RESEARCH ARTICLE

A new species of Eogruidae (Aves: Gruiformes) from the Miocene of the Linxia Basin, Gansu, China: Evolutionary and climatic implications

Grace Musser,[1,*] **Zhiheng Li,**[2,3,*] **and Julia A. Clarke**[1]

[1]The University of Texas at Austin, The Jackson School of Geosciences, Austin, Texas, USA
[2]Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China
[3]CAS Center for Excellence in Life and Paleoenvironment, Beijing, China
* Corresponding authors: Grace Musser, gmusser@utexas.edu;
Zhiheng Li, lizhiheng@ivpp.ac.cn

ABSTRACT

Despite having one of the most robust fossil records within core-gruiform birds (rails, cranes, and allies), the biogeographic history of Gruidae (cranes) and key drivers of diversification within this group remain largely unknown. The Eogruidae of Eurasia represent some of the earliest known crane-like fossils. Here, we present description of a new species represented by a well-preserved specimen of a foot from the late Miocene (7–6.5 mya) Liushu Formation of Linxia Basin, Gansu, China. It is the only eogruid fossil that has been found in this formation and is the first eogruid known from northwest China. Linxia Basin is located along the margin of the northeastern Tibetan Plateau, which allows for new insight into Miocene dispersal of the Eogruidae and potential climatological and geological connections. It is also the first specimen with an associated tarsometatarsus and nearly complete phalanges, including a claw, which provides further morphological information on this taxon. Referral of the new specimen to Eogruidae is based on extreme reduction of the trochlea of metatarsal II, which is most similar to the condition present in the eogruid subclade traditionally termed Ergilornithidae.

Keywords: biogeography, China, Eogruidae, evolution, Linxia, morphology, palaeoclimate, Tibetan Plateau

Una nueva especie de Eogruidae (Aves, Gruiformes) del Mioceno de la Cuenca de Linxia, Gansu, China: Implicancias evolutivas y climáticas

RESUMEN

A pesar de tener uno de los registros fósiles más robustos dentro del núcleo de las aves gruiformes (rálidos, grullas y aliados), la historia biogeográfica de Gruidae (grullas) y los factores claves de diversificación dentro de este grupo siguen siendo mayormente desconocidos. Los Eogruidae de Eurasia representan algunos de los primeros fósiles conocidos del tipo de las grullas. Aquí, presentamos la descripción de una nueva especie representada por un espécimen bien preservado de un pie del Mioceno tardío (7–6.5 Ma atrás) de la Formación Liushu de la Cuenca de Linxia, Gansu, China. Este es el único fósil de Eogruidae que ha sido encontrado en esta formación y es el primer Eogruidae conocido del noroeste de China. La Cuenca de Linxia está ubicada a lo largo del margen noreste de la meseta tibetana, lo que brinda una nueva mirada a la dispersión del Mioceno de los Eogruidae y las potenciales conexiones climatológicas y geológicas. También es el primer espécimen con un tarso-metatarso asociado y falanges casi completas, incluyendo una garra, lo que brinda información morfológica adicional de este taxón. La remisión de la nueva especie a Eogruidae está basada en la extrema reducción de la tróclea del metatarsiano II, el cual es más similar a la condición presente en el sub-clado Eogruidae tradicionalmente denominado Ergilornithidae.

Palabras clave: biogeografía, China, Eogruidae, evolución, Linxia, meseta tibetana, morfología, paleoclima

INTRODUCTION

The fossil record of Gruidae (cranes) is one of the most extensive within core-Gruiformes. Gruid fossils have largely been found in northern hemisphere localities (Mayr 2009, 2016a). The biogeographic history, life history, and potential drivers of diversification within extinct gruids remains little understood, and many of these fossils require phylogenetic revision. This is especially true of the Eurasian

Eogruidae, a group that contains the oldest crane-like remains after those of the Geranoididae from the early-middle Eocene of Wyoming (Wetmore 1933, Cracraft 1969, 1973; Clarke et al. 2005, Mayr 2009). The only phylogenetic study of Eogruidae (Clarke et al. 2005) recovered *Eogrus aeola* (Wetmore 1934) within an unresolved group containing Psophiidae and Gruidae using a modified dataset (Mayr and Clarke 2003). Results also placed an eogruid-like specimen (IGM 100/1447) as the sister taxon of an Aramidae

+ Gruidae sister group. Traditionally, the morphologically similar Eogruidae and Ergilornithidae were divided into separate families; however, traditional Eogruidae is likely paraphyletic with respect to Ergilornithidae (Clarke et al. 2005). Here, we use the suggested terminology of Clarke et al. (2005), and consider Eogruidae to include taxa that were historically placed within Ergilornithidae.

Originally established for the genus *Eogrus* (Wetmore 1934), the Eogruidae have largely been found in middle to late Eocene localities of Mongolia and Inner Mongolia (Figure 1; *Eogrus crudus* of central Mongolia, *Eogrus* sp. and IGM 100/447 of southeastern Mongolia [Kurochkin 1981, Clarke et al. 2005]; *Eogrus aeola* of Inner Mongolia, China [Wetmore 1934]), and were also recovered from the mid-late Eocene of eastern Kazakhstan (*Eogrus turanicus*; Bendukidze 1971). An Oligocene *Eogrus* sp. was recovered in southeastern Mongolia (Wetmore 1934). The youngest known *Eogrus* specimen is mid-Miocene in age and was found in eastern Inner Mongolia (*Eogrus wetmorei*; Wetmore 1934, Kurochkin 1981, Olson 1985, Wang et al. 2003c, Clarke et al. 2005). Known remains of *Eogrus* largely comprise isolated tarsometatarsi, although a left coracoid (originally identified as accipitriform; Mayr 2016b), proximal humerus, left manual phalanx (digit II: phalanx 1) and

several tibiotarsi have also been referred to the taxon (Wetmore 1934, Kurochkin 1976, 1981; Clarke et al. 2005).

Remains of the Late Eocene–early Oligocene *Sonogrus gregalis* (Khoer-Dzan; Kurochkin 1981) were also recovered in Mongolia. Late Eocene to early Pliocene taxa that were historically placed within Ergilornithidae have been recovered as far east as Mongolia and as far west as the Balkan Peninsula (Kurochkin 1981, Zelenkov et al. 2016; see Table 1). Four genera were originally named: *Proergilornis* (Kozlova 1960), *Ergilornis* (Kozlova 1960), *Urmiornis* (Mecquenem 1908), and *Amphipelargus* (Lydekker 1891). Today 3 genera are recognized: *Ergilornis*, *Amphipelargus*, and *Urmiornis*, with *Proergilornis* and *Ergilornis* being synonymized (Kurochkin 1981). The Paleogene ergilornithid record comprises several unknown species of *Ergilornis* from the late Eocene–early Oligocene of southeastern Mongolia (Ergilin Dzo and Khoer-Dzan; Zelenkov and Kurochkin 2011, 2015) and the late Eocene of eastern Kazakhstan (Kustovskaya svita; Kozlova 1960, Kurochkin 1981). The Neogene record of these taxa currently consists of *Urmiornis brodkorbi* from the early Miocene of western Kazakhstan (Mynsualmas and Altynshokysu; Karhu 1997); *Ergilornis* sp. from the late Middle Miocene of western Mongolia (Sharga; Zelenkov
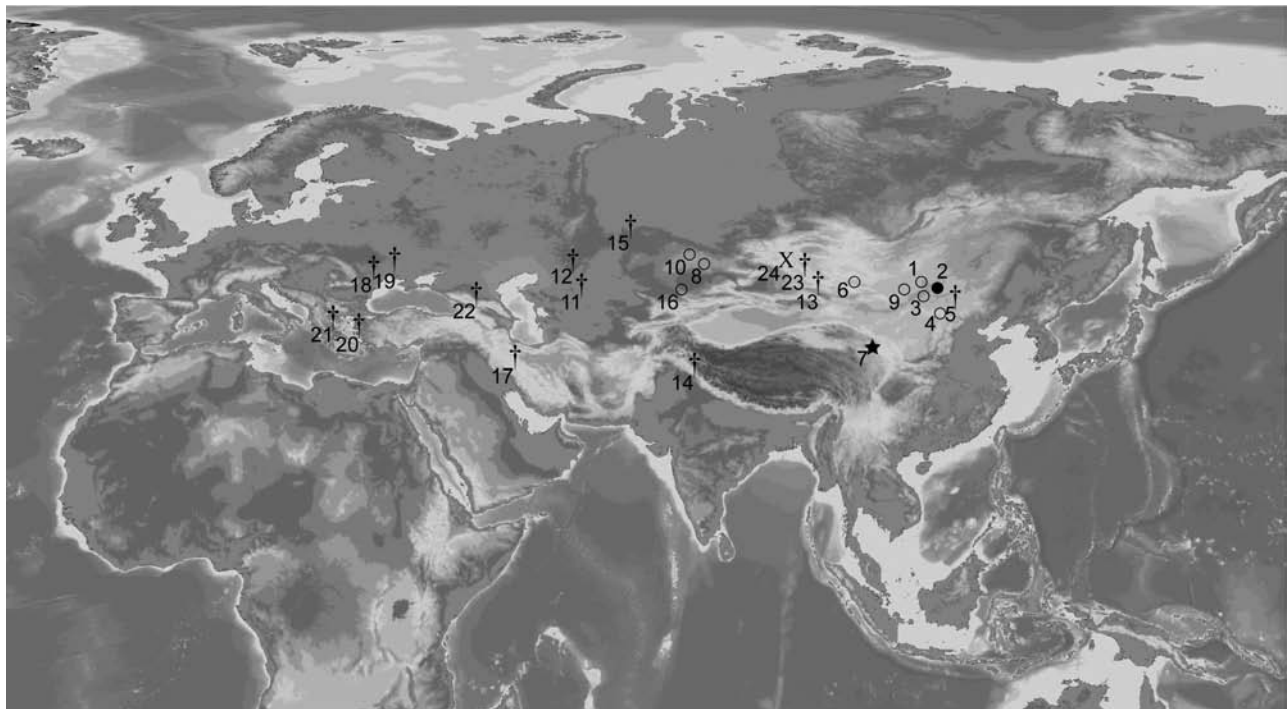

