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

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RESEARCH ARTICLE

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

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ABSTRACT

Neogene fossils of Old World vultures (Aegypiinae and Gypaetinae) are known from both Old World and New World records. There are no extant Old World vultures in the Americas today, although a large diversity of Gypaetinae is known from Miocene to late Pleistocene records. Despite a comparatively large number of North American gypaetine fossils, complete specimens have rarely been reported from Eurasia and Africa. We describe the exceptional skeleton of a new gypaetine vulture from the late Miocene deposits of the Linxia Basin in northwestern China. The specimen is the oldest record of Gypaetinae from Eurasia or Africa. A reexamination of the geographic and temporal distribution of most Old World vultures from Neogene deposits indicates a diverse radiation, coincident with early- to mid-Miocene grassland expansion for Gypaetinae. Although the diversification of Aegypiinae has been linked to the transition from C_3 to C_4 grassland, Gypaetinae diversification predates that transition in both North America and Asia. A shift in the known latitudinal distribution is also noted. Neogene records of Old World vultures are found primarily in mid- and high-latitude regions of North America and Eurasia as well as in the middle and low latitudes of Eurasia and Africa. With very few records in the middle to late Miocene, a latitudinal distribution similar to that of extant species is first seen in the early Pliocene. The new fossil provides further temporal constraints on avian subclade diversification. It is also consistent with an emerging pattern of profound recent shifts in avian diversity and distribution more generally.

Keywords: extinction, fossil, Gypaetinae, Linxia, Old World vulture

Un nuevo buitre del Viejo Mundo del Mioceno tardío de China esclarece los cambios en la diversidad pasada y la distribución de Gypaetinae

RESUMEN

Los fósiles del Neógeno de buitres del Viejo Mundo (Aegypiinae y Gypaetinae) se conocen de localidades en el Viejo y el Nuevo Mundo. Actualmente no existen buitres del Viejo Mundo en las Américas, aunque se conoce una gran diversidad de Gypaetinae a partir de registros del Mioceno al Pleistoceno tardío. A pesar de un número comparativamente grande de fósiles de Gypaetinae en Norte América, los reportes de especímenes completos en Eurasia y África son raros. En este trabajo describimos el esqueleto excepcional de un nuevo buitre gypaetino de los depósitos del Mioceno tardío de la cuenca Linxia en el noreste de China. El espécimen es el registro más viejo de Gypaetinae de Eurasia o África. La reevaluación de la distribución geográfica y temporal de la mayoría de los buitres del Viejo Mundo en depósitos del Neógeno indica una radiación diversa que coincide con la expansión de las praderas durante el Mioceno temprano a medio. Aunque la diversificación de Aegypiinae ha sido relacionada con la transición de praderas C3 a praderas C4, la diversificación de Gypaetinae precede esa transición en Norte América y Asia. También notamos un cambio en la distribución latitudinal. Los registros del Neógeno de buitres del Viejo Mundo se encuentran principalmente en regiones de latitud media y alta en Norte América y Eurasia, y también en regiones de latitud media y baja en Eurasia y África. Con tan pocos registros en el Mioceno medio a tardío, una distribución latitudinal similar a la de las especies actuales sólo se ve inicialmente en el Plioceno temprano. El nuevo fósil impone más restricciones temporales en la diversificación de subclados de aves. También es consistente con un patrón emergente de cambios profundos recientes en la diversidad y distribución de las aves en general.

Palabras clave: buitres del Viejo Mundo, extinción, fósil, Gypaetinae, Linxia

INTRODUCTION

Old World vultures do not form a monophyletic group within Accipitridae (Seibold and Helbig 1995, Lerner and Mindell 2005, Griffiths et al. 2007), and 2 subclades are commonly recognized (Lerner and Mindell 2005, Lerner 2007), the Gypaetinae (*Gypohierax*, *Gypaetus*, and *Neophron*) and Aegypiinae (*Aegypius*, *Gyps*, *Sarcogyps*, *Torgos*,

