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TWO OLD WORLD VULTURES FROM THE MIDDLE PLEISTOCENE OF NORTHEASTERN CHINA AND THEIR IMPLICATIONS FOR INTERSPECIFIC COMPETITION AND BIOGEOGRAPHY OF AEGYPIINAE

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ABSTRACT—Two new fossil crania of Old World vultures (Accipitridae, Aegypiinae), from the middle Pleistocene Jinniushan site of Liaoning Province, northeastern China, were studied. A new species of *Aegypius*, *A. jinniushanensis*, is erected and characterized by possessing a less developed processus zygomaticus and processus suprameaticus, as well as a relatively larger condylus occipitalis, compared with *A. monachus*. Another specimen, assigned to *Torgos*, is the first record of this genus from outside Africa. The presence of two large vultures, apparently in the same feeding group, in the Jinniushan faunal assemblage suggests that there were more opportunities for interspecific competition among scavengers in the middle Pleistocene of northeastern China than at present. By analogy with phylogenetically related modern vultures, we suggest that niche differentiation between the two extinct species may have reduced the degree of competition between them. The disappearance of the genus *Torgos* from northeast China might be the result of the Pleistocene extinction of a suite of large mammalian herbivores, and the loss of grassland and savannah from this region.

INTRODUCTION

Aegypiinae, the Old World vultures, is a monophyletic group containing six genera (*Necrosyrtes*, *Gyps*, *Sarcogyps*, *Trigonoceps*, *Torgos*, and *Aegypius*), presently confined in Africa and Eurasia (Seibold and Helbig, 1995; Lerner and Mindell, 2005). *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 the 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* is confined mainly to the Himalayan foothills from Kashmir to Assam and the Gangetic plain (Dickinson, 2003). In some regions, such as the Indian subcontinent, East Africa, and South Africa, up to six species of vultures coexist (Petrides, 1959; Grossman and Hamlet, 1964; Kruuk, 1967; Houston, 1975).

Sympatric vultures are divided into three different feeding groups, based mainly on observations that reveal marked differences in morphology, behavior, and ecology to reduce interspecific competition for food. Rippers (tearing; *Torgos*, *Aegypius*, and *Trigoniceps*) feed mainly on tough materials such as skin and tendons, and are characterized by large body mass, great adductor index, and a large, wide skull. Gulpers (pulling; griffon vultures) have a long, bare neck, intermediate beak strength, narrow skull, and primarily feed on the soft viscera and meat. *Necrosyrtes* and *Neophron*, a genus of Gypaetinae, belong to the third group, the scrappers (pecking), which are smaller than the other vultures and have thin, slender bills adapted to peck smaller scraps on and around the carcass (Kruuk, 1967; Hertel, 1994).

Fossil records of Old World vultures occur in both the Old and the New Worlds as early as the early Miocene and become more frequent in the Pleistocene (Feduccia, 1996; Table 1). Compared with the Old World, the New World has an unexpectedly diverse and rich fossil component of Aegypiinae, especially *Neophrontops*, which is represented by six species spanning the late Miocene to the late Pleistocene, and thus was a relatively successful group. The earliest records of extant species of Aegypiinae are from Pleistocene sites; among them, *Aegypius monachus* is the most widespread, occurring in 10 Pleistocene sites distributed in Spain, Azerbajan, Austria, Bulgaria, Belgium, Russia, Israel, Italy, Greece, France, and Portugal; followed by *Gyps fulvus* and *Neophron percnopterus* (see Tyrberg, 1998). There have been no reports of Pleistocene vultures from China until now.

The fossils we describe here are two well-preserved crania from the middle Pleistocene Jinniushan site of northeastern China, dated to 260,000 B.P., and represent two new records of aegypiins. Our findings enhance the relatively poor fossil record of aegypiins in the Old World, increase our knowledge of the evolutionary history of Old World vultures, and have implications for interspecific competition between sympatric fossil scavengers and biogeography of the subfamily Aegypiinae.

MATERIALS AND METHODS

The fossil materials, which were excavated from layer 8 of the Jinniushan limestone cave (Lü, 2003) in 1987 and 1994 by a group from the School of Archaeology and Museology at Peking University and the Cultural Relics and Archaeology Institute of Liaoning Province, are housed in the School of Archaeology and Museology, Peking University, China. Osteological terminology follows that of Baumel and Witmer (1993) and Howard (1929). In order to describe and compare the shape of

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TABLE 1. Fossil records of extinct Old World vultures.

