms a sharp, ridge-like margin that angles laterally proximally and distally encloses a deep caudomedial excavation on metatarsal III (Fig. 1B); the excavation may be somewhat exaggerated by crushing.

The most proximal preserved portion of metatarsal IV indicates that the dorsal surface was strongly convex for a portion of its length; this convexity diminishes from the most proximal preserved portion of the shaft (approximately midpoint). This is also present in *Mystiornis*, but not limited to metatarsal IV (Kurochkin et al., 2011). Metatarsal IV expands laterally along the distal quarter of its length. The lateral surface is damaged; however, the trochlea appears to be non-ginglymous and single-headed, as in some basal birds (e.g., enantiornithines, *Confuciusornis*, *Vorona*). A vascular foramen is located between metatarsals III and IV; the metatarsals are not fused as they are in *Mystiornis*—just proximal to the trochlea, metatarsal IV expands medially to distally enclose this foramen. A similar morphology is observed in *Rahonavis*, *Confuciusornis*, and avisaurid enantiornithines; in ornithuromorphs, this opening is fully closed by fusion of the metatarsals distal to the foramen (e.g., *Apsaravis*, *Patagopteryx*, *Yixianornis*). The plantar opening for the foramen is much larger than the dorsal opening. On the plantar surface, a groove extends on the lateral edge of metatarsal IV for 30% of its total length, ending at the trochlea (Fig. 1B). This is likely for one of the flexor tendons of the fourth digit. A very small foramen that does not perforate the tarsometatarsus is located just proximal to the trochlea and just medial to the groove (Fig. 1B). The medial half of the trochlea is excavated. Proximal to the trochlea, a suture is no longer visible along the distal one-third of metatarsals III and IV.

DISCUSSION

Comparative Morphology

The new specimen ZIN PH 1/154 shows a unique suite of morphologies that distinguish it from *Mystiornis cyrili* from the same formation (Kurochkin et al., 2011) and other Mesozoic birds. These differences indicate that ZIN PH 1/154 most likely represents a new form, for which we erect the name *Evgenavis nobilis*, gen. et sp. nov. Because the new tarsometatarsus bears some similarity to a number of different groups (e.g., basal pygostylians and basal ornithothoracines), we compared it with the entire range of known Mesozoic birds in addition to selected paravian taxa in order to determine its phylogenetic position. The tarsometatarsus is in some ways similar to those of basal troodontids (e.g., *Sinovenator changii*, *Mei long*), which are very different from their derived counterparts that exhibit the arctometatarsalian condition (Makovicky and Norell, 2004). However, basal troodontids differ from the new specimen in several aspects: a tubercle on the dorsal surface of metatarsal II is absent; the metatarsals are unfused; and the metatarsal IV trochlea is ginglymous (Xu and Norell, 2004). The fusion of the metatarsals to the proximal tarsals (inferred) and partial fusion of the metatarsals to each other suggests a bird (rather than a paravian dinosaur), but because fusion is incomplete, the taxon is excluded from Ornithurae. The new specimen can be further excluded from the derived clade due to the absence of a hypotarsus and a plantarly displaced proximal part of metatarsal III. A metatarsal V is most common among taxa outside Ornithothoraces, being present in long-tailed birds (e.g., *Archaeopteryx*, *Jeholornis*) and the basal pygostylian groups Confuciusornithiformes and Sapeornithiformes (O'Connor et al., 2011a); however, a metatarsal V is also present in the basal ornithothoracine taxon, *Vorona berivotrensis* (see Forster et al., 1996).

Among basal avians, ZIN PH 1/154 differs from the long-tailed jeholornithiform birds and the basal pygostylian *Sapeornis* in the proportions of the metatarsals (metatarsals II and IV are subequal in these taxa). The new specimen exhibits a strong degree of similarity with *Confuciusornis sanctus*, a basal pygostylian from the Early Cretaceous of China. Both taxa show incomplete fusion, a metatarsal V, two sites for muscle attachment on the dorsal surface of the metatarsals and staggered accordingly, distal end of metatarsal II trochlea angled, plantar projection of the medial condyle of the metatarsal II trochlea, metatarsals II and IV having non-ginglymous trochlea, unfused distal closure of the distal vascular foramen, and an excavated plantar surface (Chiappe et al., 1999). The dorsal surface of metatarsal IV is also convex in confuciusornithiforms (IVPP V12352); proximally, this feature is also weakly expressed on metatarsal III. *Evgenavis* differs from *Confuciusornis* only in size and proportions, being larger and more slender and waisted than the latter.

The new specimen differs from enantiornithines in several regards. Metatarsal IV is not reduced as it is in most enantiornithines (although to varying degrees); metatarsal II appears to be thinner than IV in ZIN PH 1/154. No enantiornithine is known to possess a metatarsal V; several early juveniles were studied and none preserve this element. Although potentially this metatarsal is lost during preservation, the large number of specimens that do not preserve this metatarsal suggests that its absence is genuine. In addition, no enantiornithine preserves more than one tubercle for muscle attachment on the proximodorsal surface.