Trigonoceps, and *Necrosyrtes*). Aegypiinae is a well-supported clade nested within Accipitridae, whereas Gypaetinae has been recovered basally within Accipitridae (Lerner and Mindell 2005, Griffiths et al. 2007). Both molecular and morphological data have indicated that Gypaetinae may be more closely related to Perninae (kites and buzzards) than to Aegypiinae (Jollie 1976, 1977a, 1977b, 1977c, Mundy et al. 1992, Seibold and Helbig 1995, Lerner and Mindell 2005). Indeed, one recent analysis has suggested that a monophyletic Gypaetinae would also include a non-vulturine accipitrid, the Madagascar Serpent-eagle (*Eutriorchis astur*; Lerner and Mindell 2005). Ecologically and morphologically, Aegypiinae and Gypaetinae are quite different. Aegypiinae usually consume carrion from large mammal carcasses and are specialized scavengers; whereas gypaetine vultures exhibit highly diverse diets and habitats (Hertel 1994, Thiollay 1994). For instance, *Neophron* (Gypaetinae) mostly occurs in open areas of dry regions and consumes a variety of foods, including dead passerines, small mammals, insects, and even ostrich eggs (Hertel 1994, Thiollay 1994). *Gypaetus* is a specialized bone feeder that inhabits rocky sites in mountainous areas, whereas *Gypohierax* is a regular fruit consumer found close to tropical forests, rivers, and lakes where palm trees are present (Thiollay 1994). Of the 16 extant accipitrid vultures, the majority of aegypiine vultures (e.g., *Necrosyrtes monachus*, *Gyps africanus*, *G. coprotheres*, *G. rueppelli*, *Torgos tracheliotos*, and *Trigonoceps occipitalis*) and one gypaetine vulture (*Gypohierax angolensis*) are restricted to Africa (Mundy et al. 1992). Only a few aegypiine species, including *Sarcogyps calvus*, *Gyps bengalensis*, *G. himalayensis*, and *G. indicus* have exclusively Asian extant distributions. *Gypaetus barbatus*, *Neophron percnopterus*, and *Aegypius monachus* have both Eurasian and African distributions.

Old World vultures have a comparatively rich fossil record in the Neogene of North America but have never been found in South America (Howard 1932, 1966, Wetmore 1936, Feduccia 1974, Rich 1980, Zhang et al. 2012a). Fossils referred to 6 species of *Neophrontops* have been described from early Miocene to late Pleistocene (0.13–16.4 mya) localities, including Nebraska, Idaho, South Dakota, and California (Howard 1932, Feduccia 1974, Rich 1983, McDonald and MacVaugh 2013). More fragmentary material referred to Old World vultures was found in Nebraska, South Dakota, and California, including *Arikarornis* (early Miocene), *Palaeoborus* (early Miocene–early Pliocene), *Anchigyps* (late Miocene–lower Pliocene), and the late Pleistocene *Neogyps* (Wetmore 1936, Miller and Compton 1939, Howard 1966, Rich 1980). All these taxa were considered to be more closely related to gypaetine vultures and to represent one, or multiple, basal divergences within Accipitridae (Rich 1980).

Compared to the rich fossils of Old World vultures in North America, pre-Pleistocene Eurasian and African records are more limited and occur mostly after the late Miocene. *Palaeohierax gervaisii* has been described from a single tarsometatarsus from the late Oligocene–early Miocene in France (Brodkorb 1964), and a new species of griffon vulture (*Gyps bochenskii*) was recently described on the basis of pectoral elements from late Pliocene deposits in Bulgaria (Boev 2010). More recently, 2 new *Aegypius* species were reported from the early Pliocene in South Africa and Europe (Manegold and Zelenkov 2014, Manegold et al. 2014). The latter species appears to be the earliest recovered for crown Aegypiinae in Europe (Manegold and Zelenkov 2014). Two pre-Pleistocene records of Old World vultures from China have been described, including a partial tarsometatarsus from the middle Miocene of Jiangsu Province (*Mioaegypius gui*; Hou 1984) and an almost complete skeleton of a large aegypiine vulture from the late Miocene of Gansu Province (*Gansugyps linxiaensis*; Zhang et al. 2010). *Gansugyps* has been placed within the Aegypiinae (Zhang et al. 2010), and its crown affinity has been debated (Manegold et al. 2014). The assignment of *Mioaegypius* to Accipitridae is questionable, given that no diagnositic features of Accipitridae have been identified in the holotype specimen (Hou 1984, Manegold et al. 2014). Meanwhile, the majority of the Pleistocene Old World vultures have been found in cave deposits in Central Europe, Southeast Asia, and northeastern China, which suggests a recent contraction in the range of extant Old World vultures (Sánchez Marco 2007, Zhang et al. 2012b, Meijer et al. 2013, Meijer 2014). In contrast to North American records, most of these Pleistocene Old World records have been referred to Aegypiinae.

Here, we describe a nearly complete specimen of a small *Neophron*-like vulture from late Miocene sediments of the Linxia Basin, Gansu Province (Figures 1–4). This specimen is the earliest and the first definite record of Gypaetinae in the Old World. Other Miocene avian taxa known from the same basin include another Old World vulture, *Gansugyps linxiaensis* (Aegypiinae), as well as a distinct species of stem kestrel (*Falco hezhengensis*) and a large ostrich (*Struthio linxiaensis*) (Hou et al. 2005, Zhang et al. 2010, Li et al. 2014). The avian diversity as well as the better-represented mammalian fauna in the Linxia Basin indicate a "savanna-like" environment in this part of northwestern China during the late Miocene (Bahean stage, 7.25–11.1 mya; Deng et al. 2013). The results of detailed pollen studies suggest that the vegetation was dominated by xerophilous grasses and a few broad-leaved trees (Ma et al. 1998).

