ORIGINAL ARTICLE

A new Old World vulture (Falconiformes: Accipitridae) from the Miocene of Gansu Province, northwest China

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Abstract A large-sized and almost complete fossil vulture was discovered from the Late Miocene Liushu Formation of Linxia Basin in northwestern China. It is the best-preserved and the most complete fossil vulture yet discovered. The new genus and species *Gansugyps linxiaensis* is proposed and assigned to the family Accipitridae; morphology and limb proportions suggest it was chiefly an arboreal and soaring bird. It is more advanced than the other two known Miocene vultures from China. This new fossil increases our knowledge of the evolutionary history of vultures, and has implications for reconstructing the paleoecology of this region.

Keywords *Gansugyps linxiaensis* gen. et sp. nov. · Late Miocene · Liushu Formation · Northwestern China · Old World vulture · Paleoecology

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Introduction

Vultures are large, carrion-eating birds represented by two distinct groups: New World vultures (Cathartidae) and Old World vultures (Accipitridae: Aegypiinae). These two groups provide a classic case of convergent evolution, in which morphological similarities are due to functional convergences (Hertel 1994). Six genera, *Necrosyrtes*, *Gyps*, *Sarcogyps*, *Trigonoceps*, *Torgos* and *Aegypius*, form subfamily Aegypiinae (Seibold and Helbig 1995; Lerner and Mindell 2005). Aegypiins are presently confined to Africa and Eurasia. *Necrosyrtes*, *Trigonoceps*, *Torgos* and three species of *Gyps* (*G. africanus*, *G. rueppelli*, *G. coprotheres*) only occur in Africa. *Aegypius* and *G. fulvus* are widely distributed in the Afro-Euro-Asiatic region. *Sarcogyps* is distributed in Pakistan, Yunnan, Indochina and Malay Peninsula. Of the other four species of *Gyps*, *G. himalayensis* is from central Asia to north India, *G. indicus* from Pakistan and India, *G. bengalensis* from south Asia and *G. tenuirostris* confined mainly in Himalayan foothills from Kashmir to Assam and the Gangetic plain (Dickinson 2003).

Old World vultures occur as early as the Lower Miocene in both the Old and New Worlds, and have been found commonly from the Pliocene and Pleistocene of North America and Europe (Feduccia 1996; Mlíkovský 2002). The fossil record of Miocene vultures is rather scarce. To date, three genera and four species have been excavated and described from Europe and North America. They are *Palaeohierax gervaisii* and *Palaeoborus rosatus* from the Lower Miocene of France and South Dakota, respectively, and *Palaeoborus howardae* and *Neophrontops vetustus* from the Middle Miocene of Nebraska (Brodkorb 1964; Mlíkovský 2002). Miocene vultures are poorly known in China; only two species, *Mioaegypius gui* and *Qiluornis*

taishanensis, have been reported from Jiangsu and Shandong provinces of eastern China (Hou 1984; Hou et al. 2000).

Recently, a nearly complete articulated skeleton of a large vulturid was discovered from the Late Miocene red clays in the Linxia Basin of Gansu province, northwestern China, and represents a new genus and species of aegypiine vultures. The new discovery increases our knowledge of the evolutionary history of Old World vultures and has implications for reconstructing the paleoecology of the region.

Materials and methods

The holotype and paratype are housed at Tianyu Natural Museum of Shandong Province. Comparisons with skeletons of extant falconiforms were conducted at the Zoological Museum of China, Institute of Zoology, Chinese Academy of Sciences, and the Natural History Museum of Los Angeles County, and by using published descriptions and illustrations from Jollie (1976, 1977a, b, c) and Fisher (1944, 1946). Osteological terminology follows that of Howard (1929) and Baumel and Witmer (1993); measurements are in millimeters and refer to the maximum length of the bone along its longitudinal axis.

Systematic paleontology

Class Aves (Linnaeus 1758)
Order Falconiformes (Seebohm 1890)
Family Accipitridae (Vieillot 1816)

Gansugyps gen. nov.