Evgenavis (and *Confuciusornis*) also shares a number of features with the basal ornithothoracine *Vorona berivotrensis* and the basal ornithuromorph *Apsaravis ukhaana*. The tarsometatarsus of *Vorona* is poorly fused, retains a metatarsal V, has two muscle attachment sites on the proximodorsal surface, a distal vascular foramen, and is plantarly excavated (Forster et al., 2002). The two taxa differ in the relative positions of the metatarsal trochlea (those of metatarsals II and IV are subequal in *Vorona*). In *Vorona*, the distal end of metatarsal II is not angled and the trochlea is ginglymous; the lateral surface bears a pit for the collateral ligament. *Apsaravis* shows a much greater degree of fusion and metatarsal V is absent; however, it shares with *Confuciusornis* and *Evgenavis* a plantarly projecting medial condyle of the metatarsal II trochlea. In *Apsaravis*, the lateral condyle of the metatarsal IV trochlea also projects plantarly. *Apsaravis* can be further distinguished from the new specimen by the plantar displacement of metatarsal III proximally and of the trochlea of metatarsals II and IV distally (Clarke and Norell, 2002).

Evgenavis can be clearly distinguished from *Mystiornis*, which occurs in the same formation. Overall, *Mystiornis* shows a greater degree of fusion, although this feature may be related to the ontogenetic age of the specimens. The proportions of the metatarsals are different in each taxon; *Mystiornis* is much more gracile and metatarsal II is reduced relative to other known Mesozoic birds, ending well above the proximal margin of the metatarsal IV trochlea (nearly reaching this margin in *Evgenavis*). *Evgenavis* has two proximal tubercles for the m. tibialis cranialis, whereas *Mystiornis* only has a single faint tubercle. The dorsal surface of metatarsal III is strongly convex in *Mystiornis* and a plantar tubercle is present proximal to the metatarsal II trochlea, whereas both of these features are absent in *Evgenavis*. In *Mystiornis*, the distal vascular foramen is closed distally by fusion between metatarsals III and IV—but these are unfused in *Evgenavis*. Furthermore, in *Mystiornis*, the distal interosseal canal originates proximal to the distal vascular foramen, but terminates inside it. The latter feature is an autapomorphy of *Mystiornis*; in neornithines, the canal originates inside the foramen, runs more distally and terminates in the intertrochlear incisure.

Systematic Position of *Evgenavis*

In order to test morphological hypotheses regarding potential relationships, we placed the new specimen (ZIN PH 1/154) in a comprehensive cladistic analysis. In light of this new discovery, we also reexamined the inferred systematic position of *Mystiornis cyrili*. This specimen was assigned to a new order of birds, rather than referred to an existing group, and published phylogenetic hypotheses for this taxon vary widely (Kurochkin et al., 2011). However, the specimen shows several features, many of which were noted by the original authors, that are consistent with enantiornithine affinities and, in particular, with a clade known as Avisauridae (Brett-Surman and Paul, 1985; Chiappe, 1992). Unlike the new specimen, the holotype of *Mystiornis cyrili* does not preserve a metatarsal V, and metatarsal IV is reduced in a way similar to that of enantiornithines (metatarsal IV is not reduced in *Evgenavis*). The convex dorsal surface of metatarsal III and the dorsally inclined proximal articular surface in *Mystiornis* are both features also present in avisaurids (e.g., *Soroavisaurus*, *Neuquenornis*). Notably, metatarsal IV is not strongly reduced in *Avisaurus archibaldi*. An excavated plantar surface formed by the keeled plantar surfaces of metatarsals II and IV is also present in a range of enantiornithine taxa, including some avisaurids (e.g., *Soroavisaurus*). However, the location of the attachment of the m. tibialis cranialis, on metatarsal III 20% from its proximal end, is consistent with ornithuromorphs, and fusion is nearly complete, and greater than in other enantiornithines. Metatarsal IV is dorsally concave (as also present in many neornithines such as cormorants, loons, procellariiforms, etc.), and the distal interosseal canal is present (however, it originates proximal to the distal vascular foramen and terminates within this foramen). These advanced features clearly distinguish *Mystiornis* from avisaurid enantiornithines. The proximal end of the holotype of *Mystiornis* is damaged and it cannot be determined if three proximal cotyla were truly present; however, this morphological assessment suggests that further information is needed before this taxon can be assigned to a particular clade (Aves incertae sedis).