FIGURE 1. Distribution of the Eogruidae. A star denotes the Linxia Basin, where the new eogruid was found. Empty circles denote Eocene specimens, filled circles denote Oligocene taxa, daggers denote Miocene taxa, and an X denotes Pliocene taxa. Numbers correspond to the names of taxa as follows: (1) *Sonogrus gregalis* (SE Mongolia); (2) *Eogrus* sp. (SE Mongolia); (3) IGM100.1447 (Mongolia); (4) *E. aeola* (NE China); (5) *E. wetmorei* (NE China); (6) *E. crudus* (Mongolia); (7) *Sinoergilornis guangheensis* (N China); (8) *Eogrus turanicus* (E Kazakhstan); (9) *Ergilornis* spp. (SE Mongolia); (10) *Ergilornis* sp. (E Kazakhstan); (11) *Urmiornis brodkorbi* (W Kazakhstan); (12) *U. brodkorbi* (W Kazakhstan); (13) *?Ergilornis* sp. (W Mongolia); (14) *?U. cracrafti* (N Pakistan); (15) *U.* sp. (N Kazakhstan); (16) *U. orientalis* (E Kazakhstan); (17) *U. maraghanus* (N Iran); (18) *U. ukrainus* (S Moldova); (19) *U. ukrainus* (S Ukraine); (20) *A. majori* (SE Greece); (21) *?Amphipelargus* sp. (N Greece); (22) *U. ukrainus* (S European Russia); (23) *U. dzabghanensis* (W Mongolia); (24) *U. dzabghanensis*. Citations in text.

TABLE 1. Summary of the species and recovered elements of all previously described didactyl Eogruidae. See Figure 1 for locality and age data of presented taxa. Boldfaced elements are those that overlap with the holotype specimen of the new species. Abbreviations: prox = proximal, dist = distal, R = right, L = left, tbt = tibiotarsus, tmt = tarsometatarsus.

Species and references	Preserved elements (Digit: Phalanx)
U. orientalis (Kurochkin 1981, Zelenkov et al. 2016)	Fragment of cervical vertebra Dist R tbt Prox and dist R tmt Pedal III:1–3 Pedal IV:1–4
U. brodkorbi (Karhu 1997, Zelenkov et al. 2016)	Dist L tbt Prox R tmt Pedal III:1 Pedal IV:2
U. ukrainus (Kurochkin 1981, Zelenkov et al. 2016)	Dist R tbt R tmt and dist L tmt Pedal III:2 Pedal IV:1
U. dzabghanensis (Kurochkin 1985)	Shaft and dist R tbt Dist L tbt Prox R tmt, dist R and L tmt
U. maraghanus (Mecquenem 1925, Cracraft 1973, Kurochkin 1981)	Dist R tbt L tmt
?U. cracrafti (Harrison and Walker 1982)	R and L prox and dist femoral epiphyses Dist L tibiotarsus
U. sp. (Kurochkin 1981)	Dist epiphysis of III:1
Amphipelargus majori (Lydekker 1891, Harrison 1981)	Dist tbt
?A. sp. (Boev et al. 2013, Zelenkov et al. 2016)	Pedal III:1 Pedal III:2
Ergilornis spp. (Kozlova 1960, Cracraft 1973, Kurochkin 1981)	Prox R humerus Shaft and dist R tbt L tmt, prox and dist R tmt Pedal III:1–3

et al. 2016); *?U. cracrafti* from the late Middle and early Late Miocene of northern Pakistan (Nagri and Chinji Formations of the Siwaliks; Harrison and Walker 1982, Karhu 1997); *U.* sp. from the late Miocene of northern Kazakhstan (Pavlodar; Zelenkov et al. 2016)); *U. orientalis* from the late Miocene of eastern Kazakhstan (Kalmakpai; Kurochkin 1981); *U. maraghanus* from the late Miocene of northern Iran (Maragheh; Mecquenem 1908); *U. ukrainus* from the late Miocene of southern Moldova (Kotlova Balka), southern Ukraine (Morozovka), and southern European Russia (Armavir; Kurochkin 1981, Zelenkov and Kurochkin 2015); *Amphipelargus majori* from the late Miocene of southeastern Greece (Samos Island; Lydekker 1891); *?A.* sp. from the late Miocene of northern Greece (Kyropigi); and *U. dzabghanensis* from the late Miocene and early Pliocene of western Mongolia (Chono-Khariakh; Zelenkov et al. 2016). In addition to hind limbs, several phalanges have been preserved from *Urmiornis orientalis*

(specimen PIN 2433/481; Kurochkin 1981); *?Amphiplargus* sp. (KRY 1300 and KRY 1807; Zelenkov et al. 2016), previously assigned to *Otis hellenica* in Boev et al. (2013); *Urmiornis brodkorbi* (PIN 4600/2; Karhu 1997); *Ergilornis* sp. (PIN 311/61; Zelenkov and Kurochkin 2015, Zelenkov et al. 2016); and *Urmiornis ukrainus* (NMNH 25–1697; Kurochkin 1981).

These genera are distinct in that digit II is further reduced relative to *Eogrus*, *Sonogrus*, and outgroups. The trochlea of this digit is developed only as a small tubercle or is absent like those of extant ostriches (Kurochkin 1981), which led some early workers to suggest a close relationship between them (Feduccia 1980, Olson 1985); however, there is currently no compelling evidence to support this (Cracraft 1973, Clarke et al. 2005, Mayr 2009, 2016a). Similarly, it has been proposed that due to this reduction, the Eogruidae were cursorial and likely flightless; however, flight loss has not been confirmed by anatomical data (Clarke et al. 2005).

Here, we describe a new eogruid taxon (Eogruidae sensu Clarke et al. 2005) from the late Miocene Liushu Formation of the Linxia Basin in Gansu, China. It is the only eogruid fossil that has been found within this formation, and the first to be located within northwest China. Avian fossils have only been recovered from the late Miocene Liushu formation and include ostriches, a pheasant, vultures, and falconids in addition to the species described here (Hou et al. 2005, Zhang et al. 2010, Li et al. 2014, 2016, 2018).

METHODS

Osteological terminology follows Baumel and Witmer (1993). The specimen was compared to osteological specimens of the Texas Memorial Museum at the University of Texas at Austin, and was scanned using x-ray microtomography (225 Micro CT) at the Key Laboratory of Vertebrate Evolution and Human Origins at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP). The specimen is housed in the collections of IVPP, Beijing, China. CT data generated during the current study is available at Dryad: https://doi.org/10.5061/dryad.jh9w0vt6j.

Systematic Paleontology
AVES Linnaeus, 1758
GRUES Bonaparte, 1854
GRUOIDEA Vigors, 1825
EOGRUIDAE Wetmore, 1934 (sensu Clarke et al. 2005)
Sinoergilornis, gen. nov. (Figures 2–6)