Type species—*Gansugyps linxiaensis* sp. nov.
Included species—Type species only.
Etymology—From the Chinese pinyin "Gansu" meaning the province where the fossil was found, and *gyps* from Greek, masculine, vulture.
Type locality and horizon—Yangwapuzijifang, Guanghe County, Gansu Province; upper Liushu Formation (Late Miocene); 7.78–6.25 Ma (Fang et al. 1997).
Diagnosis—As for the type and only species.

Gansugyps linxiaensis sp. nov.

Holotype—Preserved in dorsal view, almost complete articulated skeleton lacking the sternum and tips of both wings; the distal 2/3 of the right tarsometatarsus does not belong to the skeleton but was fabricated by the preparator of the specimen (Fig. 1). Collection number STMV002.
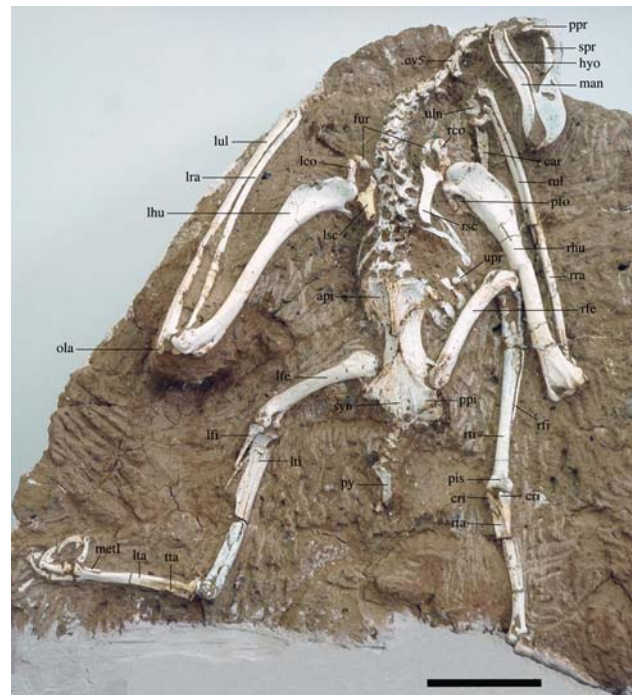
Fig. 1 The holotype of *Gansugyps linxiaensis* gen. et sp. nov. *api* Anterior part of ilium, *car* carpometacarpus, *cri* calcaneal ridge, *cv5* fifth cervical vertebra, *fur* furcula, *hyo* hyoid, *lco* left coracoid, *lfe* left femur, *lfi* left fibula, *lhu* left humerus, *lra* left radius, *lsc* left scapula, *lta* left tarsometatarsus, *lti* left tibiotarsus, *lul* left ulna, *man* mandible, *metI* metatarsal I, *ola* olecranon, *pfo* pneumatic foramen, *pis* posterior intercondylar sulcus, *ppi* posterior part of ilium, *ppr* postorbital process, *py* pygostyle, *rco* right coracoid, *rfe* right femur, *rfi* right fibula, *rhu* right humerus, *rra* right radius, *rsc* right scapula, *rta* right tarsometatarsus, *rti* right tibiotarsus, *rul* right ulna, *spr* supraorbital process, *syn* synsacrum, *tta* tubercle for M. tibialis anterior, *uln* ulnare, *upr* uncinate process. *Scale bar* 100 mm