Determining the phylogenetic placement of *Evgenavis* through comparative morphology and cladistic analysis is still problematic because of the limited material (less than a single element for comparison) and the phylogenetic distribution of its preserved features (which are found in taxa ranging from basal birds to ornithuromorphs). The result of any analysis based on such limited material is subject to change with new information (e.g., the discovery of wing elements). Nevertheless, we entered the new specimen into an existing data matrix that was targeted towards assessing Mesozoic bird relationships (O'Connor et al., 2011a). With the inclusion of the new specimen, *Mystiornis*, and two avisaurids (*Soroavisaurus* and *Avisaurus archibaldi*), the matrix included 64 taxa scored for 245 characters. The analysis was run in TNT (Goloboff et al., 2008) using a heuristic parsimony search based on 1000 replications of tree bisection reconnection (TBR). Retaining the single shortest tree from each replication produced 12 most parsimonious trees (MPTs) of 850 steps; from these, a reduced consensus tree was calculated that excluded three taxa (*Liaoningornis longidigitrus*, *Archaeorhynchus spathula*, and *Jianchangornis microdonta*), all of which are resolved both as enantiornithines and ornithuromorphs in equal length trees) (Fig. 3). This result places *Evgenavis*, *Mystiornis*, and *Vorona* within Enantiornithes; the clade itself forms a complete polytomy except for a relationship between *Buolochia* and *Longipteryx* (O'Connor et al., 2011b). An additional run of TBR produced over 1000 trees one step shorter, with Ornithothoraces collapsing in the Nelsen strict consensus. The results of this analysis are only weakly supported (consistency index [CI] = 0.382, retention index [RI] = 0.667), a result of the fragmentary nature of several of the primary taxa in this study as well as the mosaic distribution of characters, which make it difficult to infer phylogenetic relationships. The placement of *Mystiornis* within Enantiornithes is unsurprising given the number of characters shared with Avisauridae; the addition of an avisaurid taxon not included by Kurochkin et al. (2011) may have permitted the analysis to recognize this potential relationship. Alternatively, the results may reflect differences in interpretation regarding the proximal articular surface of the tarsometatarsus in this taxon. The phylogenetic placement of *Vorona* varies widely in previous analyses; the taxon has been resolved as basal to all other taxa excluding *Archaeopteryx* (Kurochkin et al., 2011), as the ornithothoracine sister taxon (Z.-H. Zhou and Zhang, 2005), as an enantiornithine (Z.-H. Zhou and Zhang, 2006), and as an ornithuromorph (Z.-H. Zhou et al., 2008). Of the taxa excluded in the reduced consensus, *Liaoningornis* is commonly regarded as an ornithuromorph, although a recent study has reassigned the species to Enantiornithes (O'Connor, 2012). The analysis resolves *Jianchangornis* and *Archaeorhynchus* (also removed) as basal members of both ornithothoracine clades as well as together in a separate clade forming the sister group to Ornithothoraces. Both taxa are basal ornithuromorphs with unusual morphologies that hint at the plesiomorphic ornithothoracine condition (e.g., deep caudal embayments in the sternum of *Archaeorhynchus*, usually considered an enantiornithine feature). New discoveries of basal ornithothoracines have blurred the once clear distinction between the two ornithothoracine clades (S. Zhou et al., 2012).

Using implied weights (Goloboff et al., 2008) to investigate the effect of homoplasy on the analysis produced different results. Setting the constant (k) at 1.0 and 3.0 resulted in similar topographies in which *Evgenavis*, *Mystiornis*, *Vorona*, *Soroavisaurus*, and *A. archibaldi* are consistently resolved together in a clade within Ornithuromorpha; their positions alternate so that in the reduced consensus tree (e.g., with *Chaoyangia* removed because it alternates between Enantiornithes and Ornithuromorpha), they form a basal polytomy with *Ambiortus* and *Schizooura* (314 trees, tree length [TL] = 80.80266, CI = 0.375, RI = 0.0657; Supplemental Data, Fig. S1). Ornithothoraces collapses with k = 2.0, resulting in the derived enantiornithine and ornithurine clades resolved in a polytomy with basal taxa. These results highlight the high amount of homoplasy that characterizes early avian evolution, which exacerbates the lack of resolution that surrounds the phylogenetic position of *Evgenavis* and other extremely fragmentary taxa. Implied weighting has a greater effect on the position