METHODS

Osteological terminology follows the English equivalents of features in Baumel and Witmer (1993). The use of "Gypaetinae Vieillot 1816" to refer to a basally divergent accipitrid clade that includes *Gypohierax*, *Neophron*,

FIGURE 1. Photograph and line drawing of the holotype specimen of *Mioneophron longirostris* (HMV 1877). Anatomical abbreviations: c = coracoid; cav = caudal vertebrae; cmc = carpometacarpus; cv = cervical vertebrae; fe = femur; fi = fibula; fu = furcula; h = humerus; il = ilium; pes = pes; py = pygostyle; r = radius; ra = radialae; rib = rib; s = scapula; sk = skull; st = sternum; tbt = tibiotarsus; tmt = tarsometatarsus; tv = thoracic vertebrae; u = ulna; ub = upper beak; ul = ulnare; II:1 = phalanx II-1.

Gypaetus, and *Eutriorchis* and their stem relatives follows Lerner and Mindell (2005). The new specimen was compared with the skeletal collections of the U.S. National Museum of Natural History and the Vertebrate Paleontology Laboratory, University of Texas at Austin. Institutional abbreviations: HMV = Hezheng Paleozoological Museum, vertebrate collection, Gansu Province, China; STM = Shandong Tianyu Museum, Linyi, China; NMNH = U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; and VPL = Vertebrate Paleontology Laboratory, University of Texas at Austin, Austin, Texas, USA.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758
ACCIPITRIDAE Vieillot, 1816
Gypaetinae Vieillot, 1816
Mioneophron longirostris, gen. et sp. nov.
(Figures 1–4)

Holotype. HMV 1877: A nearly complete skeleton (Figure 1) preserved in yellow-brownish siltstone with carbonate cementation. The proximal right tarsometatarsus and distal left tarsometatarsus have been rearranged after collection (illustrated as dark gray regions in Figure 1). Some bones have been fabricated and others recomposed in a wrong position (e.g., pedal digits). The left distal humerus is reconstructed with plaster and the proximal right tarsometatarsus appears to be a proximal tibiotarsal fragment, without any definite clue to its affinity. The position of the hallux opposite of where it should be in the right pes is one indication that the pedal digits were recomposed.

Locality and horizon. The holotype was collected from Baihua Village, Zhuangheji Town, Guanghe County, in Gansu Province, northwestern China (Figure 5: star), in the Upper Miocene Liushu Formation, Linxia Basin. All currently known fossil birds in the Linxia Basin are from the same unit, which is characterized by a distinct matrix lithology (Deng et al. 2013). The bird fossils have been acquired from local farmers and collectors. The holotype specimen is archived in the Hezheng Paleozoological Museum, Gansu Province, China.

Etymology. The genus name, "*Mioneophron*," references the Miocene age and the proposed affinity of the new

FIGURE 2. Photographs showing the anatomical details of the holotype specimen of *Mioneophron longirostris*: (**A**) lateral view of the rostrum; (**B**) cranium and right distal forearm; (**C**) anterodorsal view of the pectoral and pelvic girdle; and (**D**) dorsal view of the thoracic region. Anatomical abbreviations: accp = acrocoracoid process; acp = acromion process; C6, C7, C8 = cervical vertebrae 6, 7, and 8; cav = caudal vertebra; cp = costal process; dce = deltopectoral crest edge; dep = dorsal depression; dsp = dorsal supracondylar process; eoc = extremitas omalis claviculae; ep = extensor process; if = intertransversarial foramina; il = ilium; ils = iliosynsacral sulcus; lc = lateral margin of coracoid; nar = naris; nf = neurovascular foramina; pf = pneumotricipital fossa; popr = postorbital process; py = pygostyle; s = scapula; su = suture between ilium and ischium; sy = symphysis; tc = tomial crest; tpi = terminal process of ischium; tr = trochanteric ridge; tri = thoracic rib; ts = tendinal sulcus.

specimen with *Neophron*. The adjectival species name, *longirostris*, references an elongate rostrum.

Diagnosis. *Mioneophron longirostris* can be differentiated from all other gypaetine and aegypiine vultures by the unique presence of a combination of the following features: a long and narrow rostrum with small oval-shaped nares (Figure 1), a well-projected and globose humeral head and distinct caudal ridge on the margin of the deltopectoral crest, a much longer ulna than tibiotarsus (ratio = 1.45), and a distinct groove between the dorsal iliac ridges (Figure 2).

