

A new fossil of Galliformes with close relationship to extant turkey and grouse from Linxia Basin (Postprint)

Authors: YU Ting-Yu, LI Zhi-Heng¹, LI Zhi-Heng¹

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Abstract

The Linxia Basin, located in northwestern China on the margin of the Tibetan Plateau, preserves abundant Neogene mammal and bird fossils. We report an exquisitely preserved skeleton of a small phasianid species recovered from the Linxia Basin, dating to approximately the latest Miocene to early Pliocene. *Gracilisgallus linxia*, characterized by its small body size and slender limb bones, represents the first discovery in China of a new galliform species closely related to extant grouse (Tetraoninae) and turkey (Meleagridinae). Phylogenetic analysis confirms its close phylogenetic relationship with extant grouse and turkey. Although the scapula, carpometacarpus, femur, and tarsometatarsus of *Gracilisgallus linxia* are morphologically similar to its extant relatives, skeletal features such as the relatively long spur on its tarsometatarsus support its status as a new genus and species distinct from grouse and turkey. This fossil provides a crucial internal calibration point for the divergence of turkey and grouse during the late Miocene to early Pliocene, and reveals that this group had a complex diversification pattern in North America and East Asia during this period.

Full Text

Preamble

Vertebrata PalAsiatica

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A new fossil of Galliformes with close relationship to extant turkey and grouse from Linxia Basin

YU Ting-Yu^{1,2} LI Zhi-Heng^{1*}

¹ Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences,

Beijing 100044

² University of Chinese Academy of Sciences, Beijing 100039

*Corresponding author: lizhiheng@ivpp.ac.cn

Abstract

The Linxia Basin, located in Northwest China at the edge of the Tibetan Plateau, preserves a rich fossil record of mammals and birds. Here, we report an exquisitely preserved skeleton representing a new species of small-bodied phasianid from the Linxia Basin, dated to approximately the latest Miocene to Early Pliocene. *Gracilisgallus linxia* represents the first discovery in China of a taxon closely related to extant grouse and turkey. The new species exhibits a small body size and slender limb bones. Phylogenetic analysis supports its close relationship with extant grouse (Tetraoninae) and turkey (Meleagridinae). The scapula, carpometacarpus, femur, and tarsometatarsus of *Gracilisgallus linxia* share morphological similarities with its extant relatives, but diagnostic features—such as relatively long spurs on the tarsometatarsus—support its classification as a distinct genus and species, separate from both turkey and grouse. This fossil provides a Late Miocene to Early Pliocene calibration point for the divergence of the turkey–grouse lineages and reveals complex patterns in their radiation across North America and eastern Asia.

Key words: Linxia Basin, Neogene, Galliformes, Phasianidae, *Gracilisgallus linxia*, phylogenetic analysis, grouse, turkey

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1 Introduction

The Phasianidae is the most species-rich clade within the Galliformes, comprising 182 extant species with a wide range of body sizes (IOC world bird lists v15.1). These species occupy habitats ranging from Arctic tundra to tropical forests (Madge et al., 2002). The diversity and molecular phylogenetic relationships among extant Phasianidae taxa support the hypothesis that this core group of Galliformes originated and diversified in Asia, particularly in southeastern Asia (Zhao et al., 2012; Wang et al., 2017). Fossils from Neogene Asia are therefore crucial for understanding the timing of geological dispersal events associated with Phasianidae evolution.

Miocene Phasianidae fossils are widely distributed in Eastern China, including important localities such as Linqiu, Sihong, and Lufeng. Notable discoveries with uncertain phylogenetic relationships to extant Galliformes include *Shandonggor-*

nis shanwanensis and *Linguornis gigantis* from the Middle Miocene diatomaceous lacustrine deposits of Shanwang, Shandong Province (Ye, 1980, 1997). *Linguornis gigantis* is the largest known Asian Galliformes fossil, with a body size comparable to that of the extant green peafowl (*Pavo muticus*) (Ye, 1980).