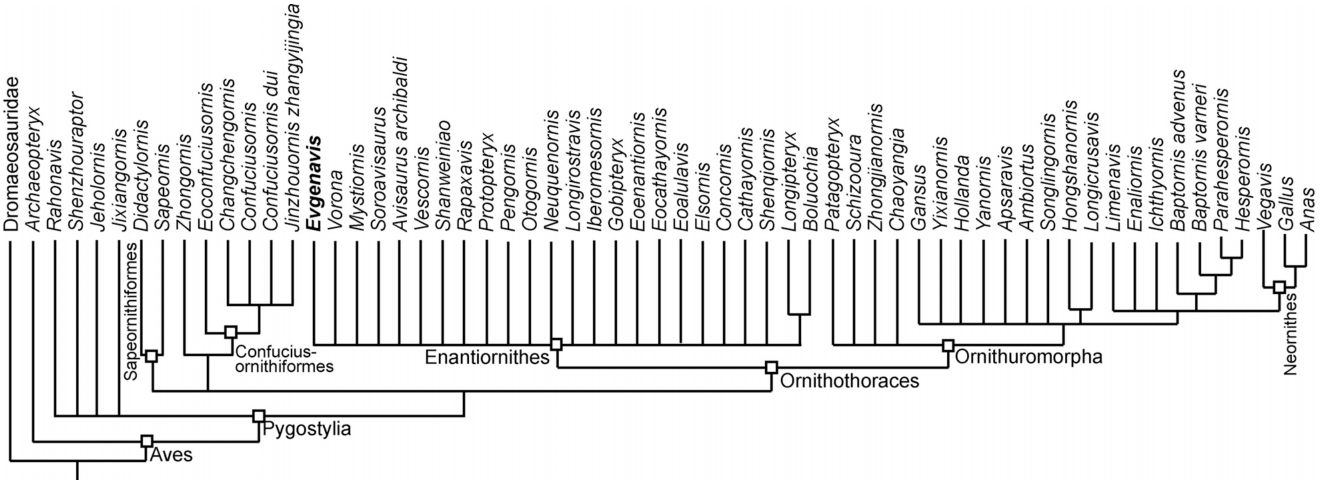

FIGURE 3. Hypothetical phylogenetic relationship of *Evgenavis nobilis*, gen. et sp. nov. Cladogram of the reduced consensus tree (12 MPTs, TL = 850 steps, CI = 0.382, RI = 0.667; excluding *Archaeorhynchus*, *Jianchangornis*, and *Liaoningornis*) with *Evgenavis* and *Mystiornis* resolved within Enantiornithes.

of fragmentary taxa and both unweighted and weighted trees are weakly supported.

Comparisons between these taxa highlighted several features of the tarsometatarsus that are not in the character matrix, but that may be phylogenetically important due to their distributions among these early birds. Such features might be especially important for understanding these fragmentary specimens. Thus, we added two new tarsometatarsal characters to the matrix (distinguishing between the presence of one versus two tubercles for muscle attachment on the dorsal surface, and the absence/presence of a plantarly projecting medial condyle on the metatarsal II trochlea; see Supplemental Data) and reran the data set. The first round of TBR produced a single highly resolved tree (TL = 858 steps) that also placed both *Evgenavis* and *Mystiornis* within Enantiornithes; an additional round of TBR resulted in over 1000 trees of the same length in which all ornithothoracine taxa form a large polytomy in the Nelsen strict consensus. Removal of *Chaoyangia* and *Liaoningornis*, taxa whose systematic positions are debatable (O'Connor, 2012; O'Connor and Zhou, 2013), produced resolution between Enantiornithes and Ornithuromorpha (Supplemental Data, Fig. S2). In the reduced strict consensus tree, as in the previous analysis, Enantiornithes forms a polytomy that also includes *Evgenavis*, *Mystiornis*, and *Vorona*, and a *Boluochia* + *Longipteryx* clade. Ornithuromorpha, however, is highly resolved, with results similar to other recent analyses (O'Connor et al., 2011a; O'Connor and Zhou, 2013). The addition of these new tarsometatarsal characters was therefore able to lend further resolution to this analysis, which had been hindered by the inclusion of very fragmentary taxa (*Vorona*, *Mystiornis*, *Avisaurus*, *Evgenavis*, *Soroavisaurus*). These results imply that these characters are highly homoplastic, and do not support a relationship between *Confuciusornis* and *Evgenavis*, despite the shared presence of these and other features.

Fossil confuciusornithiforms are the most common type of bird collected in the Jehol Group, especially in the lower Yixian Formation, and hundreds of specimens have been recovered (Chiappe et al., 2008). However, confuciusornithiforms have not been reported from any other geologic unit. The only potential specimen reported from outside China comes from Jehol Group equivalents exposed in North Korea, which are geographically continuous with exposures in northeastern China (Lee et al., 2001). The group is important because it includes the oldest known beaked bird, the first bird described with a pygostyle, and perhaps the earliest documented case of sexually dimorphic plumage within an avian species (Hou et al., 1996). Although comparative material is limited, there are no significant morphological differences between *Evgenavis* and *Confuciusornis sanctus*; differences mostly relate to size or poor preservation. Instead, the two taxa share a unique suite of morphologies that are not found in any other bird group: fifth metatarsal present; partial fusion of metatarsals II–IV; two tubercles on the dorsal surface, one distal to the other; plantarly projecting medial condyle of metatarsal II trochlea; distal margin of metatarsal II angled proximomedial-distolaterally; and non-ginglymous trochlea on metatarsals II and IV. Discovery of a confuciusornithiform in Siberia would greatly expand the known range of the clade and imply the group was not endemic to the Jehol Biota. The cladistic analyses presented here resolve *Evgenavis* as an enantiornithine, despite the presence of a metatarsal V (which is also present in *Vorona* and that is also resolved here as an enantiornithine) and other features otherwise unknown in Enantiornithes (O'Connor, 2009), indicating that this taxon and others (e.g., *Vorona*, *Mystiornis*) may currently be too fragmentary to accurately assess with cladistic analysis. Given these results, we cannot currently justify the assignment of *Evgenavis* to Confuciusornithiformes, although we also do not feel that there is a strong justification for assigning the taxon to Enantiornithes. Thus, *Evgenavis* is not referred to a specific clade and is regarded as Aves incertae sedis herein; new material is required to elucidate its phylogenetic position.