Type species. *Sinoergilornis guangheensis*, sp. nov.
Diagnosis. The didactyl foot distinguishes *Sinoergilornis guangheensis* from all Gruidae, *Eogrus*, *Ergilornis*, and *Sonogrus*. *Sinoergilornis guangheensis* is differentiated from all other Eogruidae by a unique combination of features, including the following that are novel within the remaining
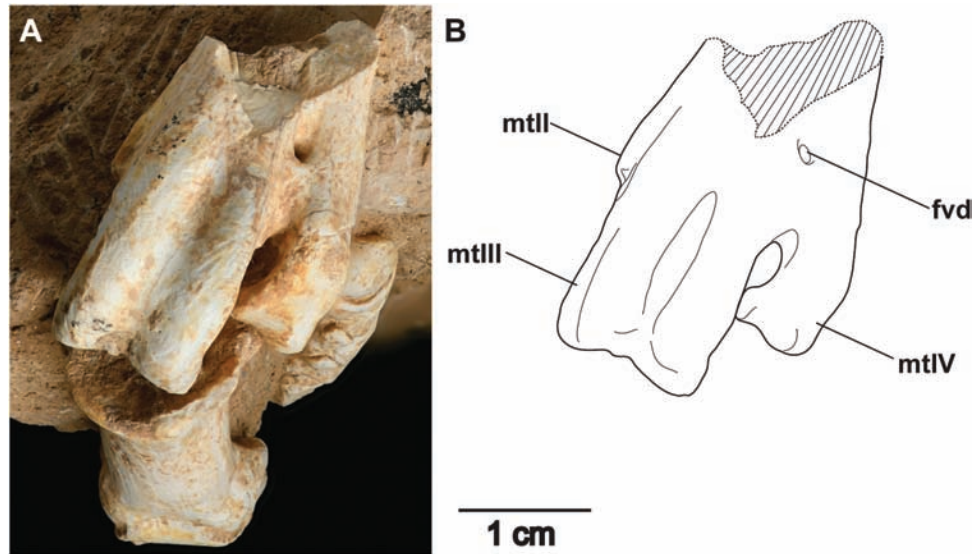
FIGURE 2. (**A**) Photograph and (**B**) line drawing of the left tarsometatarsus of *Sinoergilornis guangheensis* in dorsal aspect. Broken areas are delimited with dashed margins. Anatomical abbreviations: mtII = trochlea of metatarsal II, mtIII = trochlea of metatarsal III, mtIV = trochlea of metatarsal IV trochlea, fvd = foramen vasculare distale.
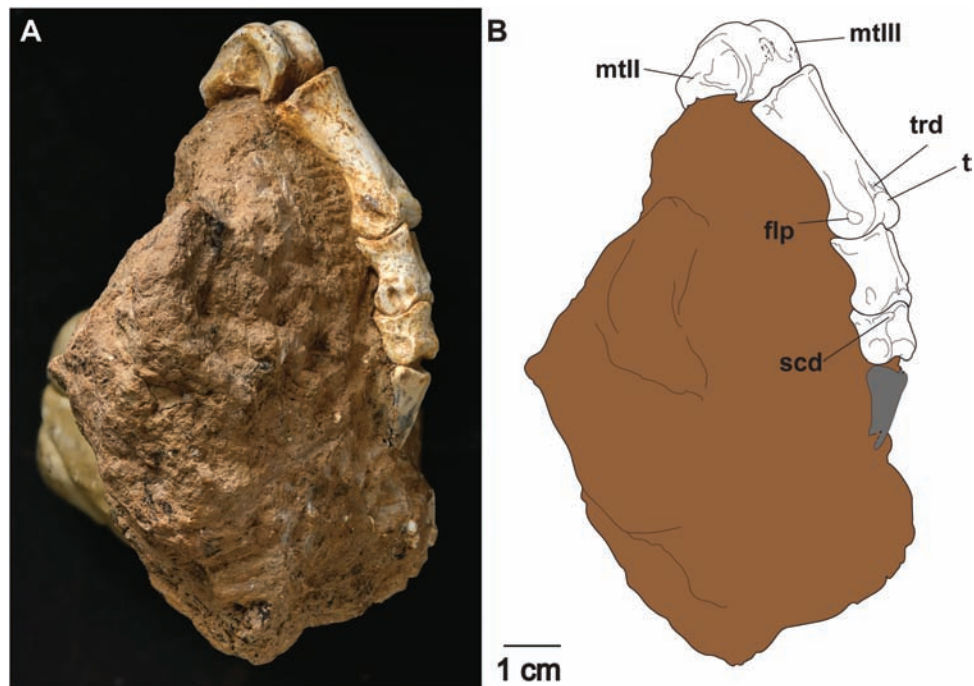

FIGURE 3. (**A**) Photograph and (**B**) line drawing of the left foot of *Sinoergilornis guangheensis* in medial aspect. Areas that are obscured by matrix or broken are delimited with dashed margins. The mammal bone is portrayed in gray. Anatomical abbreviations: mtII = trochlea of metatarsal II, trd = triangular depression, mtIII = trochlea of metatarsal III, mtIV = trochlea of metatarsal IV, t = dorsally raised trochlea, flp = flexor pit, scd = semicircular indentations.

didactyl eogruids: (1) enclosure of the intertrochlear incisura between the trochleae of metatarsals III and IV by medial extension of the mediodistal margin of trochlea IV (Figures 2, 4, and 5; mtIV); (2) lack of a laterally extensive ala along the mediodistal margin of trochlea III; (3) exceptional plantar extension of trochlea IV along its lateral margin; (4) a deep, mediolaterally wide and proximodistally elongate incisura along the ventrolateral margin of III:1 (Figure 5; inc); (5) a proximodistally short plantar eminence of III:1 (see Supplementary Material Videos 1, 2, and 3, and data
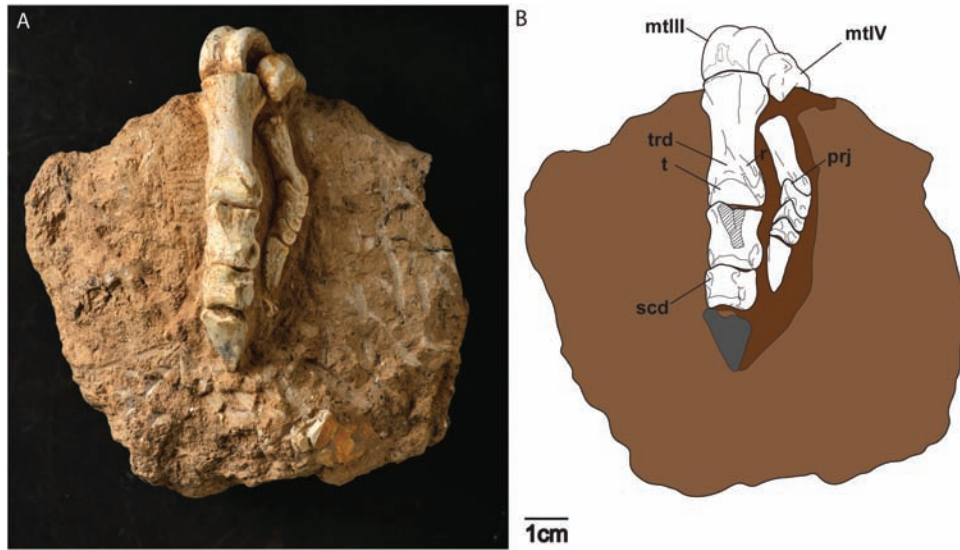
FIGURE 4. (**A**) Photograph and (**B**) line drawing of the left foot of *Sinoergilornis guangheensis* in lateral aspect. Areas obscured by matrix are delimited with dashed margins. Broken areas are shown with dashed margins and a hatched surface. The mammal bone is portrayed in gray. Anatomical abbreviations: mtIII = trochlea of metatarsal III, mtIV = trochlea of metatarsal IV, trd = triangular depression, t = dorsally raised trochlea, r = laterodorsal ridge, scd = semicircular indentations, prj = hamate projections.
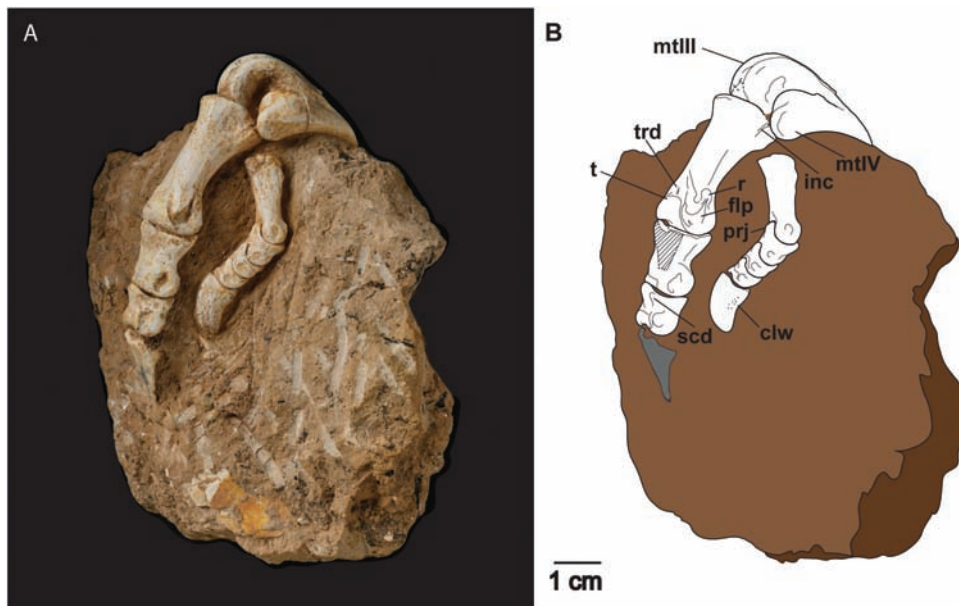

FIGURE 5. (**A**) Photograph and (**B**) line drawing of the left foot of *Sinoergilornis guangheensis* in lateral aspect. Areas obscured by matrix are delimited with dashed margins, and broken areas are shown with dashed margins and a hatched surface. The mammal bone is portrayed in gray. Anatomical abbreviations: mtIII = trochlea of metatarsal III, mtIV = trochlea of metatarsal IV, inc = incisura, t = dorsally raised trochlea, flp = flexor pit, r = laterodorsal ridge, trd = triangular depression, scd = semicircular indentations, prj = hamate projections, clw = claw (IV:5).