Other fragmentary materials, identified as relatives of *Alectoris* and *Gallus*, have been reported from Middle Miocene deposits of Sihong, Jiangsu Province, and the Late Miocene hominid site Lufeng, Yunnan Province (Hou, 1985, 1987). *Panraogallus hezhengensis*, a nearly complete skeleton with an exquisitely preserved elongated, coiled trachea from the Late Miocene, was the first galliform fossil discovered in the Linxia Basin, Gansu Province (Li et al., 2018).

Grouse and turkeys represent two distinct subfamilies within Phasianidae and are considered sister taxa that diverged from a common ancestor during the Early to Middle Miocene (10–20 Ma), based on molecular dating and fossil evidence (Zhao et al., 2012; Shen et al., 2014; Wang et al., 2017; Chen et al., 2021; Ksepka et al., 2023). Grouse (subfamily Tetraoninae) are primarily adapted to boreal and temperate regions of the Northern Hemisphere, with some species exhibiting specific adaptations to cold climates (Madge et al., 2002). Species such as *Falci pennis falci pennis*, *Lagopus lagopus*, *Lyrurus tetrrix*, and *Tetrastes bonasia* are distributed in Northeast China, particularly in Heilongjiang Province, while *Tetrastes sewerzowi* is an endemic species of central China and the only grouse species observed in Gansu Province (Madge et al., 2002). Their fossil record is highly fragmentary with a few isolated elements assigned to *Tetrao*, *Lagopus*, and *Bonasa*, dated from the Pliocene to Pleistocene ages in Eurasian deposits (Jánnosy, 1974; Tyrberg, 1998; Boev, 2002; Marco, 2009). Turkeys (subfamily Meleagridinae) are native to the Americas and are generally larger birds that inhabit forested and woodland environments (Madge et al., 2002). The oldest turkey fossils found in North America have yet to be validated (Ksepka et al., 2023). Therefore, it remains premature to infer the precise geographic origin of the common ancestor of grouse and turkey clades. Until now, no fossil records of either grouse or turkey relatives have been reported from China.

Here, we describe a new phasianid fossil species from Shi-li-dun, Linxia Basin, Gansu Province. Shi-li-dun is a well-known Late Miocene to Early Pliocene fossil locality, with representative mammal fossils including *Chasmaporthetes kani*, *Hipparion pater*, and *Gazella blacki* (Deng et al., 2013). The fossil species reported in this article is the first known bird fossil in China closely related to grouse and turkeys, providing new insights into the evolutionary history and biogeography of these lineages.

Institutional abbreviations: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China.

2 Systematics

Class Aves Linnaeus, 1758

Order Galliformes Temminck, 1820

Family Phasianidae Vigors, 1825

***Gracilisgallus linxia* gen. et sp. nov.**

Holotype: IVPP V30721. The holotype specimen consists of an almost complete articulated skeleton, including the anterior portion of the skull, cervical vertebrae, partial left coracoid, complete furcula, thoracic vertebrae, both scapulae, humeri, ulnae, radii, left carpometacarpus, and the first phalanges of the major digit. The hindlimb bones include the femur, tibiotarsus, and tarsometatarsus from both sides, though the left tibiotarsus and tarsometatarsus are partially obscured. The phalanges of the right foot are well-preserved, while only the first phalanges of toes III and IV are preserved on the left foot. The dorsal and distal parts of the pelvis are incompletely preserved [Figure 1: see original paper].

Diagnosis: *Gracilisgallus linxia* exhibits several characteristics that align it with crown Galliformes, including a slender scapus clavicularis of the furcula, a shallow cotyla scapularis of the coracoid, a cranially protruding crista deltopectoralis, an incisura capitis of the humerus separated from the fossa tricipitalis dorsalis by a ridge, and a wide spatium intermetacarpale of the carpometacarpus. Within Phasianidae, *G. linxia* is further characterized by a rounded crista bicipitalis of the humerus in cranial view, a moderately developed fossa pneumotricipitalis dorsalis, the presence of a processus intermetacarpalis on the carpometacarpus overlapping metacarpal III, and a femur longer than the humerus. The proximal apex of the crista cnemialis cranialis on the tibiotarsus is flat or rounded in cranial view.