Species	Range	Age	Materials	Literature
Palaeoborus rosatus	South Dakota	lower Miocene	Ulna	Miller and Compton, 1939
Palaeoborus howardae	Nebraska	middle Miocene	Distal tarsometatarsus	Brodkorb, 1964
Palaeoborus umbrosus	New Mexico	lower Pliocene	Nearly complete skeleton	Brodkorb, 1964
Neophrontops vetustus	Nebraska	middle Miocene	Partial humerus	Wetmore, 1943
Neophrontops dakotensis	South Dakota, Oregon	lower and middle Pliocene	Partial humerus	Compton, 1935
Neophrontops slaughteri	Idaho, Florida	upper Pliocene	Distal tibiotarsus, mandible, and limb bones	Feduccia, 1974; Emslie, 1998
Neophrontops vallecitoensis	California	middle Pleistocene	Distal tarsometatarsus	Howard, 1963
Neophrontops americanus	California, New Mexico, Wyoming	early Miocene to upper Pleistocene	Limb bones	Miller, 1916; Emslie, 1985
Neogyps errans	California, Nevada, Mexico	upper Pleistocene	Tarsometatarsus	Miller, 1916
Neophrontops ricardoensis	California	middle Miocene	Partial articulated skeleton	Rich, 1980
Neophrontops sp.	Arizona	late Miocene to early Pliocene	Coracoid, limb bones	Bickart, 1990
Arikarornis macdonaldi	South Dakota	lower Miocene	Distal tibiotarsus	Brodkorb, 1964
Palaeohierax gervaisii	France	lower Miocene	Tarsometatarsus	Brodkorb, 1964
Gyps melitensis	Monaco, Austria, France, Malta	middle–late Pleistocene	Femur, tibiotarsi, tarsometatarsi, pedal phalanges, cervical vertebrae	Brodkorb, 1964; Tyrberg, 1998; Marco, 2007
Mioaegypius gui	China	early Miocene	Tarsometatarsus	Hou, 1984
Gansugyps linxiaensis	China	late Miocene	Nearly complete skeleton	Zhang et al., 2010
Aegypius prepyrenaicus	Spain	upper Pleistocene	Ulna	Hernánde, 2001

the skull, six measurements (Table 2) were taken with a caliper to the nearest 0.1 mm, primarily following measurements defined by Fisher (1944): cranial length, distance from frontonasal hinge to supraoccipital; cranial height, vertical distance between anterior end of basitemporal plate and top of cranium; cranial width, maximum width across processus postorbitalis; temporal width, distance between fossae temporalis; opisthotic width, distance across processus paroccipitalis; postcranial height, vertical distance between processus paroccipitalis and midpoint of crista nuchalis transversa.

Comparisons with skeletons (M, male; F, female) of extant accipitriforms are based on the following USNM (National Museum of Natural History, Smithsonian Institution) specimens: *Torgos tracheliotus*, 347597M, 19990, 320977M, 321827F; *Trigonoceps occipitalis*, 320859F, 347358; *Aegypius monachus*, 18223, 428040F, 289569; *Gyps himalayensis*, 19534M; *Gyps coprotheres*, 561314; *Gyps africanus*, 587405, 19992, 431696, 430826M, 430014M, 19991, 431403F, 587404M, 431591F, 430016M; *Gyps fulvus*, 227051F; *Neophron percnopterus*, 17835, 610499; *Necrosyrtes monachus*, 614886, 291442F, 18894, 620646, 291440M, 291443F, 291441F, 620645; *Gypaetus barbatus*, 345684F, 17834, 19383; *Gypohierax angolensis*, 224820, 291078F, 226143, 18892, 291316M.

SYSTEMATIC PALEONTOLOGY

Class AVES Linnaeus, 1758
Order ACCIPITRIFORMES Voous, 1973
Family ACCIPITRIDAE Vieillot, 1816
Subfamily AEGYPIINAE Peters, 1931
Genus *AEGYPIUS* Savigny, 1809

Remarks—We assign the new specimen to the Aegypiinae as opposed to other accipitriforms by the following combined characters: large size, the zona flexoria craniofacialis closer to the

TABLE 2. Measurements (mm) of two fossil specimens and different species of Old World vultures.

	Cranial length	Cranial width	Cranial height	Opisthotic width	Temporal width	Postcranial height
Torgos sp.	72.6	>72.7	46.8	>50.2	56.4	33.2
Aegypius jinniushanensis	66.2	79.2	45.9	51.6	57.8	38.3
Aegypius monachus (n = 4)	70.4	81.0	46.4	52.2	57.4	36.8
	65.8–72.7	78.8–82.6	44.0–47.5	50.4–53.9	54.8–59.3	34.3–40.7
Torgos tracheliotus (n = 4)	69.1	80.9	48	52.6	58.2	38.1
	64.5–73.4	76.4–83.5	46.5–49.7	50.4–55.5	56.4–61.0	35.6–39.2
Trigonoceps occipitalis (n = 2)	66.1	71.1	45.8	47.6	52.6	31.1
	63.3, 68.8	69.0, 73.2	46.1, 45.5	46.7, 48.5	52.1, 53.1	28.1, 34.1
Gyps coprotheres (n = 1)	69.3	54.8	38.4	41.5	43.4	37.8
Gyps africanus (n = 10)	62.6 ± 2.86	49.4 ± 2.62	35.7 ± 1.61	35.8 ± 2.69	38.9 ± 2.03	34.5 ± 2.58
	59.8–69.6	44.8–55.4	32.8–38.7	30.6–41.2	35.7–43.4	29.3–38.3
Gyps himalayensis (n = 1)	68.4	58.3	40.3	42.3	46.0	39.2
Gyps fulvus (n = 1)	70.3	54.9	39.0	40.6	42.3	38.5
Neophron percnopterus (n = 2)	52.3	47.9	34.4	29.1	39.2	23.3
	51.6, 52.9	47.8, 47.9	33.0, 35.8	29.1, —	39.1, 39.2	23.3, —
Necrosyrtes monachus (n = 8)	52.2 ± 1.97	46.3 ± 2.07	32.4 ± 0.76	28.6 ± 1.36	37.1 ± 2.69	25.8 ± 1.00
	48.6–54.7	44.0–49.8	31.1–33.3	26.7–30.7	35.2–40.2	24.1–26.8
Gypaetus barbatus (n = 3)	69.7	68.3	41.4	48.5	52.3	31.0
	67.4–71.2	66.5–71.4	41.3–41.6	47.4–49.3	51.2–53.3	29.6–31.9
Gypohierax angolensis (n = 5)	53.2 ± 1.23	44.9 ± 0.2	32.1 ± 1.15	23.1 ± 1.32	34.6 ± 0.24	22.9 ± 0.34
	51.4–54.6	44.6–45.1	31.0–33.7	21.8–24.6	34.3–34.9	22.7–23.5