on Dryad: https://doi.org/10.5061/dryad.jh9w0vt6j); (6) recurvature of the ventral margin of the shaft of III:1 (see Supplementary Material Videos 1, 2, and 3, and data on Dryad: https://doi.org/10.5061/dryad.jh9w0vt6j); (7) a distinct, dorsolateral ridge that extends along the proximal margin of the triangular depression and flexor pit of III:1 (Figures 4 and 5; r); (8) a deep, sickle-shaped lateral flexor pit in III:1 (Figure 3; flp); and (9) semicircular, symmetrical indentations within the lateral margins of the proximal eminence of III:3 (Figures 3, 4, and 5; scd). Characters
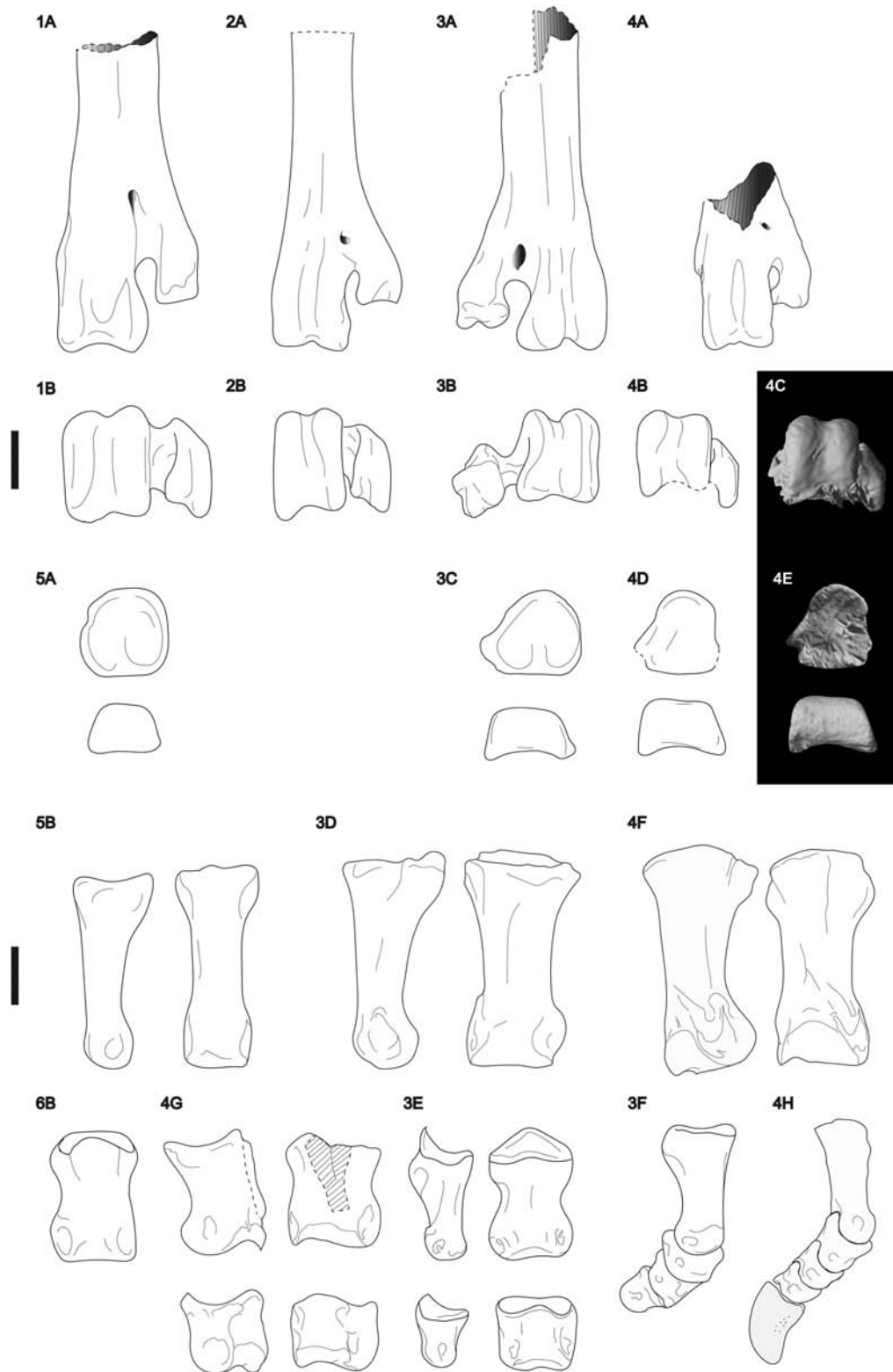
FIGURE 6. Line drawings and Micro-CT volumes of distal tarsometatarsi and pedal phalanges from *Sinoergilornis guangheensis* and previously figured members of *Urmiornis*. Scale bar is 1 cm across all images. (**1A–B**) *Urmiornis dzabghanensis* (based on line drawings of Kurochkin 1985); (**2A–B**) *U. maraghanus* (based on photographs of Cracraft 1973); (**3A–F**) *U. orientalis* (based on line drawings of Kurochkin 1981 and photographs of Zelenkov et al. 2016); (**4A–H**) *Sinoergilornis guangheensis*; (**5A–B**) *U. brodkorbi* (based on photographs of Zelenkov et al. 2016); (**6A**) *U. ukrainus* (based on photograph of Zelenkov et al. 2016).

TABLE 2. Measurements of digit III, phalanx 1 in select members of Eogruidae and several extant Gruidae. Measurements (mm): a = total length; b = distal depth; c = proximal depth; d = minimum diaphysis depth; e = distal width; f = proximal width; g = minimum width (see Boev et al. 2013 figure 3 for details). *?Amphipelargus* measurements are from Zelenkov et al. (2016). All measurements other than those of *Sinoergilornis guangheensis* are from Boev et al. (2013). Extinct taxa are denoted by daggers.

	a	b	c	d	e	f	g
†*Sinoergilornis guangheensis*, IVPP V24968 (China), Late Miocene	31.3	12.0	13.7	8.0	11.4	16.0	10.3
†*?Amphipelargus* sp., KRY 1300—Kryopigi (Greece), Late Miocene	33.4	10.1	15.0	7.2	11.8	15.7	9.4
†*Urmiornis ukrainus* NMNH 25–1696—Grebeniki (Ukraine), Late Miocene, after Kurochkin (1981)	30.7	–	–	7.6	12.3	14.3	8.9
†*Urmiornis orientalis*, specimen PIN 2433/481, Kalmakpai, Late Miocene, Kazakhstan	31.4	8.3	14.4	6.8	14.1	16.4	9.7
†*Urmiornis brodkorbi,* specimen PIN 4600/2, Mynsualmas, Early Miocene, Kazakhstan	30.0	7.3	12.7	6.1	10.2	12.9	7.5
†*Ergilornis* sp., specimen PIN 3110/61, Khoer-Dzan, Late Eocene, Mongolia	32.1	9.5	15.3	7.4	11.7	15.3	8.9
Grus grus, specimen NMNHS 2/1992, Spain	36.2	6.6	10.4	4.1	6.5	9.4	4.9
Anthropoides virgo, specimen NMNHS 1/1989, Gobi (Inner Mongolia), China	28.8	5.7	9.0	3.4	5.5	7.6	4.4

4–9 could not be assessed for *Urmiornis maraghanus* or *U. dzabghanensis*, and characters 1–3 and 9 could not be assessed for *?Amphipelargus* sp. Differentiation was not possible for *?U. cracrafti*, *U.* sp., or *A. majori*.

Etymology. The genus name, "*Sinoergilornis*," refers to this specimen being the first known eogruid from a locality in west China, and its presentation of morphology that is more similar to *Urmiornis*, *Amphipelargus*, and *Ergilornis* than to *Eogrus* and *Sonogrus*.

Sinoergilornis guangheensis, sp. nov. (Figures 2–6)

Holotype. IVPP V24968, a three-dimensionally preserved distal left tarsometatarsus and a nearly complete set of pedal phalanges preserved atop a burnt ochre colored siltstone block with carbonate cementation. We determine pedal phalanx 4 of digit III to be a modified mammal bone added by the preparator due to density recovered from micro-CT (Figures 3, 4, and 5; see Supplementary Material Videos 1, 2, and 3, and data on Dryad: https://doi.org/10.5061/dryad.jh9w0vt6j). The holotype specimen was collected from near Langwagou Village, Zhuangkeji Town, Guanghe County, in Gansu Province of northwestern China (Figure 1) from the Upper Miocene Liushu Formation, Linxia Basin. The known bird fossils of the Linxia Basin are of the same unit and have largely been acquired from local farmers and collectors (Li et al. 2016).