Gracilisgallus linxia can be further distinguished from extant turkey and grouse species, as well as other extinct Galliformes, by several distinct features. It possesses a notably small body size and slender limb bones. The processus costalis extends to half to two-thirds of the length of the cervical vertebrae. The hypocleideum of the furcula forms a right-angled triangle projection in lateral view. The sulcus ligamentous transversus of humerus is weakly developed (see Fig. 2A [Figure 2: see original paper]). The process intermetacarpalis of carpometacarpus projects laterally, forming a flat, obtuse triangle shape (see Fig. 2B). Notably, the femur is longer than the humerus. The tuberculum preacetabular of the pelvis is elongated and projects cranioventrally (see Fig. 2C). Additionally, a relatively long spur extends from the lower portion of the tarsometatarsus. The foramen between trochlea metatarsi and is absent, replaced by a shallow fossa.

Locality and horizon: Shi-li-dun village, Linxia Basin, Gansu Province, China. Upper Liushu to lower Hewangjia Formation. Late Miocene-Early Pliocene (3.6–5.3 Ma) (Deng et al., 2013).

Etymology: The generic name derives from the Latin word *gracilis* (slender)

and “gallus” (chicken), referring to the slender skeleton characteristic of this new galliform species. The specific epithet, “linxia” refers to Linxia Basin, where this fossil was collected.

Description

Skull and lower jaw: The maxilla, quadrate, and mandible of the right side are mainly exposed in lateral view. The frontal, nasal, and part of the parietal bones are preserved. The nasal is divided into the left and right parts, as is the nasal process of the premaxilla. The large external narial opening is triangular in shape. The otic and mandibular processes of the quadrate are well preserved, with the distal margin of the otic processes bearing a small, sharp projection on the lateral side. The lateral mandibular condyle protrudes distinctly laterally. The rostral and caudal mandibular fenestra of the dentary are absent, and the processus coronoideus is poorly developed.

Cervical vertebrae: The lengths of the centrum from 7th to 11th cervical vertebrae measure approximately 11.66 mm. The process costalis is elongated, extending about half to two-thirds of the length of the vertebra. The dorsal side of the centrum is flat, with a weakly developed process dorsalis.

Thoracic vertebrae: Centrum lengths of 2nd and 3rd thoracic vertebrae are approximately 9.81 mm, shorter than that of the cervical vertebrae. Other vertebrae are too poorly preserved to be measured. The neural spine is highly projected and distinctly developed.

Furcula: Only the left scapus clavicularae and hypocleideum are visible on the surface of the holotype; the right part is evaluated through x-ray Computed Tomography (CT) scanning data. The hypocleideum forms a right-triangular projection in lateral view, with ventral and cranial margins measuring 11.53 mm and 6.12 mm, respectively. The scapus clavicularae is slender, with a diameter of 2.05 mm, and presents a V-shape.

Scapula: Both left and right scapulae are preserved. Although the dorsal part of the corpus facies on the right scapula is partly broken, a slight expansion of the middle corpus is visible. The acromion extends straight and projects more cranially than the facies articularis humeralis. The facies articularis humeralis forms an acute angle relative to the corpus scapulae. There is no pneumatic foramen between the acromion and the facies articularis humeralis. The tuberculum coracoideum is weakly developed between acromion and facies articularis humeralis. The facies articularis clavicularis is represented by a small point located at the dorsal margin of the proximal end.