processus postorbitalis, a narrower and longer triangle-shaped lamina parasphenoidalis, and a flared ala parasphenoidalis (Rich, 1980). Among aegypiins, the new fossil material is clearly referable to *Aegypius* in having a large and wide cranium; long, well-developed, and lateroventrally projecting processus postorbitalis; broad fossa temporalis; distinct crista temporalis marking the gently convex surfaces of the dorsal and lateral aspects of the cranium; and moderate development of processus lateralis parasphenoidalis.

AEGYPIUS JINNIUSHANENSIS, sp. nov.
(Figs. 1A–C, 2A)

Holotype—Cranium, collection number 94. L. J. A. VIII-13.D-11.

Locality and Horizon—The specimen was excavated from layer 8 of the limestone cave at Jinniushan site near the town of Yinkou in Liaoning Province, northeastern China (N40°34′40″,

E122°26′38″); middle Pleistocene, 260 kyr (Lü, 2003; Rosenberg et al., 2006).

Etymology—The specific name is derived from the fossil locality.

Measurements—See Table 2.

Diagnosis—Differs from *Aegypius monachus*, its only congener, in the large cranium with less developed processus zygomaticus and processus suprameaticus of the squamosal, and a relatively larger condylus occipitalis.

Description and Comparisons—The cranium, except the posterior left side, is well preserved. On the dorsal surface, the bone behind the zona flexoria craniofacialis is concave as in *Aegypius monachus*. The nasal is not preserved, but the posterior tip of the nasal process of the premaxilla articulates with the frontal. The facies articularis frontonasalis is distinctly visible on both anterior sides of the frontal (Fig. 1C), indicating the presence of an unfused prefrontal (or lacrimal) in this species, as in other aegypiins. The lateral edges of the frontals, which form the supraorbital crests, are almost straight parallel lines (Fig. 1B). Compared
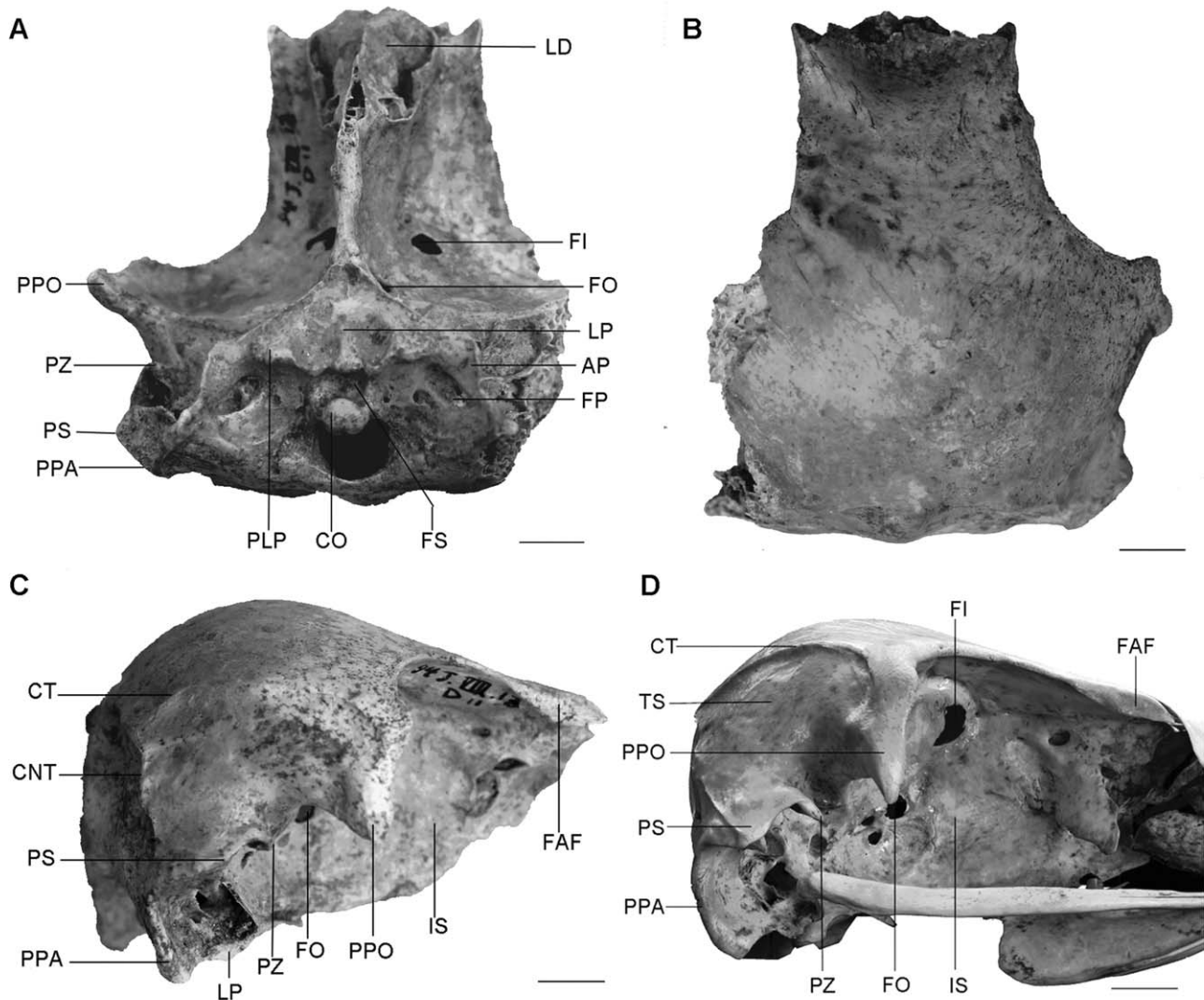