Evolution of Avian Hind Limb Musculature

One of the most interesting features of *Evgenavis* is the presence of two muscle attachment sites on the proximodorsal surface of the tarsometatarsus. Most Mesozoic birds have only one attachment site, which is inferred to be for the m. tibialis cranialis. Enantiornithes and Ornithuromorpha generally differ in that this attachment site is distomedially located in the former and proximolaterally located in the latter (O'Connor, 2009). Reptiles have very complex pedal musculature compared with birds; the m. tibialis anterior in reptiles is considered homologous with the m. tibialis cranialis of modern birds (Hutchinson, 2002). In reptiles, this muscle has a single anterior insertion point and multiple distal insertions on the medial side of the metatarsus, particularly on metatarsal I. In the avian lineage, a second anterior attachment site evolves on the femur, whereas the distal insertions move proximolaterally (Hutchinson, 2002); in living birds, the two bellies of the muscle converge into a single tendon proximal to the ankle. However, in some neornithines, the distal tendon of the m. tibialis cranialis bifurcates and there are two (sometimes three) attachment sites (Hudson, 1937; Zinoviev, 2010). This condition is also subject to individual variation (Hudson et al., 1959; George and Berger, 1966); however, where the tendon distally bifurcates, the two attachments are clearly associated with two separate tubercles. The presence of two tubercles characterizes several bird orders (Gaviiformes, Podicipediformes, Charadriiformes, Gruiformes, some Anseriformes, and a few others). This bifurcation may represent an atavism in Neornithes.

The presence of a hypertrophied tubercle on the dorsal surface of metatarsal II in some enantiornithines (e.g., *Avisaurus*, *Soroavisaurus*) is hypothesized to represent the concentration of m. tibialis cranialis insertions onto a single area of metatarsal II due to the reduction and retroversion of metatarsal I (Hutchinson, 2002). This suggests that during the evolution of the neornithine condition, the multiple distal attachments moved proximally before reducing to a single attachment. Basal birds with two tubercles (and thus attachment sites) may represent a previously unrecognized stage in the evolution of the neornithine condition (in which the attachments continued to move proximolaterally, but did not attach at a single site); however, in early birds where two tubercles were present (e.g., *Evgenavis*, *Confuciusornis*, *Vorona*), we cannot unambiguously determine whether one distally bifurcated tendon or if two separate tendons were present. In Neornithes, these tubercles are always closely positioned, whereas in *Evgenavis* the medial one is more distally located than the lateral one; this condition is also present in the ornithurine *Ichthyornis* (Clarke, 2004), suggesting that the derived condition of a single tendon evolved within neornithines.

The separation of the two tubercles may indicate that the two tendons had different functional specializations. The distance between the center of rotation of the joint and the point of insertion of the tendon constitutes the lever arm of the force acting to dorsiflex (hyperextend) the tarsometatarsus. The shorter the lever arm, the faster the speed of the flexion; simultaneously, with an increase in the lever arm, speed decreases but force increases—the latter effect may be especially important for those muscles that primarily act to stabilize joints (e.g., Cracraft, 1971). Extant birds that have a single insertion point of the m. tibialis cranialis must 'choose' between speed and force and the position of the insertion point, which varies only slightly in neornithines, reflects ecological differences (Zeffer and Norberg, 2003). Calculations by Norberg (1979) have shown that even a slight (1–2 mm for small birds) increase of the lever arm may strongly affect the resultant force. The force, for example, is greater in accipitrids, which use their feet to carry their prey. In these birds, the point of the insertion of the m. tibialis cranialis is positioned far away from the ankle joint, located even more distally than *Evgenavis* and other in early birds (e.g., *Yungavolucris*). Biomechanical study of the raptorial hind limb revealed that the m. tibialis cranialis of accipitrids is capable of maintaining maximum effectiveness through a wide range of intertarsal angles (Goslow, 1972). Tree-trunk-foraging birds also have a distally located insertion of the m. tibialis cranialis on the tarsometatarsus (Richardson, 1942); this is in response to gravitational forces, which tend to extend the ankle joint while the bird is climbing, requiring the flexor muscles of tree-trunk-foraging birds to exert a larger force. Early birds that had two insertion points of the main metatarsus flexor thus might have been capable of adjusting the force and speed of ankle flexion by distributing the force between either of the two tendons. If true, this would imply a generalized hind limb functional morphology in early birds, which is supported by studies on other aspects of hind limb morphology (Hopson, 2001).