Paratype—Partial skeleton preserved in left lateral view; the veterbral colum, the right forelimb and the right femur are missing (Fig. 2). Collection number STMV003.
Locality and horizon—Yangwapuzijifang, Guanghe County, Gansu Province; upper Liushu Formation (Late Miocene); 7.78 ~ 6.25 Mya (Fang et al. 1997).
Etymology—The fossil was found in the Linxia Basin of Gansu Province.
Diagnosis—A large-sized vulturid bird. Upper bill long, massive, strongly hooked, and more than half the total length of the skull; skull length/skull width 1.93; postorbital process well developed. Papillae of secondaries unnoticeable and restricted to the distal half of ulna. Anterior intermuscular line long and extends diagonally across the femoral shaft from the trochanteric ridge to the internal condyle. Bordering ridges of the posterior intercondylar sulcus of tibiotarsus nearly symmetrical. Terminal phalanx of digit IV longer than basal phalanx.
Differential diagnosis—The new taxon *Gansugyps* differs from extant vultures in: the ratios of skull length/skull
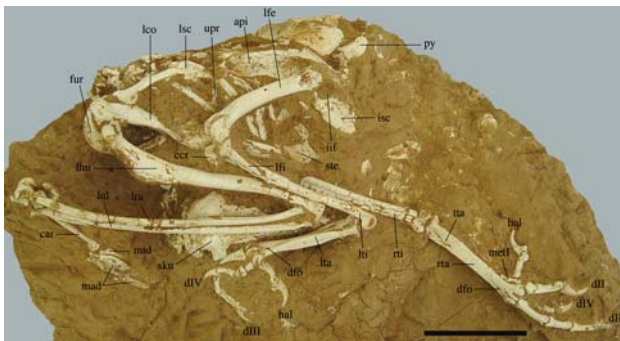
Fig. 2 The paratype of *Gansugyps linxiaensis* gen. et sp. nov. *api* Anterior part of ilium, *car* carpometacarpus, *ccr* cnemial crest, *dII* digit II, *dIII* digit III, *dIV* digit IV, *dfo* distal foramen, *fur* furcula, *hal* hallux, *iif* ilio-ischiatic foramen, *isc* ischium, *lco* left coracoid, *lfe* left femur, *lfi* left fibula, *lhu* left humerus, *lra* left radius, *lsc* left scapula, *lta* left tarsometatarsus, *lti* left tibiotarsus, *lul* left ulna, *mad* phalanges I and II of major digit, *man* mandible, *metI* metatarsal I, *mid* phalanx of minor digit, *py* pygostyle, *rta* right tarsometatarsus, *rti* right tibiotarsus, *sku* skull, *ste* sternum, *tta* tubercle for M. tibialis anterior, *upr* uncinate process. *Scale bar* 100 mm

width are 1.93 in *Gansugyps*, 2.4–2.5 in *Gyps*, 1.77 in *Trigonoceps*, 2.28 in *Necrosyrtes*, and 1.82 in *Torgos, Sarcogyps* and *Aegypius* (Hertel 1994). Furthermore, *Necrosyrtes* is characterized by the smaller size, short supraorbital process and thin bill. The supraorbital process bends down more into the orbit in *Torgos* than in *Gansugyps*. The postorbital process of *Gyps* is less developed and extends down with a pointed distal end, tubercle for M. tibialis anterior less developed, anterior proximal fossa of tarsometatarsus deeper. *Gansugyps* differs from *Aegypius* in its smaller size and relatively larger skull (Table 1). Compared to *Gansugyps*, *Sarcogyps* is peculiar in having a distinct process in the central part of the caudal margin of the orbit, length of tarsometatarsus equals that of femur, calcaneal ridges of hypotarsus shorter and lower, outer

calcaneal ridge bends laterally, hypotarsus groove broader and shallower.

Gansugyps differs from *Mioaegypius* in: smaller size, calcaneal ridges of hypotarsus developed, tubercle for M. tibialis anterior and the wing of inner trochlea more distinct. *Gansugyps* is different from *Qiluornis* in: femur longer than tarsometatarsus, external condyle of femur well-developed and more complicated, intertrochlear notches deep.

Dimensions (in mm)—See Table 1.