Differential diagnosis. Although the tarsometatarus is distinct when compared with other Neogene didactyl Eogruidae, the general shape and size of the pedal phalanges of *S. guangheensis* are most similar to the condition in *Urmiornis orientalis* (Figure 6). In addition to the diagnostic differentia of the new genus, *S. guangheensis* can be differentiated from the Miocene *U. orientalis* due to (1) the presence of further dorsally raised trochleae that grade proximally into the shaft of each phalanx (Figures 4 and 5; t); (2) a III:1 that is more dorsoplantarly greater in height than its mediolateral width (Figure 6 [4D–4E]); (3) a relatively deep triangular depression present just above the trochlea of III:1 (Figures 3, 4, and 5; trd); (4) a distinct ridge along the proximal margin of the flexor pit in III:1

that extends dorsally and continues along the margin of the triangular depression (Figures 4 and 5; r); (5) lack of a projection along the plantomedial margin of the distal articular surface of III:1 (Figure 6 [4D–4E]); (6) unique, symmetrical, and semicircular indentations along the lateral margins of the proximal eminence of III:3 (Figures 3, 4, and 5; scd); (7) proximally projecting, hamate eminences present along the midline of the proximal margins of IV:2–4 (Figures 4 and 5; prj); and (8) more dorsoplantarly compressed and proximodistally elongate phalanges of digit IV (see Figure 6 for comparative drawings of differentia). Micro-CT data (see Figure 6, Supplementary Material Videos 1, 2, and 3, and data on Dryad: https://doi.org/10.5061/dryad.jh9w0vt6j) reveals further differentiation of III:1 in *S. guangheensis*. The phalanx possesses a proximodistally truncate, plantar eminence compared to those of other didactyl eogruids. The incisura along the dorsal margin of this eminence is relatively deep, like that of *U. orientalis*, although it appears to be dorsoplantarly wider (Figure 5; inc). Characters 1–5 were only able to be assessed for *U. brodkorbi* and *U. orientalis*, and characters 6–8 were only assessable in *U. orientalis*.

Although reduction of trochlea II is similar to the condition in ostriches, complete eogruid tarsometatarsi reveal enclosed flexor canals within the hypotarsus that place this group within Neoaves, as the canals of Paleognathae are not closed (Clarke et al. 2005). *Sinoergilornis guangheensis* additionally exhibits many characters within the distal tarsometatarsus and pedal phalanges that place it firmly within Eogruidae. In the tarsometatarsus, trochlea II is more prominent than that of *Struthio*, the fovea for the collateral ligament in trochlea IV is shallow in *S. guangheensis* and is deep and circular in *Struthio*, the lateral margin of trochlea IV is much more plantarly projected in the new taxon, and the mediodistal margin of trochlea IV is markedly medially projected in *S. guangheensis*. Within the phalanges, the most notable differentia comprise a sickle-shaped flexor pit of III:1 in *S. guangheensis*, recurvature of the ventral margin of III:1 in the new taxon, and the more proximodistally shortened III:2 and IV:2–3 of

S. guangheensis (Figures 3–6). The latter phalanges are subequal in size, whereas those of *Struthio* are roughly twice as elongate as their distal counterparts. The single preserved pedal ungual IV:5 of *S. guangheensis* is additionally elongate and recurved, unlike the relatively small claw of an ostrich that is flattened along the plantar margin (Figures 5–6). *Sinoergilornis guangheensis* can be distinguished from Miocene ostrich by the plantar extension of trochlea IV of the tarsometatarsus in *S. guangheensis*, which is limited in *Struthio* cf. *karatheodoris* (Miocene, southwestern Bulgaria; Boev and Spassov 2009). If another individual of this taxon is found that is represented by other elements not contained in the holotype specimen, it will not be assignable to this taxon until further associated elements are located.

Type locality and horizon. Linxia Basin, northeastern Plateau, China, Liushu Formation. The exact locality of the specimen is unknown as it was collected by locals in 2018. The locality and horizon are similar to that of Li et al. (2016). The Linxia Basin is an intracontinental foreland basin located on the northeastern margin of the Tibetan Plateau (Wang et al. 2014). It is currently located in a transitional zone between the East Asian monsoon and the non-monsoon arid climate of the Asian inland (Fang et al. 2016). Long and continuous sedimentary succession was deposited in this basin from the Oligocene to the Pliocene and Pleistocene (Li 1995, Fang et al. 2003, 2016; Qiu et al. 2004, Deng et al. 2004, 2013; Garzione et al. 2005). The stratigraphy of Linxia Basin has previously been divided into 8 formations based on lithofacies, contacts, paleontology, and magnetostratigraphy (Li 1995, Li et al. 1997, Fang et al. 2003, 2016). While mammalian remains have been recovered in many of these deposits (Deng et al. 2004, 2013), avian remains have only been recovered in the Liushu formation (Hou et al. 2005, Zhang et al. 2010, Li et al. 2014, 2016, 2018). The most recent dates provided for the Liushu formation are late Miocene in age, from 7.78 to 6 million years ago [mya] (Fang et al. 2016). It is largely made up of mudstone and siltstone (Wu et al. 2017).

Measurements (mm). See Table 2.

Etymology. The species name, "*guangheensis*," refers to the locality.

Description and comparison. The specimen is preserved three-dimensionally and comprises the distal portion and metatarsal trochleae of the left tarsometatarsus along with nearly complete sets of pedal phalanges for digits IV and III, including a decurved ungual (IV:5, Figure 5). The size of the specimen is similar to that of a large extant gruid, such as *Grus grus*. The tarsometatarsus is preserved in dorsal aspect with both lateral and medial aspects visible, as in digit III. A large area of breakage is evident along the proximal, dorsal region of III:2. Digit IV is preserved in laterodorsal aspect. The shaft of the tarsometatarsus is not preserved, and the specimen is broken along the proximal margin of the medial groove of the trochlea of metatarsal III and the foramen vasculare distale. The foramen vasculare distale is ovoid and the proximal margin is slightly angled medially. A shallow groove extends along the length of the intertrochlear area from the distal portion of the foramen. A small amount of breakage is located along the distal margin of trochlea II.

The trochlear area is wide and exhibits dorsoplantar flattening, as in extant Gruidae (Figures 2 and 5). A small portion of the distal margin of the trochlea of metatarsal II is slightly broken. This trochlea is reduced and located much more proximally as compared to those of trochleae III and IV. It extends little medially. The trochlea of metatarsal III is the most robust trochlea both lateromedially and proximodistally and extends approximately twice the distal length of trochlea IV. This is similar to the condition in both extant Gruidae and in IGM 100/1447, the *Eogrus aeola* holotype specimen (AMNH 2936), and 2 specimens referred to *Eogrus aeola* (AMNH 2937 and AMNH 2946; Clarke et al. 2005). The depth of the medial groove of trochlea III is shallow to moderate, is mediolaterally broad, and continues along the midline of trochlea III to the small distal portion of the plantar aspect of trochlea III that is visible. The terminus of this groove cannot be determined without further preparation. The proximal margin of the groove terminates just below the level of the distal margin of the foramen vasculare distale. This is like that of IGM 100/1447 and the abovementioned *Eogrus* specimens. The lateral and medial aspects of trochlea III are deeply excavated and exhibit circular pits. The pit of the lateral aspect is deeper than that of the medial aspect.

The intertrochlear incisura between trochleae III and IV is small, only about 2 mm between the lateral margin of trochlea III and the distomedial margin of trochlea IV. This is similar to the condition in *Balearica pavonica* (M-5323) and *Grus canadensis* (M-11728), although trochlea IV does not present as much lateral torsion as that of *G. canadensis*. The distal margin of trochlea IV angles medially, which is most like that of IGM 100/1447, the *Eogrus aeola* holotype specimen, and the 2 Eocene specimens referred to *Eogrus aeola* (Clarke et al. 2005). Trochlea IV is slightly plantarly deflected, more so than that of IGM 100/1447. The degree of deflection is most similar to that of the *Eogrus aeola* holotype specimen. The ala of trochlea IV is stout, rounded, and robust. Its distoplantar extent is greater than that of IGM 100/1447. A shallow depression is present on the lateroplantar margin of the ala.

Digit III comprises the most robust elements of the preserved digits. Phalanx 1 of digit III is recurved (see Supplementary data and videos) and is more mediolaterally broad and proximodistally elongate than phalanx 1 of digit IV (Figures 4 and 5). The proximal margin of III:1 is especially broad, with a robust and acuminate plantar eminence present (see Supplementary Material Videos 1, 2,

and 3 and data on Dryad: https://doi.org/10.5061/dryad. jh9w0vt6j) that is accompanied by a deep incisura along its dorsal margin. The lateral flexor pits or collateral ligament pits of III:1 are deep and the lateral flexor pit is sickle shaped (Figure 5), with a narrow and elongate incisura extending proximally from the fovea. The trochlea of III:1 is proximodistally extensive and lateromedially wide. A triangular depression is present above the cartilaginous trochlea (Figures 3, 4, and 5). III:2 is approximately half the length of III:1 but exhibits approximately the same width as the distal portion of III:1. III:3 is similarly approximately half the length of III:1 and as lateromedially robust. The trochleae of both III:2 and III:3 are proximodistally shortened compared to that of III:1, and symmetrical, semicircular indentations are present along the lateral margins of the proximal eminence of III:3 (Figures 3, 4, and 5; scd). Deep lateral flexor pits are also present in these phalanges, although the sickle shape is less pronounced in these pits than those of III:1. "III:4" has been identified as a likely mammalian bone that was artificially attached to phalanx III:3 due to incongruous morphology and CT scanning of the specimen revealing that this bone was higher in density (i.e. more comparable to that of a mammal than of a bird; Supplementary Material Videos 1, 2, and 3 and data on Dryad: https://doi.org/10.5061/dryad.jh9w0vt6j) and set atop darker, broken matrix that was likely mixed with glue (shown in gray in Figures 3, 4, and 5).