FIGURE 1. Ventral (**A**), dorsal (**B**), and lateral (**C**) views of the cranium of *Aegypius jinniushanensis* sp. nov. (94. L. J. A. VIII-13.D-11), and lateral view (**D**) of the cranium of *A. monachus* (USNM 18223). **Abbreviations**: **AP**, ala parasphenoidalis; **CO**, condylus occipitalis; **CNT**, crista nuchalis transversa; **CT**, crista temporalis; **FAF**, facies articularis frontonasalis; **FI**, fonticuli interorbitales; **FO**, foramen opticum; **FP**, fossa parabasalis; **FS**, fossa subcondylaris; **LD**, lamina dorsalis; **LP**, lamina parasphenoidalis; **IS**, interorbital septum; **PLP**, processus lateralis parasphenoidalis; **PPA**, processus paroccipitalis; **PPO**, processus postorbitalis; **PS**, processus suprameaticus; **PZ**, processus zygomaticus; **TS**, temporal scar. Scale bars equal 1 cm. (Color figure available online.)

with large eagles such as *Aquila* and *Haliaeetus*, the dorsal and caudal edges of the orbit nearly meet at right angles in *A. jinniushanensis*, as opposed to a more obtuse angle in the eagles. The processus postorbitalis forms the caudoventral border of the orbit; as in *A. monachus*, *Trigonoceps*, and *Torgos*, it is long, well developed, and roughly triangular in shape, whereas it is relatively short and stout in *Sarcogyps*, and short and thin with a sharp-pointed end in *Gyps*. Compared with *Trigonoceps*, *Torgos*, *Gyps*, *Neophron*, and *Necrosyrtes*, the processus postorbitalis extends more laterally rather than ventrally in *A. jinniushanensis* and some specimens of *A. monachus*. The processus postorbitalis provides an attachment point for the postorbital ligament and for part of the adductor musculature of the mandible (musculus [M.] adductor mandibulae externus rostralis temporalis and M. adductor mandibulae externus rostralis lateralis; Richards and Bock, 1973). It has been suggested that its degree of development may correlate with the size of M. adductor mandibulae externus rostralis temporalis, a muscle that adducts the mandible and probably also retracts the maxilla (Richards and Bock, 1973).

The processus zygomaticus of the squamosal is short, stout, and extents ventrally, so that the tips of processus postorbitalis and processus zygomaticus are not in contact. Another process of the squamosal, processus suprameaticus, which forms part of the cotyla for the squamosal capitulum of the quadrate bone and contributes to the upper boundary of the external acoustic meatus, is less protrudent with a rounded outline, compared with that of *A. monachus* (Fig. 1C, D). These two processes in *Aegypius*, *Trigonoceps*, and *Torgos* are well developed and more protrudent, whereas in *Gyps* and *Necrosyrtes*, the processus zygomaticus is relatively thin and long and extends more anteriorly than ventrally, and the processus suprameaticus is less developed and roughly linear. The outline of the squamosal in lateral view differs greatly in *A. jinniushanensis* and different extant species of aegypiins. The convexity of the zig-zag lateral border of the squamosal is the sharpest in *A. monachus*, moderate in *Torgos* and *Trigonoceps*, gentle in *A. jinniushanensis*, and least in *Gyps* and *Necrosyrtes*. The presence of a vertical triangular lamella ventral to the processus suprameaticus indicates that the otic and squamosal capitula of the quadrate are separate, although the quadrate is not preserved. An articular facet for the otic capitulum is discernable in the opisthotic.