Description and comparisons—The skull (Fig. 1) is nearly completely preserved and exposed in dorsal and right lateral views. It differs from that of New World Vultures in morphology. Skull shape index calculated as skull length/skull width is 1.93 in *Gansugyps*, 2.4–2.5 in *Gyps*, 1.77 in *Trigonoceps*, 2.28 in *Necrosyrtes*, and 1.82 in *Torgos, Sarcogyps* and *Aegypius* (Hertel 1994). The cranium is flattened above and rounded behind in lateral view; the rounding of the cranium produces a posterior bulge extending slightly beyond the dorsal margin of the foramen magnum. As in most extant aegypiins, the massive beak is unusually long (more than 1/2 the total length of the skull) and high, with an equal height over most of its length and a deeply hooked tip. The external naris, obstructed by ossification in the lateral vestibular wall, is small and roughly oval in shape with the anterior end uppermost, a feature of extant vulturines, whereas it is large and triangular in other accipitrids (Jollie 1977b). The prefrontal is free and has a large, caudally projecting supraorbital process. The supraorbital process bends down more into the orbit in *Torgos*, and it is much shorter in *Necrosyrtes*. The superciliary that articulates with the tip of the supraorbital process, usually found in most of the accipitrids including *Aquila* and *Haliaeetus*, is absent in the fossil vulture and extant aegypiins. The postorbital process, as in *Aegypius*, is long, well developed and roughly triangular in shape, whereas it

Table 1 Measurements (mm) of selected elements of *Gansugyps linxiaensis* in comparison with *Aegypius monachus*

	Gansugyps linxiaensis		*Aegypius monachus* (n = 2)
	STMV002	STMV003	
Length of skull	145		151 (151, 151)
Width of skull	75	–	83 (81, 85)
Length of bill	79	–	83 (83, 83)
Length of mandible	123	–	123.5 (123, 124)
Length of scapula	–	95 (left)	118.5 (119, 118)
Length of coracoid	–	91 (left)	110.5 (109, 112)
Length of humerus	222 (left), 233 (right)	221 (left)	273.5 (267, 280)
Length of ulna	285 (left)	273 (left)	348.5 (338, 359)
Length of carpometacarpus	–	102 (left)	143 (141, 145)
Length of femur	127 (left), 130 (right)	123 (left)	140.5 (138, 143)
Length of tibiotarsus	174 (right)	172 (left)	208.5 (206, 211)
Length of tarsometatarsus	109 (left)	113 (right), 112 (left)	132 (130, 134)

is relatively short and stout in *Sarcogyps*, and short and thin with a pointed end in *Gyps*. Similar to most of the aegypiins, such as *Aegypius*, *Sarcogyps* and *Necrosyrtes*, the postorbital process of *Gansugyps* extends anterolaterally, but it projects down from the posterior border of the orbit in *Gyps*. The otic process and articular process of the quadrate are well shown in the lateral and posterior views, respectively. The mandibular ramus is deep and lacks the posterior fenestra; it is about 85% the length of the skull.

In the holotype, the cornu branchiale of the hyoid apparatus is represented by a slender osseous bar below the mandible.

The vertebral column of the holotype is preserved in articulation and 19 free presacral vertebrae can be discerned; the vertebrae series becomes elongate to broad from anterior to posterior (Fig. 1). The spinous process of the axis is high. The third cervical vertebra has an osseous bridge from the processus transverses to the articularis caudalis (Mayr and Clarke 2003). The fifth to eighth cervical vertebrae are more strongly elongate than the others behind the eighth, and the postzygapophysis is significantly longer than the prezygapophysis. The spinous processes of the 13th–19th vertebrae are much higher and form a marked ridge. Being preserved in dorsal and lateral views, the number of vertebrae in the synsacrum cannot be counted. Five free caudal vertebrae can be discerned.

Pectoral girdle. It is clear from the dorsal view of the holotype, and the left lateral view of the paratype that the three components of the pectoral girdle are preserved in their natural position. The coracoid is robust with the head bends forward. The clavicular facet projects anteroventrally; the scapular facet is cup-like which is in concordance with the presence of a distinct inflated tuberculum coracoideum on the scapula as in most Accipitridae. The exact shape of the sternal end cannot be discerned.