Differential diagnosis. In comparison with other extant and extinct Old World vultures, the new specimen has a slender and elongated rostrum, close to that of the Egyptian Vulture (*Neophron percnopterus*; Gypaetinae) and the Hooded Vulture (*Necrosyrtes monachus*; Aegypiinae). However, it differs from these 2 small vultures in other skeletal features, including the distinct groove between the

dorsal iliac crests and the caudal ridge on the margin of the deltopectoral crest of the humerus (Figure 4). Unlike widespread extinct taxa from the Neogene in North America, such as *Neophrontops* and *Neogyps*, the new specimen shares with other crown gypaetine vultures (e.g., *Neophron*) a dorsally projected acrocoracoid process on the coracoid and a blade-like acromion on the furcula. In addition, the deltopectoral crest of the humerus is more dorsally expanded in *Mioneophron* than in *Neophrontops* (Rich 1980). Recently described *Anchigyps*, a basal gypaetine vulture, displays a slightly longer ulna than tibiotarsus. The difference in the length of the ulna and tibiotarsus is much greater in *Mioneophron*, in which it more closely resembles extant Old World vultures. In addition, the mandibular symphysis is slightly longer but narrower in *Mioneophron* than in *Anchigyps*.

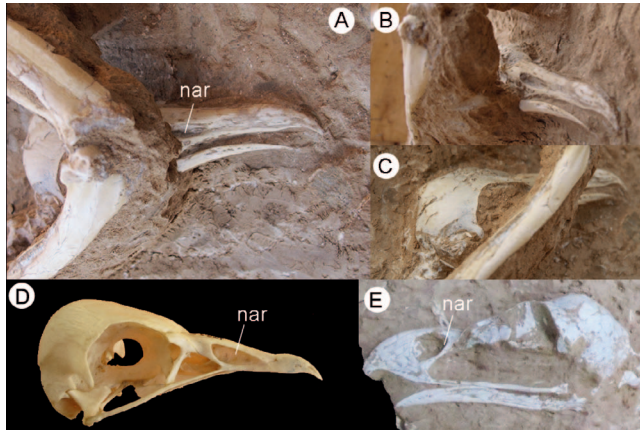**Systematic placement of the new species.** The new species shares several features with gypaetine vultures,

FIGURE 3. Morphology of the cranium in *Mioneophron longirostris* (HMV 1877): (**A**) lateral view, (**B**) cranial view, and (**C**) dorsolateral view; compared with (**D**) *Neophron percnopterus* (NMNH 17835; Gypaetinae) and (**E**) referred specimen of *Gansugyps linxiaensis* (STM 20-4; Aegypiinae). Abbreviation: nar = naris.

FIGURE 4. Morphology of the pelvis in *Mioneophron longirostris* (HMV 1877) compared with that of other Old World vultures (dorsal view): (**A**) *Mioneophron longirostris* (HMV 1877); (**B**) *Neophron percnopterus* (NMNH 17835; Gypaetinae); (**C**) *Necrosyrtes monachus* (NMNH 620646; Aegypiinae); (**D**) *Gypaetus barbatus* (NMNH 345684; Gypaetinae); and (**E**) *Gyps africanus* (NMNH 431696; Aegypiinae). Anatomical abbreviations are the same as in Figures 1 and 2.

including the relatively weakly projected transverse nuchal crest on the basicranium as well as the broad humeral deltopectoral crest. It also has fewer cervical vertebrae (14, vs. 15–17 in Aegypiinae; Rich 1980, Holdaway 1994), and the postacetabular ilia are incompletely fused to the sacrum (Figure 4; Jollie 1976, 1977a, 1977b, 1977c), both of which are features consistent with gypaetine vultures. However, *Mioneophron* has a wider deltopectoral crest than aegypiine vultures, a deeper humeral capital incisure, a gentler bicipital crest, and a shorter mandibular symphysis. Furthermore, unlike in aegypiine vultures, no pneumatic foramina are present on the proximal surface of the pisiform process of the carpometacarpus (Manegold et al. 2014). The medial hypotarsal crest is slightly higher than that of the lateral one in the cranial view, whereas in *Aegypius*, *Trigonoceps*, and *Torgos* the 2 hypotarsal crests are very similar in height.

Measurements (mm). Skull, 113.2; scapula, 74.7; coracoid, 65.5; humerus, 146.0; ulna, 180.9; radius, 169.0; carpometacarpus, 82.0; synsacrum (length and width), 84.8 and 47.4; femur, 80.4; tibiotarsus, 124.7; tarsometatarsus, >74.4; manual phalanges I-1, 26.6; II-1, 33.5; II-2, 25.6; III-1, 15.7; pedal phalanges II-1,18.1; II-2, 14.2; II-3, 8.3; III-1, 19.4; III-2, 16.0; III-3, 13.3; IV-1, 12.0; IV-2, 7.9. Maximum length is given for all measurements except as noted. The size of the new specimen is similar to *Neophron* in terms of element length and proportions.