IV:1 is relatively slender, approximately two-thirds the length of III:1 and half as wide. The lateral and medial flexor pits of this phalanx are shallow and circular. IV:2, IV:3, and IV:4 are markedly proximodistally shorter than IV:1, with IV:2 being only slightly more elongate than IV:3 and IV:4. The proximal eminences of each phalanx are distinctly projected proximally and are proximally acuminate. Shallow, circular lateral and medial flexor pits are similarly located on all 3 of these phalanges. IV:4 is exposed in lateral view, but appears to be broad at the base and robust. The claw tapers to what appears to be a rounded terminus, although this is somewhat obscured by matrix.

DISCUSSION

Compared to *Urmiornis*, *Amphipelargus*, and *Ergilornis*, *Sinoergilornis guangheensis* exhibits the largest III:1 measurements for distal depth, minimum diaphysis depth, and minimum width, and has one of the largest measurements for proximal width after that of *Urmiornis orientalis* (see Table 2). Zelenkov et al. (2016) suggested that flattening of III:1 was indicative of running adaptation, and that the more robust phalanx of the Greek *Amphipelargus*-like specimen KRY 1300 suggests that it was less adapted to running, perhaps indicating that it lived in a more humid and vegetated environment than its eastern counterparts. *Sinoergilornis guangheensis* shares similar

depth measurements and overall shape with this specimen. Kurochkin (1982) hypothesized that Eogruidae grew larger in body mass over time as their cursorial adaptations became more apparent; however, it is unclear how depth and width of the phalanges are related to body mass in this group. The length of III:1 in *Sinoergilornis guangheensis* is within the range of those of the extant cranes *Anthropoides virgo* (Demoiselle Crane) and *Grus grus* (Common Crane), although its width and depth measurements are approximately twice as robust (see Table 2).

Several workers have suggested that the Eogruidae were flightless (Wetmore 1934, Kurochkin 1976, Feduccia 1999), although the morphological evidence known from recovered specimens needs confirmation (Clarke et al. 2005). A humerus (PIN 3110–60; Kurochkin 1976) exhibiting characteristics of flightlessness was attributed to *Ergilornis* sp. (Clarke et al. 2005); however, it is an isolated bone and it is unclear whether it was assigned correctly to Eogruidae rather than to an ostrich. In addition, a coracoid assigned to *E. aeola* does not exhibit flightless characteristics (Clarke et al. 2005, Mayr 2016b). The curved, elongate claw of digit IV in *Sinoergilornis guangheensis* is less suggestive of a cursorial, flightless locomotor strategy than the straightened and relatively truncate and dorsoplantarly flattened condition exhibited in claws of extant *Struthio* (Birn-Jeffery et al. 2012). Further fossil evidence, namely of elements more directly related to flight such as those of the pectoral girdle and forelimb, is needed to thoroughly assess the flight capabilities of the Eogruidae.

Sinoergilornis guangheensis provides additional insight into the diversification and differentiation of the Eogruidae due to its age and locality. Current fossil evidence suggests that the Eogruidae were largely present in southeastern Mongolia during the Eocene and that they largely diversified during the Miocene, during which time *Eogrus* and *Sonogrus* disappeared and the distribution of Eogruidae expanded westward to the Balkan peninsula, northward to northern Mongolia, and southward to the northeastern and southwestern Tibetan Plateau (Figure 1). This burst of diversity and range expansion corresponds approximately with the beginning of monsoon-dominated climate patterns around the Oligocene–Miocene boundary (Liu et al. 1998, Guo et al. 2002, 2008; Wang et al. 2003a, 2003b, 2005; Sun and Wang 2005, Qiao et al. 2006, Wang 2009, Qiang et al. 2011), the onset of the East Asian monsoon (Wu et al. 2017), and northwestern encroachment of the humid belt into the arid/semi-arid belts of China (Guo et al. 2008). The late Oligocene mammalian assemblage of giant rhino fauna in the Linxia Basin also support the onset of the East Asian monsoon around this time, as their presence indicates a warm and humid habitat (Deng et al. 2004, Deng et al. 2013).

The presence of Eogruidae in the late Miocene Liushu Formation additionally corresponds with the timing of

northeastern Tibetan Plateau uplift and intensification of the East Asian monsoon around the pre–late Miocene (~8 mya; Wang et al. 2014, Wu et al. 2017, Xu et al. 2018). Tibetan Plateau uplift has been linked to East Asian monsoon intensification by several studies, although its exact relationship with this climatic phenomenon remains uncertain (Wang et al. 2014). Grain size evidence from Linxia has similarly shown that the Asian winter monsoon intensified ~7.4 mya (Fan et al. 2007). Range and diversity shifts of Eogruidae coupled with the timing of the onset and intensification of the East Asian monsoon, associated Tibetan Plateau uplift, and the northwestern expansion of the humid belt may indicate the Monsoon as a potential driver of eogruid diversification and dispersal to more open and arid environments in western Eurasia.

Mammalian diversity and faunal similarity of *Hipparion* fauna in the Liushu Formation along with evidence from lithology, carbon isotopes, and paleobotany suggest a subarid, open steppe environment during the late Miocene in the Linxia Basin that was dominated by C_3 plants. Xerophilous and subxerophilous grasses were additionally present, indicating a dry grassland environment (Deng 2006). Conversely, *Hipparion* fauna of Greece indicate the presence of a sclerophyllous, evergreen woodland environment during the late Miocene. This is likely the environment that western late Miocene eogruid genera such as the morphologically similar *Amphipelargus* experienced.

The appearance of Eogruidae in the Nagri and Chinji Formations of the Siwaliks in Pakistan (late middle and early late Miocene, *?Urmiornis cracrafti*; Harrison and Walker 1982, Karhu 1997) corresponds roughly with the timing of the intensification of the Asian monsoon along the southern Tibetan Plateau during the mid- to late Miocene (as early as 11–7 mya; Quade et al. 1989, Sanyal et al. 2010) and the uplift of the Himalayas to their present elevation around 11–9 mya (Garzione et al. 2000, Rowley et al. 2001, Saylor et al. 2009, Quade et al. 2011). Intensification of the Asian monsoon in this area is indicated by a dramatic environmental shift from C_3 to C_4 plants in the Siwalik Basin, and Himalayan uplift has been linked to the onset and intensification of the Asian monsoon (Araguás-Araguás et al. 1998, Wang et al. 2014). Eolian sediments in China and the marine sediment record of the Indian and North Pacific oceans additionally support onset of the Indian and East Asian monsoon around 9–8 mya (An et al. 2001). As in Linxia, carbon (Barry et al. 2002) and oxygen (Behrensmeyer et al. 2007) isotope evidence indicates that the late Miocene environment of the Siwaliks shifted to a drier and more seasonal environment that contains fluvial sediments indicating the presence of floodplains (although these were surrounded by C_4 grasslands). Similar environmental shifts were associated with the first appearance of eogruids, as the Eocene and Oligocene sediments of southeastern Mongolia and the adjacent portion of China that have produced eogruid fossils contain lacustrine and lacustrine–alluvial facies that represent lacustrine–alluvial plains (Dashzeveg and Devyatkin 1986).

Additional climate phenomena highlight uncertainty surrounding possible drivers of the diversification and dispersal of both Eogruidae and gruid-like extinct taxa. Eocene–Oligocene global cooling may have had an effect on crane-like taxa globally, including the Eogruidae, although sampling and rock record biases cannot be ruled out to explain Oligocene sampling. Preservation bias and locality sampling bias generally must be considered when drawing conclusions from the fossil record. Crane-like taxa of uncertain phylogenetic placement (see Table 2) are abundant in Europe and North America during the Eocene, with only one Oligocene taxon (*Parvigrus pohli*) being known from Europe (Mayr 2005, Mayr 2013). Similarly, few eogruids have been found in Oligocene sediments, and those that are known are limited to southeastern Mongolia.

Faunal shifts within Linxia since the late Miocene suggest that large environmental change occurred, and the presence of Eogruidae in this locality further emphasizes this (Li et al. 2014, 2016). It is unclear why Eogruidae are only known until the early Pliocene while undoubted extinct crown gruids are not abundant in Asia until the Pliocene and Pleistocene (Zelenkov 2015). Only one eogruid, *Urmiornis dzabghanensis*, is known from the early Pliocene, and was recovered from western Mongolia (Zelenkov and Kurochkin 2015, Zelenkov et al. 2016). Other than the east coast of China, the Tibetan Plateau currently holds the highest amount of extant crane diversity in the world, with 4 species having overlapping or nearly overlapping distributions within the margins of the Tibetan Plateau (del Hoyo et al. 2019). Phylogenetic reassessment of the Eogruidae within the context of extinct crown gruids and other stem gruid-like fossils is needed to better understand the biogeographic history of these taxa and better estimate the primary drivers of eogruid extinction and extant crane diversification.