The fossa temporalis (temporal fossa) is relatively broad, mainly because of the well-developed and laterally projected processus postorbitalis. The dorsal and caudal parts surrounding the fossa present a distinct but shallow excavation known as the temporal scar; the crista temporalis (temporal crest) and the lateral part of crista nuchalis transversa bound the upper and rear margins of the scar, respectively. The two crests are sharp and most evident in *A. jinniushanensis*, *A. monachus*, and *Torgos*. In *Gyps*, the fossa temporalis and the caudal part of the scar are broader and deeper, respectively, than in *Aegypius*, *Torgos*, and *Trigonoceps*, but the upper part of the scar is more restricted. The fossa temporalis and the scar provide the insertion for M. adductor mandibulae externus temporalis; the size and depth of the fossa are specifically related to the manner of feeding (Fisher, 1944). The processus paroccipitalis is well preserved on the right side, and forms the caudal wall of the ear. The process of the new fossil is as thick and flared as in *Aegypius* and *Torgos*, so differing from the thin process in other aegypiin species. In particular, the process is least expanded and projects more caudally than laterally in *Gyps*. The septum interorbitale is well preserved with a big and nearly rounded foramen opticum in its caudal part and smaller fonticuli interorbitales in the upper part of the septum.

In ventral view (Fig. 1A), the lamina dorsalis shows as a marked depression surrounded laterally and caudally by highly raised margins. There is no occurrence of the sulcus nervi olfactorii. The lamina parasphenoidalis more resembles a right-angled triangle in profile, with the apex directed anteriorly and the central part a little concave. The processus lateralis parasphenoidalis is stout. The height of this process is high in *Gyps*, moderate in *A. jinniushanensis*, *A. monachus*, *Torgos*, and *Trigonoceps*, and low in *Necrosyrtes* and *Sarcogyps* (Rich, 1980). The ala parasphenoidalis is well developed and extends laterocaudally, forming part of the margin of the external acoustic meatus. The condylus occipitalis (occipital condyle) of the new species is bigger and broader than in all extant species. The incisura mediana condyli is distinct on the dorsum of the condylus occipitalis; the tip of the dens of the axis rides in the incision during dorsiflexion of the atlanto-occipital joint. The basal occipital presents as a depression, the fossa subcondylaris, between the condylus occipitalis and the central part of the lamina parasphenoidalis; the raised anterior border of this fossa gives rise to a pair of
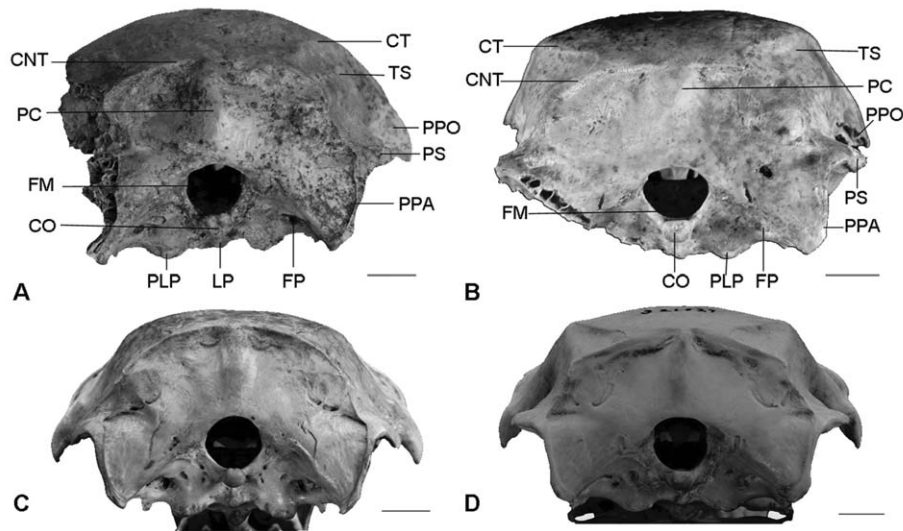

FIGURE 2. Posterior view of crania. **A**, *Aegypius jinniushanensis* sp. nov. (94. L. J. A. VIII-13.D-11); **B**, *Torgos* sp. (87. L. J. A. VIII-0: 50); **C**, *Aegypius monachus* (USNM 18223); **D**, *Torgos tracheliotus* (USNM 321827). **Abbreviations**: **CNT**, crista nuchalis transversa; **CO**, condylus occipitalis; **CT**, crista temporalis; **FM**, foramen magnum; **FP**, fossa parabasalis; **LP**, lamina parasphenoidalis; **PC**, prominentia cerebellaris; **PLP**, processus lateralis parasphenoidalis; **PPA**, processus paroccipitalis; **PPO**, processus postorbitalis; **PS**, processus suprameaticus; **TS**, temporal scar. Scale bars equal 1 cm. (Color figure available online.)

tubercula basilare and a median tubercle serving for insertion of cervical muscles. The tubercula basilare are medial of and in line with the processus lateralis parasphenoidalis. Regarding the shape of the cranial base, *Gyps* is unique among aegypiins in having a nearly quadrangular lamina parasphenoidalis, the best developed processus lateralis parasphenoidalis, the more restricted ala parasphenoidalis, and the most caudally situated tuberculum basilare. The fossa parabasalis lies posterior to the ala parasphenoidalis and medial to the ventral margin of the tympanic cavity. Two or three foramina can be observed in this fossa, but it is difficult to ascertain what they are (may be foramen nervi glossopharyngealis, foramen nervi vagi, ostium canalis carotici, or ostium canalis ophthalmici externi). Due to the preservation, the foramen nervi hypoglossal can be perceived only on the left side.