The scapula appears as a curved blade-shaped bone. The acromial process (furcular articulation) is longer and truncated obliquely, forming an apex with a more pointed tip (Fig. 1). The coracoid articulation is marked by a well-defined, inflated projection.

The furcula is arc-shaped in lateral view. The diaphysis is flat craniocaudally; the extremitas omalis expands greatly, attenuates and points posteriorly. There is a distinct gap between the tip of extremitas omalis and the acromial process of the scapula (Figs. 1, 2), but in large eagles, such as *Aquila* and *Haliaeetus*, the tip of the clavicle is in contact with that of the scapula (Jollie 1977b).

The sternum is partly exposed in the paratype and allows the recognition of only a few osteological details, however a large fenestra is visible in the distal end.

Forelimb. The humeri of the holotype are exposed in anconal view and have a slightly sigmoid profile in general (Fig. 1); they are more elongated and exceed the tibiotarsus in length. The humeral head is well developed; the capital groove between the prominent internal tuberosity and the head is deep. There is an obvious large pneumatic foramen on the anconal surface of the proximal humerus. Both the bicipital crest and the deltoid crest are less expanded and proportionally short, measuring about 1/5 and 1/4 of the humerus, respectively, whereas in extant birds of prey, the deltoid crest is nearly 1/3 of the humerus (Mayr 2006). The distal end of the humerus is expanded and less angular. The internal condyle projects distally slightly than the adjacent processes, and the entepicondylar prominence is nearly rounded. External tricipital groove, internal tricipital groove and olecranal fossa are slightly indicated. Ectepicondylar prominence projects as a narrow plate.

The ulna is the longest limb element. In the anconal surface of the proximal end, there is an obvious pneumatic fenestration between the olecranon and the tricipital attachment. The anconal papillae for the secondaries are less prominent than that of extant vultures, and only occur at the distal half (six protuberances can be palpated), but in large-sized vultures, 16–17 anconal papillae can usually be discerned along the entire length of the ulna and are situated on a more conspicuous definite ridge.

The radius is nearly 1/2 the width of the ulna and shows two flexures: one toward the anterior in the proximal half and another curves posteriorly in the mid-shaft, resulting in a spindle-like space between the proximal halves of ulna and radius (Fig. 1).

The skeletal elements of the hand are partially preserved in the holotype and the paratype. The ulnare (cuneiform) is visible in the right hand of the holotype. The minor metacarpal is relatively robust compared to that of living vulturid birds. The phalanx of the minor digit is small and vestigial, while phalanx I of the major digit is broad and flat (Fig. 2).

Pelvic girdle. The posterior part of the synsacrum turns more gradually (not abruptly) ventrally posterior to the acetabulum and fuses to the ilium as in extant aegypiins. There is no distinct crack along the line of synsacrum-ilium junction. The medial dorsal crests of the anterior ilia are raised as high above the level of the intervening vertebral column and lie in contact anteriorly (Fig. 1). A raised crest provides a stronger point of origin for the iliotibialis and iliofibularis muscles. The anterior half of the face of the ilium reflects the steeper inclination, and shows a horizontal plane only in the anterolateral corner. The posterior dorsal iliac crests, viewed from the lateral, curve ventrally more gently toward their fusion with the ischium than in other accipitrids, and present a nearly straight and parallel outline in dorsal view (Figs. 1, 2).

The ischium extends farther posteriorly than in *Aquila* and other accipitrids, and faces upwards and outwards. The ilio-ischiatic foramen (Fig. 2) is rounded and relatively

small, and lies in the proximal third of the ischium, but it is nearly ovoid-shaped and occupies the proximal half of the ischium in extant vultures.