Coracoid: Only the omal half part of the left coracoid is well-preserved. The scapular cotyle is a shallow, flat surface. The processus procoracoideus is weakly developed and extends slightly more medially than the shaft. The processus acrocoracoid is strongly deflected ventromedially, creating a concavity below it. Both the foramen nervi supracoracoidei and fossa pneumaticum on the dorsal surface are absent. A small, blunt ventral projection is located adjacent to the

facies articularis clavicularis at the omal end. The impressio m. sternocoracoidei is marked by a shallow, large concavity at the distal end of the coracoid.

Humerus: The humeri on both sides are well-exposed. The robust shaft is slightly curved. The bicipital crest is rounded in cranial view and extends ventrally, forming a semicircular projection. The fossa pneumotricipitalis dorsalis is moderately developed, creating a large, shallow, round concavity. The incisura capitis is separated from fossa pneumotricipitalis dorsalis by a bony ridge. The crista deltopectoralis is well-developed and curves cranially. The sulcus ligamentous transversus is extremely weakly developed, forming a shallow concavity at the medial margin of the humeral head on caudal view. The condylus ventralis protrudes markedly more distally than the condylus dorsalis. The epicondylus dorsalis is weakly developed, barely projecting from the shaft.

Ulna and radius: The lengths of the ulna and radius are slightly shorter than that of the humerus. The ulna (middle shaft diameter = 3.95 mm) is noticeably wider than the radius (middle shaft diameter = 2.29 mm). The ulna is curved, in contrast to the straight shape of the radius. The distal end of the radius curves slightly medially. The dorsal cotyla of the ulna is an extended, flat surface, while the olecranon process forms a bony ridge at the proximal end. The ventral condyle of the ulna extends more distally than the dorsal condyle. The cotyla humeralis of the radius is a shallow, cup-like structure. The sulcus tendineus is a deep, round concavity located at the distal end of the radius. Both the ulnare and radiale are preserved. The proximal border of the radiale is flat, and its distal margin, connecting with the carpal trochlea of the carpometacarpus, curves proximally.

Carpometacarpus and phalanges: The first phalanges of digits I, II, III, IV, V, majoris, and minoris articulate with the carpometacarpus. The first phalange of digits I and minoris are thin cylinders, while the digit majoris is a thin, rectangular-shaped bone. The pila cranialis is well-developed and located on the radialis margin of the first phalange of digit majoris. The dorsal surface of the first phalange of digit majoris is nearly flat, with a small, round concavity at the distal end. The spatium intermetacarpalis is wide, measuring 3.38 mm. The processus intermetacarpalis projects laterally, slightly overlapping metacarpal I. Metacarpal I forms a general arched shape, and its shaft is untwisted. The cranial surface is rounded, with no large bony spur present. The margin of the trochlea carpalis is positioned proximally relative to the processus extensorius. The proximal rim of the trochlea carpalis is rounded. On the medial side of the trochlea carpalis, a bony ridge separates it from the processus extensorius.

Pelvis: The left and dorsal part of the pelvis are partially preserved. The tuberculum preacetabular is elongated and projects cranioventrally. The foramen ilioischadicum is a large, enclosed, oval-shaped foramen. The lamina ischiadica is substantially developed in comparative depth on the lateral side.

Femur: The femur is distinctly longer than the humerus. The crista trochanteris extends more proximally than the femoral head, forming a thin,

short bony ridge on the lateral side of the shaft. Instead of extending straight proximally along the shaft, the crista trochanteris projects inward, giving the lateral margin of the proximal end a rounded appearance. The femoral head is expanded, forming a spherical structure. The sulcus patellaris is a deep, wide groove, with its width nearly equal to that of the femoral shaft. The condylus lateralis extends more distally than the medial one, which is relatively narrow.

Tibiotarsus: The tibiotarsus is long and slender. Both the crista cnemialis cranialis and crista cnemialis lateralis project as thin, elongated ridges. The medial condyle extends significantly more distally than the lateral one. The proximal end of the fibula articulates with the tibiotarsus.