In posterior view (Fig. 2A), the crista nuchalis transversa is an obvious ridge separating the supraoccipital, parietal, and squamosal, and extends to the caudolateral border of the processus paroccipitalis; it is prominent in *A. jinniushanensis*, *A. monachus*, and *Torgos*. The outline of the crest is a rough arc in aegypiins. The arc is relatively highest in *Gyps* (Table 2). The transverse diameter of the foramen magnum is shorter than that of the longitudinal diameter. The prominentia cerebellaris is variably prominent caudally in aegypiins; it is best developed, resulting in a rounded postcranium, in *Gyps* and *Necrosyrtes*.

Remarks—*Aegypius jinniushanensis* differs markedly from *Gyps* in every view of the cranium. *Gyps* is characterized by a shorter, more pointed, and ventrally projecting processus postorbitalis, a broader fossa temporalis, a less protruding processus suprameaticus, and more prominent crista nuchalis transversa, processus lateralis parasphenoidalis, and tuberculum basilare. The monotypic genera *Aegypius*, *Torgos*, *Sarcogyps*, and *Trigonoceps* are very closely related; they have all been considered to be in the genus *Aegypius* (e.g., Brown et al., 1982) or at least that the first two should be merged (Seibold and Helbig, 1995). The size index represented by dimensions and ratios of *Aegypius* and *Torgos* is identical (Table 2), and only minor morphological differences can be detected between these two genera (see below). *Sarcogys* differs from *A. jinniushanensis* and *A. monachus* in having a distinct process in the central part of the caudal margin of the orbit, a shorter and less pointed processus postorbitalis and a lower processus lateralis parasphenoidalis (Rich, 1980; Zhang et al., 2010). Another heavy billed and large-sized vulture, *Trigonoceps*, shows minor differences from the new species in its relatively small temporal scar, less distinct crista temporalis and crista nuchalis transversa, and a better developed prominentia cerebellaris, enabling us to distinguish it from *Aegypius*. Besides its small size, *Necrosyrtes* is easily differentiated from *Aegypius* by a low processus lateralis parasphenoidalis, a less depressed fossa temporalis, the least development of the processus suprameaticus, and a less distinct crista temporalis. Compared with *A. monachus*, both the processus zygomaticus and processus suprameaticus are less protrudent in the new specimen and the condylus occipitalis is relatively larger (Figs. 1, 2A, C). Thus, a new species is erected as *Aegypius jinniushanensis*.

The processus postorbitalis provides an attachment point for part of the adductor musculature of the mandible, M. adductor mandibulae externus rostralis temporalis and M. adductor mandibulae externus rostralis lateralis. The long, triangular, well-developed processus postorbitalis in *Aegypius*, *Torgos*, and *Trigonoceps* reveals the size of M. adductor mandibulae externus rostralis temporalis that adducts the mandible and probably also retracts the maxilla (Richards and Bock, 1973). The fossa temporalis and temporal scar provide extensive insertion for M. adductor mandibulae externus rostralis temporalis, the extent of which is a character specifically related to the manner of feeding (Fisher, 1944). The relatively broad and distinct development of these two features in *A. jinniushanensis*, *A. monachus*, *Torgos*,
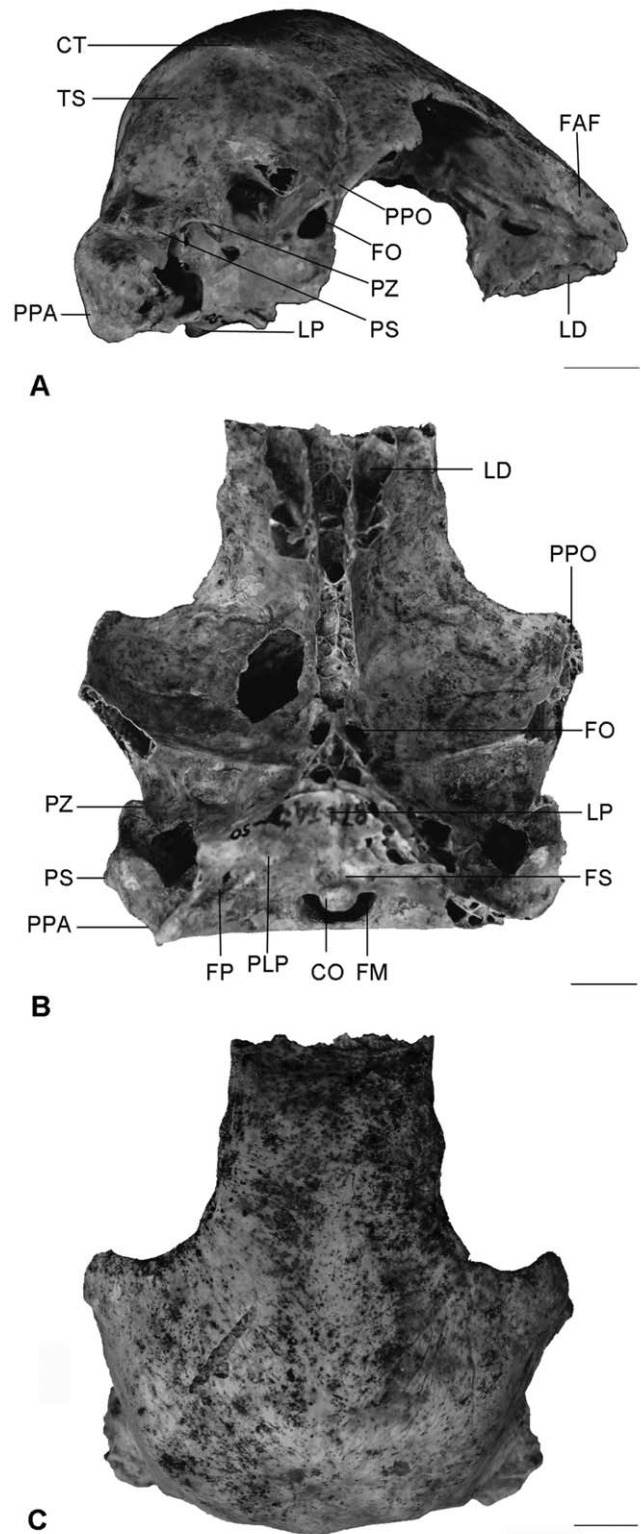