Another important aspect of the new specimen is the plantar projection of the medial trochlea of metatarsal II, a feature that is also present in *Confuciusornis* and *Apsaravis*, and to a lesser degree in *Hesperornis* and *Hongshanornis*. This projection acts as a medial barrier for muscle tendons, preventing them from slipping away from the long axis of the digit and allowing for the second digit to be splayed medially (Zelenkov and Dyke, 2008). The presence of this feature is more probably related to functional similarities or the necessity for a similar range of motion, but within different environments (e.g., the extremely specialized foot-propelled marine diving bird, *Hesperornis*, versus the continental form *Apsaravis*) rather than phylogenetic proximity; our phylogenetic results indicate that this feature evolved several times within Aves. In the foot-propelled diving hesperornithiforms, a group with highly specialized tarsometatarsal morphology, a moderately developed wing-like flange is present on the trochlea of metatarsal II; medial movement of the second digit was probably important to increase the surface area of the foot in order to facilitate propulsion. The presence of the wing-like flanges on both trochleae in *Apsaravis* indicates the ability to splay the second and fourth digits. In extant birds, these wing-like flanges are most developed in birds of prey, i.e., owls and mousebirds (Zelenkov and Dyke, 2008), forms that have a high degree of pedal mobility but lack specialized structures of the foot like those of zygodactyl birds (e.g., 'sehnenhalter' of Pici) (Steinbacher, 1935).

Evgenavis also preserves two tendinal grooves on the plantar surface of the tarsometatarsus. The first groove is positioned on the ventroproximal surface of the second metatarsal just medial to the tubercle on the ventral labrum of the medial cotyla (Figs. 1–2). This groove is interpreted as the sulcus for the distal tendon of the m. flexor digitorum longus. In Neornithes, the sulcus for this tendon is often the deepest and most medially positioned sulcus within the complex avian hypotarsus. In *Apteryx* and dinornithids, the sulcus for this tendon is the only excavation present (Owen, 1879; Brinkmann, 2010), somewhat resembling the condition in *Evgenavis*. This allows us to hypothesize that the sulcus for the tendon of the m. flexor digitorum longus was the first to evolve in the avian hypotarsus.

The second groove is located on the plantar surface of the fourth metatarsal, proximal and lateral to the distal vascular foramen (Fig. 2). The topography of this groove suggests that it supported a tendon that passed from the plantar surface of the tarsometatarsus to its lateral surface just proximal to the trochlea. As such, we assume that this groove corresponds to the tendon of m. abductor digiti IV, an intrinsic muscle of the foot that originates from the lateroplantar surface of the tarsometatarsus in Neornithes; the distal tendon of this muscle runs along the lateral margin of the plantar surface of the tarsometatarsus and then passes on the lateral surface to insert onto the basal phalanx of the fourth digit (George and Berger, 1966). This muscle is usually weak in Neornithes, being strongly developed in only a few groups (George and Berger, 1966). In those groups where this muscle is strong (e.g., Accipitridae, Sulidae), there is a deep fossa on the lateroplantar surface of the tarsometatarsus (vestigial or completely absent in most birds). In *Evgenavis*, the medial plantar crest is located on the plantar surface of metatarsal II, whereas the lateral plantar crest is formed by the keeled lateroplantar margin of metatarsal IV so that the plantar fossa is laterally displaced. We interpret this as further evidence of a strongly developed m. abductor digiti IV. In *Evgenavis*, this fossa is, however, too large to accommodate just the belly of this muscle, and we infer that it contained other intrinsic foot flexors, most probably the short flexors of the third and second digits.

The deep pit distally located on the plantar surface of the second metatarsal (Fig. 2) in *Evgenavis* may represent the origin site of the m. adductor digiti II. Among living birds, this muscle is distally positioned only in primitive groups (Palaeognathae, Galloanseres); in more advanced birds, the belly of this muscle extends proximally as far as the hypotarsus (Hudson, 1937; George and Berger, 1966; Zinoviev, 2010). Thus, the distal origin of this muscle interpreted for *Evgenavis* may represent a basal feature, plesiomorphic for Neornithes and retained in some taxa.

Living birds typically possess a shallow but distinct excavation on the ventromedial proximal tarsometatarsus that houses the belly of the m. flexor hallucis longus. This excavation is completely absent in some birds (e.g., Gaviidae), in which the hallux is nonfunctional. This excavation is also absent in *Evgenavis*, suggesting that this short muscle was either very weak or was not yet isolated from the common reptilian plantar flexors. The latter assumption seems more plausible given that the hallux is large and clearly functional in the morphologically similar *Confuciusornis* (Chiappe et al., 1999). Therefore, we suggest that there was no short specialized hallucal flexor in *Evgenavis*, implying that flexion of the first digit was controlled by a long flexor in basal birds as in reptiles.

CONCLUSIONS

New discoveries continue to change our understanding of Mesozoic bird diversity. The new Siberian specimen is distinct from all other known Mesozoic birds and thus is considered a new taxon for which we erect the name, *Evgenavis nobilis*. The new taxon shares features with the Late Cretaceous basal ornithothoracine *Vorona*, the ornithuromorph *Apsaravis*, and enantiornithine avisaurids, but most closely resembles the Chinese Early Cretaceous clade, Confuciusornithiformes. This specimen highlights the mosaic distribution of 'derived' avian features that characterizes the early evolution of Aves. Fragmentary specimens of basal taxa are particularly difficult to identify: cladistic analysis resolves the new specimen as an enantiornithine, but implied weighting causes the taxon to be resolved as a basal ornithuromorph. The addition of two new tarsometatarsal characters returns *Evgenavis* to Enantiornithes and lends resolution to Ornithuromorpha. *Evgenavis nobilis* is referred to Aves incertae sedis pending additional discoveries. The specimen documents the earliest occurrence of the short muscles characteristic of modern birds.