ACKNOWLEDGMENTS

Data deposits: Data is available on DRYAD at https://doi.org/10.5061/dryad.jh9w0vt6j.

Conflict of interests: The authors declare no conflict of interests.

LITERATURE CITED

An, Z. S., J. Kutzbach, W. Prell, and S. Porter (2001). Evolution of Asian monsoons and phased uplift of the Himalaya-Tibetan plateau since Late Miocene times. Nature 411:62–66.

Araguás-Araguás, L., K. Froehlich, and K. Rozanski (1998). Stable isotope composition of precipitation over southeast Asia. Journal of Geophysical Research 103:28721–28742.

Barry, J. C., M. E. Morgan, L. J. Flynn, D. Pilbeam, A. K. Behrensmeyer, S. M. Raza, I. A. Khan, C. Badgley, J. Hicks, and J. Kelley (2002). Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan. Paleobiology 28:1–71.

Baumel, J. J., and L. M. Witmer (1993). Osteologia. In Handbook of Avian Anatomy: Nomina Anatomica Avium (J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans, and J. C. Vanden Berge, Editors). Publications of the Nuttall Ornithological Club, Cambridge, MA, USA. pp. 45–132.

Behrensmeyer, A. K., J. Quade, T. E. Cerling, J. Kappelman, I. A. Khan, P. Copeland, L. Roe, J. Hicks, P. Stubblefield, B. J. Willis, and C. Latorre (2007). The structure and rate of late Miocene expansion of C_4 plants: Evidence from lateral variation in stable isotopes in paleosols of the Siwalik Group, northern Pakistan. GSA Bulletin 19:1486–1505.

Bendukidze, O. (1971). Novyj prestavitel' semeist-va Geranoididae (Aves, Gruiformes) iz eotsen- ovykh otlozhenij Zaisan. Soobtzhenija Akade-mii Nauk Gruzinskoj SSSR 63:749–751.

Birn-Jeffery, A. V., C. E. Miller, D. Naish, E. J. Rayfield, and D. W. Hone (2012). Pedal claw curvature in birds, lizards and Mesozoic dinosaurs–complicated categories and compensating for mass-specific and phylogenetic control. PLOS One 7:e50555.

Boev, Z., and N. Spassov (2009). First record of ostriches (Aves, Struthioniformes, Struthionidae) from the late Miocene of Bulgaria with taxonomic and zoogeographic discussion. Geodiversitas 3:493–507.

Boev, Z. N., G. Lazaridis, and E. Tsoukala (2013). *Otis hellenica* sp. nov., a new Turolian bustard (Aves: Otididae) from Kryopigi (Chalkidiki, Greece). Geologica Balcanica 42:59–64.

Clarke, J. A., M. A. Norell, and D. Dashzeveg (2005). New avian remains from the Eocene of Mongolia and the phylogenetic position of the Eogruidae (Aves, Gruoidea). American Museum Novitates 3494:1–17.

Cracraft, J. (1969). Systematics and evolution of the Gruiformes (class, Aves). 1. The Eocene family Geranoididae and the early history of the Gruiformes. American Museum Novitates 2388:1–41.

Cracraft, J. (1973). Systematics and evolution of the Gruiformes (Class Aves). 3. Phylogeny of suborder Grues. Bulletin of the American Museum of Natural History 151:1–127.

Dashzeveg, D., and E. B. Devyatkin (1986). Eocene-Oligocene boundary in Mongolia. In Terminal Eocene Events: Developments in Paleontology and Stratigraphy (C. Pomerol and I. Premoli-Silva, Editors). Elsevier Science Publishers, Amsterdam, The Netherlands. pp. 153–157.

del Hoyo, J., A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, Editors (2019). Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona, Spain.

Deng, T. (2006). Paleoecological comparison between late Miocene localities of China and Greece based on Hipparion faunas. Geodiversitas 28:499–516.

Deng, T., X. Wang, X. Ni, and L. Liu (2004). Sequence of the Cenozoic mammalian faunas of the Linxia Basin in Gansu, China. Acta Geologica Sinica 78:8–14.

Deng, T., Q. Zhan-Xiang, B. Y. Wang, X. Wang, and S. K. Hou (2013). Late Cenozoic biostratigraphy of the Linxia Basin, northwestern China. In Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology (X. Wang, L. J. Flynn, and M. Fortelius, Editors). Columbia University Press, New York, NY, USA. pp. 243–273.

Fan, M. J., D. L. Dettman, C. H. Song, X. M. Fang, and C. N. Garzione (2007). Climatic variation in the Linxia Basin, NE Tibetan Plateau, from 13.1 to 4.3 Ma: The stable isotope record. Palaeogeography, Palaeoclimatology, Palaeoecology 247:313–328.

Fang, X. M., C. Garzione, R. Van der Voo, J. J. Li, and M. J. Fan (2003). Flexural subsidence by 29 Ma on the NE edge of Tibet from the magnetostratigraphy of Linxia Basin, China. Earth and Planetary Science Letters 210:545–560.

Fang, X., J. Wang, W. Zhang, J. Zan, C. Song, M. Yan, E. Appel, T. Zhang, F. Wu, Y. Yang, and Y. Lu (2016). Tectonosedimentary evolution model of an intracontinental flexural (foreland) basin for paleoclimatic research. Global and Planetary Change 145:78–97.

Feduccia, A. (1980). The Age of Birds. Harvard University Press, Cambridge, MA, USA.

Feduccia, A. (1999). The Origin and Evolution of Birds, 2nd edition. Yale University Press, New Haven, CT, USA.

Garzione, C. N., D. L. Dettman, J. Quade, P. G. DeCelles, and R. F. Butler (2000). High times on the Tibetan Plateau: Paleoelevation of the Thakkhola graben, Nepal. Geology 28:339–342.

Garzione, C. N., M. J. Ikari, and A. R. Basu (2005). Source of Oligocene to Pliocene sedimentary rocks in the Linxia basin in northeastern Tibet from Nd isotopes: Implications for tectonic forcing of climate. GSA Bulletin 117:1156–1166.

Guo, Z. T., W. F. Ruddiman, Q. Z. Hao, H. B. Wu, Y. S. Qiao, R. X. Zhu, S. Z. Peng, J. J. Wei, B. Y. Yuan, and T. S. Liu (2002). Onset of Asian desertification by 22 Myr ago inferred from loess deposits in China. Nature 416:159–163.

Guo, Z. T., B. Sun, Z. S. Zhang, S. Z. Peng, G. Q. Xiao, J. Y. Ge, Q. Z. Hao, Y. S. Qiao, M. Y. Liang, J. F. Liu, Q. Z. Yin, and J. J. Wei (2008). A major reorganization of Asian climate by the early Miocene. Climate of the Past 4:153–174.

Harrison, C. J. O. (1981). A re-assignment of *Amphipelagus majori* from Ciconiidae (Ciconiiformes) to Ergilornithidae (Gruiformes). Tertiary Research 3:111–112.

Harrison, C. J. O., and C. A. Walker (1982). Fossil birds from the Upper Miocene of Northern Pakistan. Tertiary Research 4:53–69.

Hou, L., Z. Zhou, F. Zhang, and Z. Wang (2005). A Miocene ostrich fossil from Gansu Province northwest China. Chinese Science Bulletin 50:1808–1810.

Karhu, A. A. (1997). A new species of *Urmiornis* (Gruiformes: Ergilornithidae) from the Early Miocene of western Kazakhstan. Paleontological Journal 31:102–107.

Kozlova, E. V. (1960). Novye iskopaemye ptitsy iz yugo-vostochnoi Gobi (New fossil birds from south-eastern Gobi). Trudy problemnykh i tematicheskikh soveshanii ZIN 9:323–329.

Kurochkin, E. N. (1976). A survey of the Paleogene birds of Asia. In Collected Papers in Avian Paleontology Honoring the 90th Birthday of Alexander Wetmore (S. L. Olson, Editor). Smithsonian Contributions to Paleobiology 27:75–86.

Kurochkin, E. N. (1981). New representatives and evolution of two archaic gruiform families in Eurasia. Trudy Sovmestnaja Sovetsko-Mongol-skaja Paleontologicheskaja Ekspeditsija 15:59–85.

Kurochkin, E. N. (1982). On the evolutionary pathways of didactylous Tertiary gruids under increasing aridization. In Evolution and Environment (A. Novak and J. Milíkovsky, Editors). CSAV, Prague, Czech Republic. pp. 731–736.

Kurochkin, E. N. (1985). Birds of the Central Asia in Pliocene. Joint Soviet-Mongolian Paleontological Expedition, Transactions 26:1–120.