FIGURE 3.   The cranium of *Torgos* sp. (87. L. J. A. VIII-0: 50) in lateral (**A**), ventral (**B**), and dorsal (**C**) views. **Abbreviations**: **CO**, condylus occipitalis; **CT**, crista temporalis; **FAF**, facies articularis frontonasalis; **FM**, foramen magnum; **FO**, foramen opticum; **FP**, fossa parabasalis; **FS**, fossa subcondylaris; **LD**, lamina dorsalis; **LP**, lamina parasphenoidalis; **PLP**, processus lateralis parasphenoidalis; **PPA**, processus paroccipitalis; **PPO**, processus postorbitalis; **PS**, processus suprameaticus; **PZ**, processus zygomaticus; **TS**, temporal scar. Scale bars equal 1 cm. (Color figure available online.)
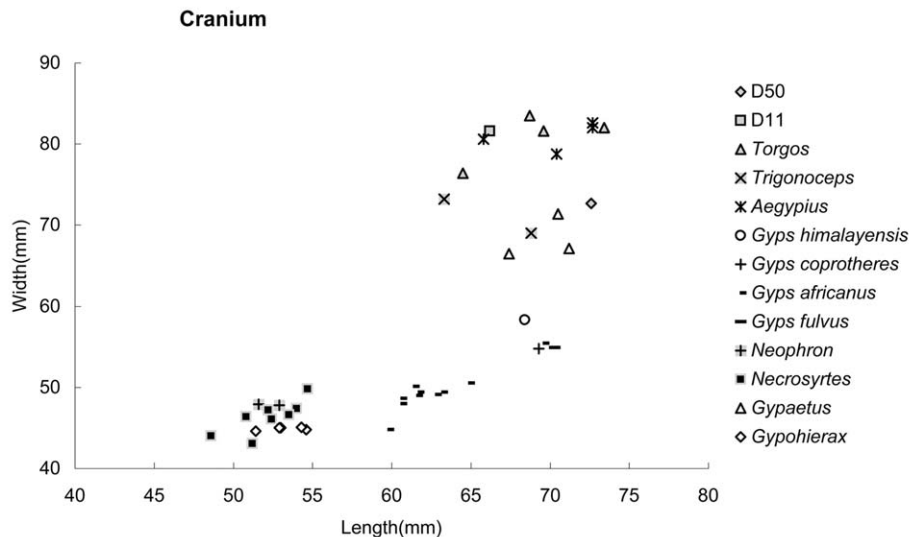
FIGURE 4.   Scatter plots comparing the width and length of the cranium of *A. jinniushanensis* (D11) and *Torgos* sp. (D50), with extant species.

and *Trigonoceps* are indicative of their manner of feeding (see Discussion).

Genus *TORGOS* Kaup, 1828
TORGOS sp.
(Figs. 2B, 3)

Material—Partly preserved cranium missing processus postorbitalis, septum interorbitale, rostrum parasphenoidale, left ala parasphenoidalis, and left part of the lamina parasphenoidalis. Collection number 87. L. J. A. VIII-0: 50.

Description—This is a second large cranium, similar in size to that of *Aegypius jinniushanensis* (Table 2), found in the same site. Because it is morphologically similar to *Aegypius jinniushanensis* in many aspects, only the differences are described here: the processus zygomaticus of the squamosal is relatively thin, long, and points anteroventrally; the processus suprameaticus is well developed and extents laterally rather than lateroventrally (Figs. 2B, 3A); ventral to the process, there is a relatively long, broad triangular lamina. Like *Torgos tracheliotus*, the crista temporalis has a sharp edge marking an abrupt transition from the near flat plane of the frontal to the steep, roughly vertical plane of the upper part of the temporal scar (Fig. 2B, D). Posterior to the fossa temporalis, mainly as a result of the lateral projection of the processus suprameaticus, the upper and the lower parts of the temporal scar form a right angle in posterior view.