Tarsometatarsus: A distinct and large-sized spur, with a length of about 11.45 mm, projects caudally and perpendicularly from the medial side of the tarsometatarsus shaft. The foramen between trochlea metatarsi and at the distal end is absent. The foramen between trochlea metatarsi and is long and narrow-oval shaped. The three trochleae metatarsi are closely positioned and vary in distal extension: trochlea metatarsi extends the most distally, while trochlea metatarsi extends farther distally than trochlea metatarsi. The total digital lengths of digits and are distinctly shorter than the tarsometatarsus. The hallux is shorter than other digits and is positioned more proximally. Since the limb bones of *G. linxia* are well ossified, and it has a relatively long spur, we infer that this skeleton belongs to a male adult individual.

3 Phylogenetic analysis

A morphological character matrix comprising 105 osteological characters, one arthrological character, 16 plumage characters, 10 miscellaneous soft tissue characters and four eggs and reproductive behavior characters was analyzed (Ksepka et al., 2023). Sixty-six taxa, including *Gracilisgallus linxia*, are contained in this matrix and the analysis was performed using PAUP version 4.0a169 (matrix data see appendix). The fossil species contain only the osteological characters, while extant species are coded with plumage, soft tissue and reproductive characters. The analysis aims to determine the phylogenetic relationships of the new species within Galliformes and Phasianidae. A molecular backbone constraint was applied to constrain the relationships of extant taxa (Hosner et al., 2017). A heuristic search was conducted with 3000 random taxon addition sequences and tree bisection and reconnection (TBR) branch swapping. Palaeognathae and Anseriformes were designated as outgroups to the galliform taxa. The analysis resulted in 5600 most parsimonious trees with a tree length of 457 steps (see Appendix). The strict consensus tree (tree length of 470 steps) places *G. linxia* within a derived clade in Phasianidae, aligned with grouse and turkeys in a polytomy [Figure 3: see original paper].

Gracilisgallus linxia is placed in the crown group of Galliformes by the presence of the following shared derived characters: the scapus clavicularae of the furcula

is slender; the cotyla scapularis of the coracoid is shallow; the incisura capitis of humerus is separated from the fossa tricipitalis dorsalis by a ridge; the spatium intermetacarpale is wide. It is further supported to be a member of Phasianidae by the following synapomorphies: the crista bicipitalis of the humerus is rounded in cranial view; the fossa pneumotricipitalis dorsalis is not weakly developed; the processus intermetacarpalis of the carpometacarpus is present and overlapping metacarpal ; the femur is longer than the humerus; the proximal apex of the crista cnemialis cranialis on the tibiotarsus is flat or rounded in cranial view. The characters uniting *Gracilisgallus linxia* with grouse and turkeys include: the scapus clavicularae has uniform thickness (character 43); the acromion of the scapula is straight (character 55).

4.1 Comparisons with turkey and grouse species

The phylogenetic analysis places *Gracilisgallus linxia* in a polytomy with grouse and turkeys, although it exhibits significant differences in body-size. Compared to the smallest extant grouse, *Tetrastes* (Madge et al., 2002), *G. linxia* is slightly smaller. In comparison to *Meleagris gallopavo* (IVPP OV1222), *G. linxia* exhibits distinctly more slender limb bones, including the humerus, femur, and tarsometatarsus, and is of overall smaller size .