Li, J. J. (1995). Uplift of Qinghai-Xizang (Tibet) Plateau and Global Change. Lanzhou University Press, Lanzhou, Gansu, China.

Li J. J., X. M. Fang, R. Van der Voo, J. J. Zhu, C. Mac Niocaill, J. X. Cao, W. Zhong, H. L. Chen, J. Wang, J. M. Wang, and Y. C. Zhang (1997). Late Cenozoic magnetostratigraphy (11–0 Ma) of the Dongshanding and Wangjiashan sections in the Longzhong Basin, western China. Geologie en Mijnbouw 76:121–134.

Li, Z., J. A. Clarke, C. M. Eliason, T. A. Stidham, T. Deng, and Z. Zhou (2018). Vocal specialization through tracheal elongation in an extinct Miocene pheasant from China. Scientific Reports 8:8099.

Li, Z., J. A. Clarke, Z. Zhou, and T. Deng (2016). A new Old World vulture from the late Miocene of China sheds light on Neogene shifts in the past diversity and distribution of the Gypaetinae. The Auk: Ornithological Advances 133:615–625.

Li, Z., Z. Zhou, T. Deng, Q. Li, and J. A. Clarke (2014). A falconid from the Late Miocene of northwestern China yields further evidence of transition in Late Neogene steppe communities. The Auk: Ornithological Advances 131:335–350.

Liu, T. S., M. P. Zhengand, and Z. T. Guo (1998). Initiation and evolution of the Asian monsoon system timely coupled with the ice-sheet growth and the tectonic movement in Asia. Quaternary Science 3:194–204.

Lydekker, R. (1891). Catalogue of the Fossil Birds in the British Museum. British Museum, London, UK.

Mayr, G. (2005). A chicken-sized crane precursor from the early Oligocene of France. Naturwissenschaften 92:389–393.

Mayr, G. (2009). Paleogene Fossil Birds. Springer-Verlag, Berlin, Germany.

Mayr, G. (2013). Parvigruidae (Aves, core Gruiformes) from the early Oligocene of Belgium. Palaeobiodiversity and Palaeoenvironments 93:77–89.

Mayr, G. (2016a). Avian Evolution: The Fossil Record of Birds and its Paleobiological Significance. John Wiley and Sons, West Sussex, UK.

Mayr, G. (2016b). On the taxonomy and osteology of the Early Eocene North American Geranoididae (Aves, Gruoidea). Swiss Journal of Palaeontology 135:315–325.

Mayr, G., and J. A. Clarke (2003). The deep divergences of neornithine birds: A phylogenetic analysis of morphological characters. Cladistics 19:527–553.

Mecquenem, R. (1908). Contribution a l'étude du gisement des vertébrés de Maragha et de ses environs. Annales d'Histoire Naturelle 1:27–79.

Mecquenem, R. (1925). Contribution a l'étude des fossiles de Maragha. Annales de Paléontologie 24:26–36.

Olson, S. L. (1985). The fossil record of birds. In Avian Biology, volume VIII (D. S. Farner, J. R. King, and K. C. Parkes, Editors). Academic Press, New York, NY, USA. pp. 79–238.

Qiang, X., Z. An, Y. Song, H. Chang, Y. Sun, W. Liu, H. Ao, J. Dong, C. Fu, F. Wu, et al. (2011). New eolian red clay sequence on the western Chinese Loess Plateau linked to onset of Asian desertification about 25 Ma ago. Science China Earth Sciences 54:136–144.

Qiao, Y., Z. Guo, Q. Hao, Q. Yin, B. Yuan, and T. Liu (2006). Grain-size features of a Miocene loess-soil sequence at Qinan: Implications on its origin. Science China Series D-Earth Sciences 49:731–738.

Qiu, Z. X., B. Y. Wang, and T. Deng (2004). Mammal fossils from Yagou, Linxia Basin, Gansu, and related stratigraphic problems. Vertebrata Pal Asiatica 42:276–296.

Quade, J., D. O. Breecker, M. Daeron, and J. Eiler (2011). The paleoaltimetry of Tibet: An isotopic perspective. American Journal of Science 311:77–115.

Quade, J., T. Cerling, and J. Bowman (1989). Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan. Nature 342:163–166.

Rowley, D. B., R. T. Pierrehumbert, and B. S. Currie (2001). A new approach to stable isotope-based paleoaltimetry: Implications for paleoaltimetry and paleohypsometry of the High Himalaya since the Late Miocene. Earth and Planetary Science Letters 188:253–268.

Sanyal, P., A. Sarkar, S. K. Bhattacharya, R. Kumar, S. K. Ghosh, and S. Agrawal (2010). Intensification of monsoon, microclimate and asynchronous C_4 appearance: Isotopic evidence from the Indian Siwalik sediments. Palaeogeography, Palaeoclimatology, Palaeoecology 296:165–173.

Saylor, J. E., J. Quade, D. L. Dettman, P. G. DeCelles, P. A. Kapp, and L. Ding (2009). The late Miocene through present paleoelevation history of southwestern Tibet. American Journal of Science 309:1–42.

Sun, X. J., and P. X. Wang (2005). How old is the Asian monsoon system?—Palaeobotanical records from China. Palaeogeography, Palaeoclimatology, Palaeoecology 222:181–222.

Wang, C., J. Dai, X. Zhao, Y. Li, S. A. Graham, D. He, B. Ran, and J. Meng (2014). Outward-growth of the Tibetan Plateau during the Cenozoic: A review. Tectonophysics 621:1–43.

Wang, E. Q., J. L. Wan, and J. Q. Liu (2003a). Late Cenozoic geological evolution of the foreland basin bordering the West Kunlun range in Pulu area: Constraints on timing of uplift of northern margin of the Tibetan Plateau. Journal of Geophysical Research: Solid Earth 108: B8, 2401. doi:10.1029/2002JB001877

Wang, P. X. (2009). Global monsoon in a geological perspective. Chinese Science Bulletin 54:1113–1136.

Wang, P., S. Clemens, L. Beaufort, P. Braconnot, G. Ganssen, Z. Jian, P. Kershaw, and M. Sarnthein (2005). Evolution and variability of the Asian monsoon system: State of the art and outstanding issues. Quaternary Science Reviews 24:595–629.

Wang, P., Q. Zhao, Z. Jian, X. Cheng, W. Huang, J. Tian, J. Wang, Q. Li, B. Li, and X. Su (2003b). Thirty million year deep-sea records in the South China Sea. Chinese Science Bulletin 48:2524–2535.

Wang, X., Z. Qiu, and N. D. Opdyke (2003c). Litho-, bio-, and magnetostratigraphy and paleoenvironment of Tunggur Formation (middle Miocene) in central Inner Mongolia, China. American Museum Novitates 3411:1–31.

Wetmore, A. (1933). Fossil bird remains from the Eocene of Wyoming. The Condor 35:115–118.

Wetmore, A. (1934). Fossil birds from Mongolia and China. American Museum Novitates 711:1–16.

Wu, F., X. Fang, Q. Meng, Y. Zhao, F. Tang, T. Zhang, W. Zhang, and J. Zan (2017). Magneto- and litho-stratigraphic records of the Oligocene-Early Miocene climatic changes from deep drilling in the Linxia Basin, Northeast Tibetan Plateau. Global and Planetary Change 158:36–46.

Xu, Y., K. Zhang, Y. Yang, G. Wang, M. Luo, J. Ji, and B. Song (2018). Neogene evolution of the north-eastern Tibetan Plateau based on sedimentary, paleoclimatic and tectonic evidence. Palaeogeography, Palaeoclimatology, Palaeoecology. doi:10.1016/j.palaeo.2018.05.012

Zelenkov, N. V. (2015). The fossil record and evolutionary history of cranes. Cranes of Eurasia (Biology, Distribution, Captive Breeding) 5:88–90.

Zelenkov, N. V., and E. N. Kurochkin (2011). Sovremennoe sostoyanie izuchennosti neogenovykh ptits Tsentralnoi Azii [The current state of knowledge of Neogene birds of Central Asia]. In A. Ya. Tugarinovu posvyashaetsya… Sbornik nauchnykh statei [Dedicated to A. Ya. Tugarinov. A collection of scientific papers] (N. V. Martynovich, Editor). Krasnoyarskii kraevoi kraevedcheskii musei, Krasnoyarsk, Russia. pp. 44–70.

Zelenkov, N. V., and E. N. Kurochkin (2015). Class Aves. In Fossil Vertebrates of Russia and Adjacent Countries, Fossil Reptiles and Birds, Part 3 (E. N. Kurochkin, A. V. Lopatin, and N. V. Zelenkov, Editors). GEOS, Moscow, Russia. pp. 86–290.

Zelenkov, N., Z. Boev, and G. Lazaridis (2016). A large ergilornithine (Aves, Gruiformes) from the Late Miocene of the Balkan Peninsula. Paläontologische Zeitschrift 90:145–151.

Zhang, Z., X. Zheng, G. Zheng, L. Hou (2010). A new Old World vulture (Falconiformes: Accipitridae) from the Miocene of Gansu Province, northwest China. Journal of Ornithology 2:401–408.