Description and comparison. The skull is preserved in the lateral view with a matrix-filled orbit (Figures 1–3). The rounded caudal cranium is similar to *Neophron* (Gypaetinae) in the vaulted shape (Figure 3A–3C). The dorsoventrally narrowed rostrum is seen elsewhere only in extant *Neophron percnopterus* (Gypaetinae) and *Ne-*
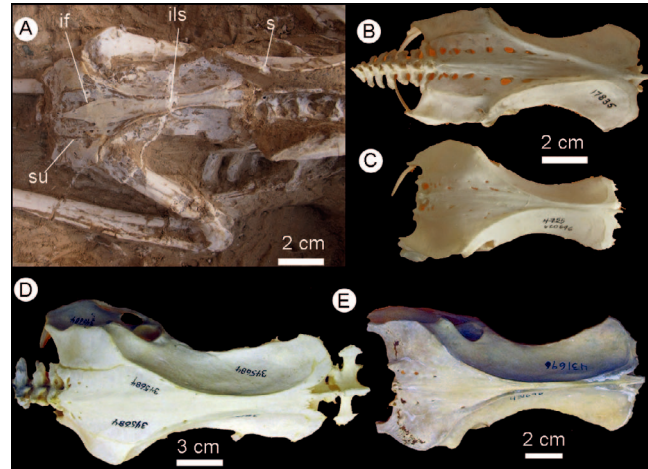
crosyrtes monachus (Aegypiinae) and the extinct *Neophrontops*. In other basal Accipitridae, such as *Polyboroides* and *Elanus*, the rostrum is much shorter and more dorsoventrally expanded. The rostrum length is about half the length of the skull, similar to all other gypaetine vultures. The pre-narial portion of the upper beak in the new specimen is also longer than that of *Neophron* (Figure 3). The tomial margin of the beak is curved (Figure 2A). In the lateral view, the dorsal surface of the upper beak is depressed cranial to the terminus of the external nares (Figure 2A). The ventral extent of the postorbital process (Figure 2B) surpasses that in aegypiine species. In the caudal view, the paraoccipital process expands ventrolaterally; a transverse nuchal crest (crista nuchalis transversa; Baumel and Witmer 1993) is weakly projected on the basicranium and provides a distinct dorsal margin to the exoccipital region (Figure 3C). The mandible is partially exposed in lateral view and curved ventrally near the rostral tip (Figures 1 and 2A). The symphysis is narrow and appears to be short (Figure 2A). Numerous neurovascular foramina are seen on the lateral surface of the rostrum and mandible. Both the upper jaw and the mandible are significantly thinner and weaker than those of most other vultures, especially aegypiine vultures.

The cervical series comprises 14 vertebrae and is primarily exposed in dorsal view (Figure 1). Cervical number varies from 15 to 17 (Rich 1980, Holdaway 1994) in *Gyps* or other Aegypiinae, and an elongated "S-shaped" naked neck is present (Thiollay 1994). By contrast, cervical number generally ranges from 12 to 14 in Gypaetinae (e.g.,
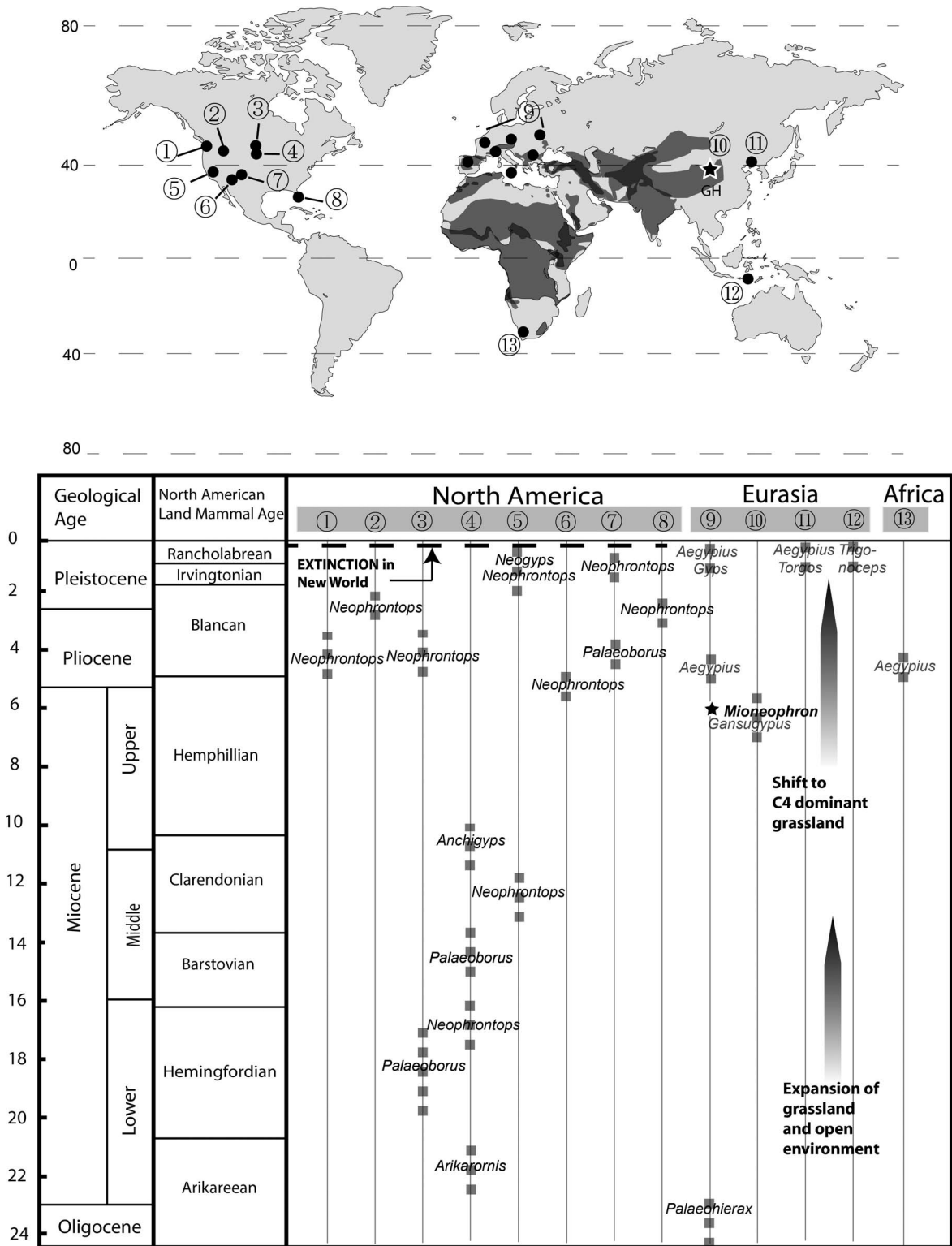
FIGURE 5. Geographic distribution and age of Old World vulture fossils and extant Gypaetinae. Black dots and star indicate fossil occurrences in North America (1 = Oregon; 2 = Idaho; 3 = South Dakota; 4 = Nebraska; 5 = California; 6 = Arizona; 7 = New Mexico; 8 = Florida); Eurasia (9 = Europe; 10 = Guanghe County, Linxia Basin, China; 11 = northeastern China; 12 = Southeast Asia); and Africa (13 = South Africa). The star marks Guanghe County, where the holotype specimens of *Mioneophron* and *Gansugyps* were discovered. The dark gray areas represent the current distribution of Gypaetinae; where extant species' ranges overlap, the color grades to black. Age data are from Rich (1980), Ludvigson et al. (2009), and Zhang et al. (2012a, 2012b).