Turkeys are quite variable in their morphology (Bochenski and Campbell, 2006; Stidham, 2011), but we can still compare some common characters existing throughout the genus *Meleagris* with *G. linxia*. The left and right nasal part of the premaxilla are completely separated along the internarial bar in both *G. linxia* and *Meleagris* [FIGURE:4A, E] (Bochenski and Campbell, 2006). However, while this separation extends to the rostral portion in *Meleagris*, it does not extend as far rostrally in *G. linxia*. The fenestra mandibularis caudalis of the jaw is absent in both *Meleagris* and *G. linxia*. The processus costalis of the cervical vertebrae in *M. gallopavo* extends less than half the length of the articulated cervical vertebrae, which is shorter than that in *G. linxia*. The hypocleideum of *G. linxia* is a large, triangular projection in lateral view, whereas in *Meleagris*, it is poorly developed. The scapulae of these two species are generally similar, except for the presence of a pneumatic foramen between the acromion and facies articularis humeralis in *Meleagris*, which is absent in *G. linxia* (Figs. 1A, 4F). The facies articularis humeralis on the coracoid is larger in *Meleagris* than in the new species. The fossa pneumotricipitalis dorsalis of the humerus is weakly developed in *Meleagris*, appearing shallow [Figure 4G: see original paper]. In contrast, it is moderately developed in the new species [Figure 4B: see original paper]. The sulcus ligamentous transversus is extremely weakly developed in both species (*M. gallopavo* and *G. linxia*). The processus intermetacarpalis in *Meleagris* is well developed, extending laterally to form an acute triangle. In contrast, in the new species, this process does not extend as far laterally and instead forms a flat, obtuse triangle (Figs. 2B, 4H). Additionally, the dorsal surface of the first phalanx of digit majoris is nearly flat in *Meleagris*, while a

small, round concavity is present at the distal end in *G. linxia*.

The tuberculum preacetabular in *G. linxia* is longer and more projected than the small tubercle found in *M. gallopavo*. Both species possess a large, closed oval-shaped foramen ilioischadicum. The femur of *Meleagris* is similar to that of *G. linxia*, in that both exhibit a wide, deep sulcus patellaris, which is nearly equal in width to the shaft [FIGURE:4C, I]. However, the femur of *Meleagris* is shorter than the humerus, whereas in *G. linxia* the femur is longer than the humerus. The spur on the tarsometatarsus of *G. linxia* is relatively longer compared to the total length of the tarsometatarsus. The foramen between the trochlea metatarsi and is present in *Meleagris* but absent in *G. linxia* [FIGURE:4D, J]. In addition, the foramen between the trochlea metatarsi and is larger in *Meleagris* than in *G. linxia*. A character shared by the two species is that trochlea metatarsi extends farther distally than trochlea metatarsi .

Compared to extant grouse, *G. linxia* is distinct in retaining the elongated spur on the tarsometatarsus, which is absent in both sexes of grouse (Madge et al., 2002). Grouse represent a relatively homogeneous group within the Phasianidae clade, sharing several osteological characteristics, including: the presence of a fenestra mandibularis caudalis, a pneumatic foramen between the acromion and facies articularis humeralis of the scapula, a strongly distally projected condylus ventralis of the humerus, a reduced tuberculum preacetabular, a shallow recessus caudalis fossa of the pelvis, and a wide and shallow ischium (Ksepka et al., 2023). However, both the fenestra mandibularis caudalis and the pneumatic foramen between the acromion and facies articularis humeralis of the scapula are absent in *G. linxia*. *Gracilisgallus linxia* also has a developed, long tuberculum preacetabular. The more distally extended condylus ventralis is a shared feature between grouse and *G. linxia*. Due to the fragmented condition of the pelvis in *G. linxia*, the fossa iliocaudalis is not preserved. Based on the preserved portion, it can be inferred that *G. linxia* likely had a conceivably wider and shallower ischium compared to most other members of Phasianidae. The overall shape of the preserved pelvis appears to be relatively flat.

Another Late Miocene Phasianidae species, *Centuriavis lioae*, which shares a close relationship with grouse and turkeys, was found in Nebraska, North America (Ksepka et al., 2023). This species represents a basal split that coexisted with early turkey and grouse. Similar to *G. linxia*, the premaxilla of *Centuriavis lioae* is completely separated along the internarial bar. The fenestra mandibularis caudalis of the lower jaw is absent in both *C. lioae* and *G. linxia*, but present in members of Tetraoninae. Both species possess a long process costalis on the cervical vertebrae, although it is slightly stouter in *C. lioae* than in *G. linxia*. The acromion of scapula in *C. lioae* is medially deflected, in contrast to the straight condition in *G. linxia*. The scapula in both species lack a pneumatic foramen at the proximal end. Additionally, the processus acrocoracoideus of *C. lioae* is not hooked, while it deflects ventromedially to form a blunt hook in *G. linxia*. The fossa pneumotricipitalis dorsalis of the humerus is moderately developed in both species, but it is slightly larger and more rounded in *G. linxia*.