Hindlimb. The femora are exposed in anterior and posterior-external views in the holotype, and lateral view in the paratype. It is stout and longer than tarsometatarsus. The shaft is nearly circular in cross-section and slightly bent anteriorly. The trochanteric ridge is better developed and markedly projects cranially forming a crescent-shaped flange. The anterior intermuscular line is long and extends diagonally across the femoral shaft from the trochanteric ridge to the internal femoral condyle, whereas it is relatively short, arises medial to the ridge and extends lateral to the midline to the proximal 1/2–3/5 shaft in most accipitrids including vultures. The distal femur shows more details than the proximal. The rotular groove is wide and deep with high ridges bordering it, and contains a small patella; the inner ridge is a little longer and higher than the outer one. A pronounced sturdy process protruding from the lateral surface of the fibular condyle provides attachment for the flexor muscles. The fibular groove, bordered by the external condyle and the fibular condyle, is deep and articulates with the fibular head. The popliteal area is broad and deep.

The tibiotarsus is about 1.5 times the length of the femur; it is wide, straight and flares at the distal end (Fig. 2). The cnemial crests are low and short. The fibular crest is restricted to the proximal 2/5 of the shaft and is represented by a distinct long bony edge. The external condyle is nearly rounded from the lateral view. It can be discerned from the holotype that the posterior intercondylar sulcus is broad and shallow. The ridges bordering the sulcus are nearly symmetrical (Fig. 2), whereas the medial ridge is oblique, lower and longer than the lateral one in extant aegypiins. The right tibiotarsus of the paratype is exposed in anterior view, but unfortunately it cannot be determined if there is an ossified pons supratendineus for the passage of the tendons of the extensor muscles of the toe, because the distal end of the tibiotarsus was crushed to some extent. The fibula is needle-like and measures about 2/3 the length of the tibiotarsus, and the head is enlarged anteroposteriorly (Figs. 1, 2).

The tarsometatarsus is robust and similar to the tibiotarsus in width. The shaft is nearly straight and shows much less expansion at the distal end, with the trochleae flaring more gradually. Proximally, the level of the inner cotylar is slightly higher than that of the outer cotylar as viewed from in front, a feature of extant vulturines (Jollie 1977b); the opposite condition occurs in most accipitrids, including large eagles like *Aquila* and *Haliaeetus*. The anterior aspect of the proximal fourth has a shallow but distinct proximal fossa, and just distal to it, has a developed elongated M. tibialis anterior tubercle lying laterally to the midline

(Figs. 1, 2). The frenula scars are absent in this fossil vulture, as in extant vulturines (Jollie 1977b). In posterior view, the hypotarsus bears two protruding calcaneal ridges, which are separated by a deep groove (Fig. 1). The morphology of the proximal hypotarsus provides a better support and maintenance to the flexor tendons when they pass through. Similar to extant aegypiins, the inner (medial) calcaneal ridge of *Gansugyps* is a little higher than the outer (lateral), and shifts laterally to fuse with the outer process at the distal ends, thus forming a nearly V-shaped outline; the distal connection of calcaneal processes gives rise to a low rounded ridge which extends down the shaft and fades into the outer posterior margin. However, there is no distal connection in calcaneal ridges in accipitrids except in Aegypiinae (Jollie 1977b). The outer proximal foramen is distinct and lies on the slope of the outer calcaneal ridge in the holotype (Fig. 1). The distal end of the tarsometatarsus bears three articular trochleae that are separated by deep notches. The inner and middle trochleae of *Gansugyps* are equal in length to those of *Aegypius*, *Trigonoceps*, *Torgos* and *Sarcogyps*, but different from that of *Necrosyrtes* whose middle trochlea exceeds the inner one and extends furthest. The trochlea for digit II (inner trochlea) is broad with a plantarly projecting wing-like flange, and the distal contour is nearly straight (*Aquila* slightly indented near the tip). Trochlea metatarsi III (middle trochlea) has a distinct groove between two rims of identical size (in *Aquila*, the external edge is noticeably more developed antero-posteriorly than the internal edge), and the dorsal surface is higher than that of the second and the fourth trochleae. The trochlea for digit IV (outer trochlea) is the smallest and deflects laterally; it bears a small plantarly projecting wing on the outer edge. The paratype shows the occurrence of a distal foramen lying proximal to the incision between the trochleae for the third and fourth toes. The lateral aspect of the shaft is convex anteriorly and posteriorly, thus giving it a long, roughly spindle-like shape (Fig. 2). Metatarsal I can be discerned in the holotype and paratype; it is about 1/6 the length of the tarsometatarsus and points posteriorly.