Neophron, 12; *Gypaetus*, 14), and in some non-vulturine basal Accipitridae (e.g., *Elanus*) the cervical number is also 12 (Holdaway 1994). The small number of cervicals (i.e. 12–14) in Gypaetinae and other basal accipitrids, including the new specimen, may be plesiomorphic for Accipitridae and possibly shared by the last common ancestor of Gypaetinae and Accipitridae. The third cervical vertebra of *Mioneophron* has an osseous bridge extending from the transverse process to the caudal articular process (Mayr and Clarke 2003). This feature is present in *Neophron* but not obvious in other Gypaetinae (e.g., *Gypaetus*) or Aegypiinae. The axis, third cervical, and fourth cervical possess a prominent spinous process. Mid-serial cervical vertebrae (e.g., vertebrae 5–8) are elongate and have prominent dorsal tori (torus dorsalis; Baumel and Witmer 1993). The postzygapophyses are longer than the prezyga-pophyses in these mid-serial vertebrae (Figure 2). The thoracic vertebrae have broad neural spines that extend nearly the length of these vertebrae and closely approach each other, possibly enabling an accessory articulation (Figure 2D). The broad transverse processes have expand-ed tips with caudally directed spine-like extensions, indicating strong ligamentous attachment. One incom-plete proximal caudal vertebra and the pygostyle are preserved near the synsacrum (Figure 2D).

The sternum and other pectoral elements are incom-pletely exposed. The acrocoracoid process of coracoids is deflected cranially, with the clavicular facet well projected medially (Figure 2C). The acrocoracohumeral ligament impression curves and slopes gently toward the sternal. The right coracoid shaft has a concave lateral margin and a broad lateral process (Figure 2C), and the furcula is characterized by an expanded omal end (Figure 2D). The acromial process of the furcula curves caudoventrally and tapers to a narrow point; this deflection is similar to that observed in *Neophron*, less significant than in *Gyps*, and more significant than in other basal accipitrids. The scapulae are well exposed in lateral and dorsal views. The scapular corpus is strongly curved and expands before tapering to a point distally (Figure 2C). In other taxa, for instance *Aegypius* and *Torgos*, the distal scapula is more rounded and relatively broad rather than forming a sharp point. The acromion of the scapula is elongate with an articular facet of the furcula (Figure 2D). A major portion of the sternum is embedded in the matrix, and only a few costal processes are discernible (Figure 2C) in the dorsal view; the incisura intercostalis (Baumel and Witmer 1993) is much smaller than in other larger vultures.