In *C. liaoe*, the distal margin of the crista deltopectoralis merges abruptly with the shaft, creating a squared outline. In contrast, the crista deltopectoralis of *G. linxia* merges smoothly with the shaft. Furthermore, while the sulcus ligamentous transversus is unusually deep and well-defined in *C. liaoe*, it is weakly developed in *G. linxia*. The ulna of *C. liaoe* is also distinctly straighter than that in *G. linxia*. The tarsometatarsus of both species shares the following characters: the absences of a foramen between trochlea metatarsi and at the distal end, the presence of a long and thin oval-shaped foramen between trochlea metatarsi III and IV, the extension of trochlea metatarsi IV farther distally than trochlea metatarsi II. However, the absence of spur in *C. liaoe* distinctly distinguishes it from *G. linxia*.

The genus *Paralyra*, a fossil member of Tetraoninae, was discovered in Bulgaria, Hungary, Poland, and Russia, with material dating to the Early Pliocene (Jánossy, 1974; Zelenkov, 2024). The shaft of the tarsometatarsus in *Paralyra* is noticeably widened, which is distinctly different from the slender shape observed in *G. linxia*. Similar to extant grouse, *Paralyra* lacks a spur, further distinguishing it from *G. linxia*. Both *Paralyra* and *G. linxia* lack a foramen between trochlea metatarsi II and III at the distal end, and in both species, trochlea metatarsi IV extends farther distally than trochlea metatarsi II. However, the foramen between trochlea metatarsi and is nearly round in *Paralyra*, while it is elongated and oval-shaped in *G. linxia*.

4.2 Comparisons with other Asian Phasianidae fossil species

Shandongornis shanwanensis is poorly preserved and its description is quite simple, but its body size is distinctly smaller than *Gracilisgallus linxia* (Ye, 1977). *Linguornis gigantis* is the largest Galliformes fossil discovered in China to date, similar to the extant green peafowl, much larger than *G. linxia* (Ye, 1980). A spur is absent on the tarsometatarsus of *Linguornis gigantis*, distinctly differentiating it from *G. linxia*. However, both species share the characteristic that the trochlea metatarsi IV extends farther distally than trochlea metatarsi II.

Diangallus mious is represented by an incomplete right tarsometatarsus with a spur. Its tarsometatarsus measures approximately 60 mm, slightly larger than that of *G. linxia*. The spur of *Diangallus mious* projects cranioposteriorly, forming an acute angle with the medial side of the tarsometatarsus shaft, in contrast to the perpendicular projecting spur in *G. linxia*.

Paleolectoris songlinensis was discovered in the Middle Miocene deposit of Sihong, Jiangsu Province, China. It is similar to extant *Alectoris* in body size and is therefore distinctly smaller than *G. linxia*. The distal end of the left tarsometatarsus is preserved and shows similarities to *G. linxia* in having a slightly shorter trochlea metatarsus II and lacking a foramen between trochlea

metatarsi and . However, the foramen between trochlea metatarsi and in *Paleolectoris songlinensis* is small and round, different from the elongated and thin oval-shaped foramen in *G. linxia*.