Digit I (Fig. 2) is nearly as long and robust as digit II. Phalanx 1 arches dorsally slightly, and it can be seen that the groove for the flexor tendons on the plantar view is well developed. The flexor attachment (tuberculum flexorium) on the proximal of the claw is sturdy and long. Two canals, one at the base of the tuberculum flexorium and another at the medial surface between the tuberculum flexorium and extensorium (Mayr and Clarke 2003), are visible in the paratype as in extant aegypiins. The relative shortness of digit II is due principally to a greatly abbreviated phalanx 1, and the stout proximal phalanx measures about 1/3 the length of phalanx 2. The claw of the second toe is as strong as that of the first toe, and exceeds those of the other

Table 2 Skeletal differences between Aegypiinae and other accipitrids

Aegypiinae	Other accipitrids
1. Usually very large-sized	Medium- to large-sized (*Aquila*, *Haliaeetus*)
2. Upper bill relatively massive and long (more than half of the skull length)	Upper bill usually compressed, short (less than 40% of the skull length)
3. Obstructed by ossification in the lateral vestibular wall, external naris small and oval-shaped	External naris large and roughly triangular in shape
4. Superciliary bone absent	Superciliary bone present in most genus
5. The level of inner cotylar on the tarsometatarsus slightly higher than that of the outer cotylar	The outer cotylar surface higher than the inner one
6. The inner and outer calcaneal ridges of the hypotarsus fuse at the distal ends	The inner and outer calcaneal ridges not fused
7. The outer proximal foramen of the tarsometatarsus lies laterally or on the slope of the outer calcaneal ridge	The outer proximal foramen is on the medial side of the outer calcaneal ridge in the bulk of accipitrids
8. Frenula scars absent on the anterior aspect of the proximal tarsometatarsus	Frenula scars present

Primarily from Jollie (1977a, b, c)

anterior toes in size. The third toe is the longest of the four toes, but shorter than tarsometatarsus. The basal and terminal phalanges are nearly the same length, and the second phalanx is shortest. The second and third phalanges of digit IV are greatly shortened; phalanx 4 is two times longer than phalanx 1, whereas in most aegypiins, the basal phalanx of the fourth digit is slightly longer than or nearly equal to the terminal one. The profile of the pedal claws in *Gansugyps* matches that of extant vultures, but is moderate in size and curvature compared with that of large eagles.

Discussion

The diurnal birds of prey (Falconiformes), which are characterized by several external morphological characters (hooked beak and curved talons) and internal characters (large and round ilioischiatic fenestra, deep ilioischiatic plate, strongly curved pubes; Cracraft 1981), are made up of five families of living birds: Cathartidae, Sagittariidae, Accipitridae, Pandionidae and Falconidae (Gill 1994). Cathartidae and some species in Accipitridae are very large-sized scavengers, but differ greatly in osteology. The morphology of *Gansugyps* clearly indicates that it is a member of the Accipitridae, and the supporting features are: (1) well-developed supraorbital process; (2) nostril not perforate; (3) mandible without a posterior fenestra; (4) hypotarsus represented by two longitudinal calcaneal processes; (5) a shallow proximal fossa and one M. tibialis anterior tubercle in the anterior aspect of the tarsometatarsus; and (6) the basal phalanx of the second digit and the second and third phalanges of the fourth digit strongly abbreviated. Among Accipitridae, Aegypiinae is peculiar and differs from other accipitrids in many aspects,

especially the morphology of the skull and tarsometatarsus (Table 2). With a comparison of the differences in the skeleton, *Gansugyps* presents typical characteristics of aegypiines (see description and Table 2) and represents a new genus of this subfamily. Features which set *Gansugyps* apart from all other genera of Aegypiinae are as follows: skull shape index is 1.93; postorbital process is well developed and extends more laterally; papillae of secondaries not very prominent and restricted to the distal half of ulna; anterior intermuscular line long and extends diagonally across the femoral shaft from the trochanteric ridge to the internal condyle; bordering ridges of the posterior intercondylar sulcus of the tibiotarsus nearly symmetrical; and terminal phalanx of digit IV longer than basal phalanx.

