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

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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 (ráldidos, 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 especimen 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 especimen 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, paleoclíma

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 extant 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 Geranoioidae 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 et al. 2016).
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 Dist R tbt L tmt |
| *U. maraghanus* (Mecquenem 1925, Cracraft 1973, Kurochkin 1981) | R and L prox and dist femoral epiphyses Dist L tibiotarsus Dist epiphysis of III:1 Dist tbt |
| ?*U. cracraftii* (Harrison and Walker 1982) | Pedal III:1 Pedal III:2 |
| *U. sp.* (Kurochkin 1981) | Amphipelargus majori (Lydekker 1891, Harrison 1981) Pedal III:1–3 |
| ?*A. sp.* (Boev et al. 2013, Zelenkov et al. 2016) | Ergilornis spp. (Kozlova 1960, Cracraft 1973, Kurochkin 1981) |

et al. 2016); ?*U. cracraftii* 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 Miocene of northern Kazakhstan (Pavlodor; 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 (Kotlovka 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
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. 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, flp = flexor pit, r = laterodorsal ridge, scd = semicircular indentations, prj = hamate projections.
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 dzabghaneensis* (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. All measurements other than those of Sinoergilornis guangheensis are from Boev et al. (2013). Extinct taxa are denoted by daggers.

| Species                      | a  | b  | c  | d  | e  | f  | g  |
|------------------------------|----|----|----|----|----|----|----|
| †Sinoergilornis guangheensis | 31.3 | 12.0 | 13.7 | 8.0 | 11.4 | 16.0 | 10.3 |
| †Amphipelargus sp.           | 33.4 | 10.1 | 15.0 | 7.2 | 11.8 | 15.7 | 9.4 |
| †Urmiornis ukrainus          | 30.7 | –   | –   | 7.6 | 12.3 | 14.3 | 8.9 |
| †Urmiornis orientalis        | 31.4 | 8.3  | 14.4 | 6.8 | 14.1 | 16.4 | 9.7 |
| †Urmiornis brodkorbi         | 30.0 | 7.3  | 12.7 | 6.1 | 10.2 | 12.9 | 7.5 |
| Ergilornis sp.               | 32.1 | 9.5  | 15.3 | 7.4 | 11.7 | 15.3 | 8.9 |
| Grus grus, specimen MNHS 2/1992, Spain | 36.2 | 6.6  | 10.4 | 4.1 | 6.5  | 9.4  | 4.9 |
| Anthropoides virgo, specimen MNHS 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 the 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 tarsometatarsus 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 trochlea that grade proximally into the shaft of each phalanx (Figures 4 and 5; trd); (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 Neaves, 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 plantarily projected in the new taxon, and the mediiodistal 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, recurvate 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. karateodoris (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 2004, 2013), avian remains have only been recovered in many of these deposits (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 trochlea 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 intertrocchlear area from the distal portion of the foramen. A small amount of breakage is located along the distal margin of trochlea II.

The intertrocchlear 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 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.

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and 3 and data on Dryad: https://doi.org/10.5061/dryad.jh9w0vt6) 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 trochlea 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.jh9w0vt6) 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 medi al 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 guan gheensis* 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 C₃ 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 C₄ to C₃ 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 C₄ 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.

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