The humeral head is quite well rounded and globose. Preservation does not allow a detailed assessment of the capital groove, but it seems to be shallow (Figure 2C). The pneumotricipital fossa contains matrix, but the outline of a large, round, perforating foramen is visible (Figure 2C). The deltopectoral crest has a rounded dorsal edge (Figure 2C). Caudally, a ridge is present along the margin of the dorsal edge. The deltopectoral crest is comparatively elongate, extending more than a third the length of the humeral shaft. The distal margin of the bicipital crest tapers into the shaft rather than meeting it at an abrupt angle as in *Necrosyrtes*. The ulna is much longer than the humerus (see above), in contrast to the relatively shorter ulna observed in *Anchigyps* (Zhang et al. 2012a).

The carpometacarpi are visible ventrally and dorsally on the left and right wings, respectively. Unlike in Aegypiinae, no pneumatic foramina are discernible proximal to the pisiform process on the carpometacarpus (Manegold et al. 2014). A long tendinous sulcus (where the M. extensor digitorum communis passed; Stegmann 1978) is well developed along the major metacarpus (Figure 2B). The extensor process appears to be more prominent and broader than that of *Neophron* and other Gypaetinae (Figure 2B), and the indentation between the process and the carpal trochlea seems to be flat. The major and minor metacarpals are approximately equal in the distal extent, and their relative extension is quite different compared to *Torgos* and *Aegypius*, in which the minor metacarpal extends farther distally. There are 2 depressions on the dorsal surface of the first phalanx of the major digit, a feature shared with *Neophron* and other non-vulturine Accipitridae (e.g., *Pandion*). The medial side bears a long, narrow groove (for the M. interosseus palmaris; Stegmann 1978); and the second phalanx of the major digit is short, with a prominent knob close to the caudal side of its base.

The synsacrum is well exposed in dorsal view (Figure 4). Caudally, open sutures are visible between the ilia and the sacrum (Figures 2 and 4) as in other Gypaetinae. By contrast, in Aeypiinae the ilia and the sacrum are largely fused. The preacetabular portion of the synsacrum is twice as long as the postacetabular portion, an attribute similar to basal Accipitridae. In Aegypiinae the preacetabular region of the synsacrum is only slightly longer. In dorsal view, the margin of the caudal iliac crest is straight, differing from the "S" shape in most accipitrids (Jollie 1977a, 1977b). The craniolateral edges of the preacetabular ilia are slightly flared laterally, similar to those in *Neophron*, whereas in *Gyps* the preacetabular ilia meet and fuse to the sacrum, enclosing the iliosynsacral canals and forming the distinct dorsal iliac ridge. A conspicuous groove is formed between the 2 ridges (Figure 4) in the new specimen.

Several foramina intertransversaria are present in the new specimen (Figures 2 and 4). These foramina are similar in size to those in *Neophron percnopterus*; those in *Gyps*, *Gypaetus*, and other Old World vultures are much smaller or almost negligible. The iliac crest is well projected laterally, below which the surface of the postacetabular ischium is markedly concave. The post-acetabular portion of the synsacrum is depressed dorso-

ventrally, and the ilioischiadic fenestra is not well exposed. The ischial margin slopes markedly ventrally, and its caudal tip tapers to a point. The pubes are not preserved.

The femur of the new specimen is short and robust (Figure 1). A pneumatic foramen is present on the craniolateral side of the proximal femur as in other Accipitridae. Distally, the patellar groove is deep and narrow, and a shallow depression is present on the medial condylar surface. The tibiotarsus is ~1.5 times the length of the femur. In medial view, the medial condyle on the left tibiotarsus appears more rounded than that of aegypiine vultures, in which the condyle protrudes cranially with a flat ventral margin. The proximal tarsometatarsus is similar to that observed in *Neophron*, characterized by a medial hypotarsal crest that is higher than the lateral crest. The intercotylar eminentia (Baumel and Witmer 1993) is raised slightly higher than that of aegypiine vultures. Unfortunately, parts of the leg bones have been fabricated, including both the left and right pedes and the proximal portion of the right tarsometatarsus.

DISCUSSION

Gypaetine fossils are well documented in the Neogene deposits of North America but are rather scarce in the Old World (Rich 1980, Campbell 2015). Among these North American fossils, *Neogyps* shares a number of tarsometatarsal features with *Gypaetus* (bearded vulture), including a proportionally much wider cranium in relation to height and the trochlea of metatarsal III, which is slightly more distally projected than the trochlea of II (Howard 1932). *Anchigyps*, a recently described accipitrid vulture from the late Miocene of Nebraska, resembles *Gypohierax* in several of its tarsometatarsal features. For instance, the lateral hypotarsal crest is slightly less projected plantarly than the medial one; the distal extension of trochlea II is about the same as that of III, and the medial divergence of trochlea II from midline is quite strong (Zhang et al. 2012a). These North American taxa lack several derived features that would suggest a basal positioning within Gypaetinae. For instance, *Neogyps* does not display a distolateral foramen on its sternal plate (Howard 1932), *Neophrontops* is without an enlarged acromion on its furcula, and *Anchigyps* lacks a proportionally longer ulna in relation to tibiotarsus length, similar to other non-vulturine accipitrids. On the basis of the incomplete and disarticulated available material, these taxa have tentatively been described as "mosaic form," suggesting that early Old World vultures originated from eagle- or harrier-like accipitrids (Rich 1980, Griffiths et al. 2007). In contrast to Gypaetinae, aegypiine vultures are found exclusively in the Old World within slightly younger deposits until the late Miocene (Figure 5). The complete disappearance of gypaetine vultures from North America (e.g., *Neophron-*