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LITERATURE CITED

Baumel, J. J., and L. M. Witmer. 1993. Osteologia; pp. 45–132 in J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans, and J. C. Vanden Berge (eds.), Handbook of Avian Anatomy: Nomina Anatomica Avium, second edition. Nuttall Ornithological Club, Cambridge, Massachusetts.

Brett-Surman, M. K., and G. S. Paul. 1985. A new family of bird-like dinosaurs linking Laurasia and Gondwanaland. Journal of Vertebrate Paleontology 5:133–138.

Brinkmann, J. 2010. Vergleichende Untersuchungen an der Hinterextremität palaeognather Vögel im Hinblick auf deren phylogenetische Systematik. Ph.D. dissertation, Eberhard Karls Universität, Tübingen, 502 pp.

Chiappe, L. M. 1992. Enantiornithine (Aves) tarsometatarsi and the avian affinities of the Late Cretaceous Avisauridae. Journal of Vertebrate Paleontology 12:344–350.

Chiappe, L. M. 1993. Enantiornithine (Aves) tarsometatarsi from the Cretaceous Lecho Formation of northwestern Argentina. American Museum Novitates 3083:1–27.

Chiappe, L. M., S. Ji, Q. Ji, and M. A. Norell. 1999. Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the late Mesozoic of northeastern China. Bulletin of the American Museum of Natural History 242:1–89.

Chiappe, L. M., J. Marugán-Lobón, S. Ji, and Z. Zhou. 2008. Life history of a basal bird: morphometrics of the Early Cretaceous *Confuciusornis*. Biology Letters 4:719–723.

Clarke, J. A. 2004. Morphology, phylogenetic taxonomy, and systematics of *Ichthyornis* and *Apatornis* (Avialae: Ornithurae). Bulletin of the American Museum of Natural History 286:1–179.

Clarke, J. A., and M. A. Norell. 2002. The morphology and phylogenetic position of *Apsaravis ukhaana* from the Late Cretaceous of Mongolia. American Museum Novitates 3387:1–46.

Cracraft, J. 1971. The functional morphology of the hind limb of the domestic pigeon, *Columba livia*. Bulletin of the American Museum of Natural History 144:171–268.

Forster, C. A., L. M. Chiappe, D. W. Krause, and S. D. Sampson. 1996. The first Cretaceous bird from Madagascar. Nature 382:532–534.

Forster, C. A., L. M. Chiappe, D. W. Krause, and S. D. Sampson. 2002. *Vorona berivotrensis*, a primitive bird from the Late Cretaceous of Madagascar; pp. 268–280 in L. M. Chiappe and L. M. Witmer (eds.), Mesozoic Birds: Above the Heads of Dinosaurs. University of California Press, Berkeley, California.

George, J. C., and A. J. Berger. 1966. Avian Myology. Academic Press, New York, 500 pp.

Goloboff, P. A., J. S. Farris, and K. C. Nixon. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.

Goslow, G. E., Jr. 1972. Adaptive mechanisms of the raptor pelvic limb. The Auk 89:47–64.

Hopson, J. A. 2001. Ecomorphology of avian and nonavian theropod phalangeal proportions: implications for the arboreal versus terrestrial origin of bird flight; pp. 211–235 in J. Gauthier and L. F. Gall (eds.), New Perspectives on the Origin and Early Evolution of Birds. Peabody Museum of Natural History, New Haven, Conneticut.

Hou, L., L. D. Martin, Z. Zhou, and A. Feduccia. 1996. Early adaptive radiation of birds: evidence from fossils from northeastern China. Science 274:1164–1167.

Hudson, G. E. 1937. Studies on the muscles of the pelvic appendage in birds. American Midland Naturalist 18:1–108.

Hudson, G. E., P. J. Lanzillotti, and G. D. Edwards. 1959. Muscles of the pelvic limb in galliform birds. American Midland Naturalist 61:1–67.

Hutchinson, J. H. 2002. The evolution of hindlimb tendons and muscles on the line to crown-group birds. Comparative Biochemistry and Physiology Part A 133:1051–1086.

Kurochkin, E. N. 1985. A true carinate bird from Lower Cretaceous deposits in Mongolia and other evidence of Early Cretaceous birds in Asia. Cretaceous Research 6:271–278.

Kurochkin, E., N. Zelenkov, A. Averianov, and S. Leschchinskiy. 2011. A new taxon of birds (Aves) from the Early Cretaceous of Western Siberia, Russia. Journal of Systematic Palaeontology 9:109–117.

Kurochkin, E. N., S. V. Saveliev, A. A. Postnov, E. M. Pervushov, and E. V. Popov. 2006. On the brain of a primitive bird from the Upper Cretaceous of European Russia. Paleontological Journal 40:655–667.

Lee, Y.-N., K.-M. Yu, and C. B. Wood. 2001. A review of vertebrate faunas from the Gyeongsang Supergroup (Cretaceous) in South Korea. Palaeogeography, Palaeoclimatology, Palaeoecology 165:357–373.