Gansugyps is the third genus of fossil vultures to be described from China. Of the other two genera, *Mioaegypius* is from the Early Miocene Xiacaowan Formation of Jiangsu Province and is represented only by a 140-mm-long left tarsometatarsus (Hou 1984), and *Qiluornis* from the Middle Miocene Shanwang Formation of Shandong Province is known by an incomplete individual including partial vertebral column, pelvis and complete right hindlimb. *Gansugyps* is very different from and more advanced than *Mioaegypius* and *Qiluornis* (see Differential diagnosis), but closely resembles modern Old World vultures in morphology, especially *Aegypius*. *Gansugyps* is presumably an arboreal bird in possessing a relatively longer femur and shorter tarsometatarsus (Berger 1952; Dilger 1956; Osterhaus 1962). Such an interpretation is also supported by the fact that the basal phalanges are relatively shorter than the distal phalanges (Fisher 1946). The discovery of this typical Old World vulture indicates that the evolutionary history of aegypiines might be traced back before the Miocene, longer than the suggested Pliocene

(Jollie 1977c) or Pleistocene ages (Seibold and Helbig 1995).

The palaeoenvironment of Linxia Basin was probably tropical semiarid savanna with strong seasonal variation in the Late Miocene (Deng 2004). Open and semi-open areas provide better thermals (Gavashelishvili and McGrady 2006), and with the help from thermals *Gansugyps* might have soared effortlessly for hours while searching visually for prey. The mammalian fauna of this region was dominated by a diverse assemblage of large herbivores, including hipparionine horses, rhinoceros, proboscideans, cervines, and bovines during the Late Miocene (Deng et al. 2004; Deng 2005). We assume that *Gansugyps* fed on carcasses of large plains-dwelling herbivores. As no other scavenging bird is known from this region, it is reasonable to assume that *Gansugyps* filled that niche. The palaeoenvironment and mammalian fauna of Linxia Basin in the Late Miocene broadly resemble that of the extant African savanna. From the detailed studies on competitive interactions between avian scavengers in the African plain (Petridges 1959; Kruuk 1967; Houston 1975), and the suggestion of Jollie (1977c) that the radiation of aegypiins is a result of the abundance of large herbivores, we expect that some other new vulturid birds of different size will be excavated from Linxia Basin and will constitute a guild of sympatric avian scavengers with *Gansugyps*.

Zusammenfassung

Ein neuer Altweltgeier (Falconiformes: Accipitridae) aus dem Miozän der Gansu Provinz im Nordwesten Chinas

In der Liushu Formation im Linxia Becken im Nordwesten Chinas wurde ein großes und nahezu vollständiges Fossil eines Geiers aus dem späten Miozän gefunden. Es ist das beste und vollständigste Fossil eines Geiers, das je gefunden wurde. Wir schlagen vor, die neue Gattung und Art *Gansugyps linxiaensis* der Familie Accipitridae zuzuordnen. Die Morphologie und die Proportionen der Extremitäten lassen vermuten, dass es sich um einen hauptsächlich Baum bewohnenden und segelnden Altweltgeier handelte. Die Art ist höher entwickelt als die zwei anderen bekannten chinesischen Geier aus dem Miozän. Das neue Fossil erweitert unser Wissen über die Evolutionsgeschichte der Geier und hat Konsequenzen für die Rekonstruktion der Paleoökologie dieser Region.

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