tops and *Anchigyps*) led to a major shift in the global distribution of Old World vultures in the Neogene. The patterns of diversification and extinction of the Gypaetinae and Aegypiinae are more complex.

Plotting the geographic and temporal range of these fossil records from the late Oligocene through the Pleistocene reveals that Old World vultures have mostly been found in a distinct zone around 40°N latitude in North America and Eurasia (Figure 5). The early–middle Miocene transition of mid-latitude landscapes from forest to more open grassland and woodland (Janis et al. 2004, Kita et al. 2014) coincides with the early appearance of gypaetine vultures in North America (Figure 5). The Middle Miocene Climatic Optimum (15–17 mya), which has been linked to high speciation rates in mammals (MacFadden 1994), is also synchronous with Gypaetinae radiation in North America. Discoveries of Old World vultures in these Miocene sites (e.g., in Oregon and South Dakota) are usually associated with a diverse array of mammal species as well (Retallack 2004, Deng et al. 2013).The expansion of open habitats by 12 mya (early Clarendonian; Kita et al. 2014), and the increase in the number of grazing as opposed to browsing mammals in North America in the middle Miocene, may have led to an increase in the availability of the mammal carcasses upon which these extinct vultures relied (Janis et al. 2000).

The spread of C_4 grassland worldwide has been linked to the Neogene diversification of several avian taxa, including Falconidae (Zhan et al. 2013, Fuchs et al. 2015), *Gyps* (Johnson et al. 2006), *Aegypius* (Manegold et al. 2014), and some starlings (Zuccon et al. 2008), all of which prefer open environments. C_4 dominant plants expanded in the Linxia Basin only in the Pliocene, around 2–3 mya (Wang and Deng 2005), which is later than in north-central China, North America, and Africa (Cerling et al. 1997, Ségalen et al. 2007, Edwards et al. 2010, Kita et al. 2014, Ciner et al. 2015). *Mioneophron* therefore predates the C_3-to-C_4 transition in Linxia, whereas major aegypiine vulture diversification (*Gyps* and *Aegypius*) may indeed track this shift. The distribution of Gypaetinae and Aegypiinae is broader in the Miocene and Pliocene, but their ranges had contracted by the end of the Pleistocene; for example, they had disappeared from North America, Southeast Asian islands, and eastern China (Howard 1966, Rich 1980, Hou 1984, Zhang et al. 2012b, Meijer 2014). The disappearance of Late Pleistocene mammalian megafauna likely had a further impact on the food resources of Old World vultures, contributing to their ultimate disappearance from North America (Martin and Klein 1989) and some regions in Asia (Zhang et al. 2012b, Meijer 2014).

The rostral morphology and body size of *Mioneophron* are more consistent with having a mixed diet similar to that of the Egyptian Vulture than with being a carrion

specialist. Skull measurements and beak shape are often used to characterize the feeding modes of vultures (Hertel 1994). It is very likely that *Mioneophron* shared an opportunistic foraging behavior similar to that of *Neophron* (Hertel 1994) and relied on similar food resources, including insects, feces, ostrich eggs, and smaller scraps of carcasses (Mundy et al. 1992, Hou et al. 2005). By contrast, *Gansugyps*, from the same deposits in Linxia, has been placed in the crown or stem Aegypiinae (Zhang et al. 2010, Manegold et al. 2014). Its robust rostrum (Figure 3E) and its larger body size are more consistent with such a carrion-based diet (Zhang et al. 2010). Therefore, *Mioneophron* may have avoided direct competition for food with the much larger *Gansugyps*.

Copresent in the late Miocene in northwestern China, the Aegypiinae and Gypaetinae have undergone markedly different patterns of diversification later in the Neogene. *Mioneophron* is one of the few fossils to offer insight into the evolution of Gypaetinae in the Old World. Early records of Old World vultures from Eurasia remain generally rare, and specimens from localities in the Linxia Basin and elsewhere in Asia, Europe, or Africa would contribute importantly to a more nuanced understanding of potential Cenozoic drivers of avian diversification. Many of these taxa have experienced profound shifts in range over very short timescales. A better understanding of their fossil records and detailed geochronological data will be critical for untangling the potentially complex relationship between vulture diversification, aridification, and changes in mammalian faunas.

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