Linnaeus, C. 1758. Systema Naturae per Regna tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Volume 1: Regnum Animale. Editio decima, reformata. Laurentii Salvii, Stockholm, 824 pp.

Makovicky, P. J., and M. A. Norell. 2004. Troodontidae; pp. 184–195 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria, second edition. University of California Press, Berkeley, California.

Nessov, L. A. 1992. Mesozoic and Paleogene birds of the USSR and their paleoenvironments; pp. 465–478 in K. E. Campbell Jr. (ed.), Papers in Avian Paleontology Honoring Pierce Brodkorb. Natural History Museum of Los Angeles County, Los Angeles, California.

Nessov, L. A., and A. A. Jarkov. 1989. New Cretaceous-Paleogene birds of the USSR and some remarks on the origin and evolution of the class Aves. Trudy Zoologicheskogo Instituta Akademii Nauk SSSR 197:79–97.

Nessov, L. A., and A. A. Jarkov. 1993. Hesperornithiforms in Russia. Russian Journal of Ornithology 2:37–54.

Norberg, U. M. L. 1979. Morphology of the wings, legs and tail of three coniferous forest tits, the goldcrest, and the treecreeper in relation to locomotor pattern and feeding station selection. Philosophical Transactions of the Royal Society, Series B 287:131–165.

O'Connor, J. K. 2009. A systematic review of Enantiornithes (Aves: Ornithothoraces). Ph.D. dissertation, University of Southern California, Los Angeles, California, 600 pp.

O'Connor, J. 2012. A revised look at *Liaoningornis longidigitrus* (Aves). Vertebrata PalAsiatica 5:25–37.

O'Connor, J. K., and Z.-H. Zhou. 2013. A redescription of *Chaoyangia beishanensis* (Aves) and a comprehensive phylogeny of Mesozoic birds. Journal of Systematic Palaeontology 11(7):889–906.

O'Connor, J. K., L. M. Chiappe, and A. Bell. 2011a. Pre-modern birds: avian divergences in the Mesozoic; pp. 39–114 in G. D. Dyke and G. Kaiser (eds.), Living Dinosaurs: The Evolutionary History of Birds. Wiley Blackwell, Chichester, U.K.

O'Connor, J., Z.-H. Zhou, and F.-C. Zhang. 2011b. A reappraisal of *Boluochia zhengi* (Aves: Enantiornithes) and a discussion of intraclade diversity in the Jehol avifauna, China. Journal of Systematic Palaeontology 9:51–63.

Owen, R. 1879. Memoirs on the Extinct Wingless Birds of New Zealand, with an Appendix on Those of England, Australia, Newfoundland, Mauritius, and Rodriguez. John Van Voorst, London, Volume 1: x + 520 pp., Volume 2: xiv pp., 126 pls.

Richardson, F. 1942. Adaptive modifications for tree-trunk foraging in birds. University of California Publications in Zoology 46:317–368..

Steinbacher, G. 1935. Funktionell-anatomische Untersuchungen an Vogelfüssen mit Wendezehen und Rückzehen. Journal für Ornitholgie 83:214–282.

Xu, X., and M. A. Norell. 2004. A new troodontid dinosaur from China with avian-like sleeping posture. Nature 431:838–841.

Zeffer, A., and U. M. L. Norberg. 2003. Leg morphology and locomotion in birds: requirements for force and speed during ankle flexion. Journal of Experimental Biology 206:1085–1097.

Zelenkov, N. Z., and G. D. Dyke. 2008. The fossil record and evolution of mousebirds (Aves: Coliiformes). Palaeontology 51:1403–1418.

Zhou, S., Z.-H. Zhou, and J. K. O'Connor. 2012. A new toothless ornithurine bird (*Schizooura lii* gen. et sp. nov.) from the lower Cretaceous of China. Vertebrata PalAsiatica 50:9–24.

Zhou, Z.-H., and F.-C. Zhang. 2005. Discovery of an ornithurine bird and its implication for Early Cretaceous avian radiation. Proceedings of the National Academy of Sciences of the United States of America 102:18998–19002.

Zhou, Z.-H., and F.-C. Zhang. 2006. A beaked basal ornithurine bird (Aves, Ornithurae) from the Lower Cretaceous of China. Zoologica Scripta 35:363–373.

Zhou, Z.-H., J. Clarke, and F. Zhang. 2008. Insight into diversity, body size and morphological evolution from the largest Early Cretaceous enantiornithine bird. Journal of Anatomy 212:565–577.

Zhou, Z.-H., F.-C. Zhang, and Z.-H. Li. 2009. A new basal ornithurine bird (*Jianchangornis microdonta* gen. et sp. nov.) from the Lower Cretaceous of China. Vertebrata PalAsiatica 47:299–310.

Zinoviev, A. V. 2010. Comparative Anatomy, Structural Modifications and Adaptive Evolution of Avian Apparatus of Bipedal Locomotion. KMK Scientific Press, Moscow, 285 pp.

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