Panraogallus hezhengensis is also found from the Liushu Formation in Linxia Basin and it is slightly older than *G. linxia* (Li et al., 2018). *Panraogallus hezhengensis* is larger than *G. linxia* with much longer humerus (74.0 mm), femur (81.5 mm) and tarsometatarsus (76.0 mm). The mandible of both *P. hezhengensis* and *G. linxia* lack fenestra. The acrocoracoid process is hooked in both species. The fossa pneumotricipitalis dorsalis is moderately developed in *G. linxia*, while in *P. hezhengensis*, this structure is shallow or absent. The condylus ventralis protrudes markedly more distally than the condylus dorsalis in both species. The process intermetacarpalis in *P. hezhengensis* is an acute triangle shaped, in contrast to the obtuse triangle shaped in *G. linxia*. The tuberculum preacetabular of *P. hezhengensis* is small and short, different from the long process of *G. linxia*. The femur of both species is longer than the humerus. The trochanteric crest of *P. hezhengensis* extends more cranially. However, due to the limitation of the preservation angle in *P. hezhengensis*, it is difficult to determine whether it projects inwardly like in *G. linxia*. The tarsometatarsus of *P. hezhengensis* is similar in the length to the femur; however, the tarsometatarsus is distinctly shorter than the femur in *G. linxia* (see Table 1). Although the tarsometatarsus of *P. hezhengensis* does not preserve a spur, a blunt tarsometatarsal callosity exists and it is potentially associated with the attachment of a spur. Trochlea metatarsi extends more distally than trochlea metatarsi in *G. linxia*, while in *P. hezhengensis*, the trochlea metatarsi extends approximately as far distally as trochlea metatarsi IV. The length of digit is only slightly shorter than the length of the tarsometatarsus in *P. hezhengensis*, in contrast to the situation where the lengths of all digits are distinctly shorter than the length of the tarsometatarsus in *G. linxia*.

Tologuica is a fossil genus found in Sharga, Mongolia, in the Middle Miocene, and it is similar to extant *Ammoperdix* in size (Zelenkov and Kurochkin, 2009a). It is distinctly smaller than *G. linxia*. The processus intermetacarpalis of *Tologuica* is poorly developed, in contrast to the triangle shaped process in *G. linxia*. *Perdix margaritae*, *Plioperdix ponticus*, and *Bantamys georgicus* from the Neogene of Mongolia and Transbaikalia (in Russia) are all small phasianids (Zelenkov and Kurochkin, 2009b). They are all similar to extant *Coturnix* in body size, distinctly smaller than *G. linxia*. Larger fossil Phasianidae species found in Asia include *Lophogallus naranbulakensis* and *Syrnaticus kozlovae* (Zelenkov and Kurochkin, 2010). *L. naranbulakensis* was discovered in Naran Bulak, Mongolia, in the Middle Miocene, and it is similar to extant *Gallus* in body size, slightly larger than *G. linxia* (Zelenkov and Kurochkin, 2010). The epicondylus dorsalis does not project dorsally in *L. naranbulakensis*, similar to *G. linxia*. The sulcus patellaris is narrow and shallow in *L. naranbulakensis*, in contrast to the deep and wide groove in *G. linxia*.

4.3 The biogeographic distribution

Although the precise evolutionary relationship between the new species and either turkeys or grouse remains unresolved, *Gracilisgallus linxia* may represent a split lineage that is ancestral to one or both groups. Given the ambiguous identification of fragmentary fossils from North America, the geographic origin of grouse and turkeys remains indeterminate. Research based on extant species indicates that the turkey + grouse lineage originated from Asia (Wang et al., 2017). The presence of *G. linxia* may support this hypothesis.

The complex transcontinental dispersal events that occurred between North America and Eurasia within the grouse clade are thought to be related to adaptation to global cooling and could have been driven by climate change in the Pliocene (Persons et al., 2016). The existence of *Gracilisgallus linxia* in the Late Miocene and Early Pliocene Linxia Basin indicates its adaptation to a savanna environment (Deng et al., 2013), much warmer than the cold regions where extant grouse are distributed. The early existence of *G. linxia* may represent a savanna-like climate adaptation of the ancestor of turkeys and grouse, and it also indirectly supports the idea that the dispersal of grouse was related to cold climates in the Pliocene.

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