Remarks—The measurements and the osteological features of *Torgos* are basically similar to *Aegypius* (Table 2). *Aegypius* differs from *Torgos* in that the surfaces of the temporal scar and posterior frontal form a unit, giving a gently and continuously convex contour (in caudal view), thus no abrupt transition can be seen between the frontal and the temporal scar (Fig. 2A, B). The new specimen is tentatively assigned to *Torgos* because no obvious morphological differences could be discerned in the cranium between the fossil and *Torgos*. It might represent a new species but this could only be determined with more material.

DISCUSSION

The sedimentological analysis and the co-occurrence of *Macacus robustus*, *Felis tigris*, *Ursus arctos*, *Equus sanmeniensis*, *Megaloceros pachyosteus*, *Dicerorhinus mercki*, *Bison* sp., *Cervus* sp., and *Gazella* sp. indicate that the climate at the Jinniushan site 260,000 years ago was warmer than at present, and that the environment was dominated by woodland to open grassland plain (Jinniushan Lianhe Fajuedui, 1976; Rosenberg et al., 2006). There was a diverse assemblage of large herbivores that would have provided scavenging vultures with abundant large carcasses as a food resource. Old World vultures have three chief forms of feeding: pulling, tearing, and pecking (see above; Kruuk, 1967; König, 1983; Hertel, 1994). The large-sized *A. monachus*, *Torgos*, and *Trigonoceps* belong to the tearing type, characterized by a more compact, wider skull with a powerful beak adapted for opening carcasses and tearing off tough and coarse parts. The relatively wider skulls of our new materials (Table 2, Fig. 4) provide greater moment arms or mechanical advantage for neck muscles that control skull movements and thus probably reflect a greater ability of the skull to twist and rip tough parts from a carcass (Hertel, 1994). The broader fossa temporalis and more distinct temporal scar in the two new fossils provide extensive insertion for M. adductor mandibulae externus rostralis (musculus temporalis) that produces the main strength for jaw closing. These above-mentioned features probably enabled these fossil species to open carcasses and feed on the skin, tendons, and some other tough parts, and indicate that they belong to the tearing food group along with the modern vultures *Aegypius monachus* and *Torgos tracheliotus* (see Hertel, 1994). The apparent sympatry of two large vultures raises questions about whether they partitioned food resources by each feeding on different types of carcasses or different parts of carcasses. By inference from morphological analyses of modern sympatric Old World and New World vultures, we suggest that *A. jinniushanensis* and *Torgos* sp. fed on similar parts of the carcass and preferred the tougher parts of the carcasses of large herbivores. Studies on modern vultures reveal that competition for food between those species that are most likely to use the same resource will be reduced by aggressive behavior, differing habitat preference, differing flight ability, and by having relatively little geographical overlap (Kruuk, 1967; Houston, 1975; Wallace and Temple, 1987; Lemon, 1991). Between the two vultures in the middle Pleistocene of Jinniushan, interspecific competition would have been augmented by sharing a preference for certain parts of the carcass, but could have been reduced by ecological differentiation. By inference from the ecology of

TABLE 3. Sympatric fossil species of Agypiinae reported from Pleistocene Palaearctic sites.

Range	Age	Species
Binagady, Azerbaijan	MP	*Gyps fulvus, Aegypius monachus, Neophron percnopterus*
Sandalja, Croatia	LP	*Gyps fulvus, Aegypius monachus, Neophron percnopterus*
Cueva de Zafarraya, Spain	LP	*Gyps fulvus, Neophron percnopterus*
Grotte de la Vache, France	LP	*Gyps fulvus, Aegypius monachus*
Grotte de l'Observatoire, France	LP	*Gyps fulvus, Aegypius monachus*
Liko cave (Crete), Greece	LP	*Gyps fulvus, Gyps melitensis*
Hayonim cave (Galilee), Israel	LP	*Gyps fulvus, Aegypius monachus, Neophron percnopterus*
Kebara + Qafzeh (Galilee), Israel	LP	*Gyps fulvus, Aegypius monachus*
Grotta del rincipe (Liguria), Italy	LP	*Gyps fulvus, Aegypius monachus, Gyps melitensis*
Ksâr'Akil, Lebanon	LP	*Gyps fulvus, Aegypius monachus*
Gandia fissure, Malta	?	*Gyps melitensis, Gyps* sp.
"Malta," Malta	?	*Gyps melitensis, Gyps* sp.
Gabasa, Spain	LP	*Aegypius prepyrenaicus, Aegypius monachus*
Jinniushan, China	MP	*Aegypius jinniushanensis, Torgos* sp.

Summarized primarily from Tyrberg (1998). **Abbreviations**: **LP**, lower Pleistocene; **MP**, middle Pleistocene.

extant counterparts, we expect that *A. jinniushanensis* inhabited wooded mountain areas where it relied on wind movement and high frequency of slope updrafts rather than thermals for soaring (Hiraldo and Donázar, 1990), enabling it to cover a broad foraging range and feed early in the morning. *Torgos* sp., by analogy with its congener *T. tracheliotus*, probably inhabited the bush savanna with a relatively small home range, and mainly relied on thermals for flight. *Torgos tracheliotus* was reported to be more aggressive than other vultures (Kruuk, 1967), although we cannot know whether the fossil *Torgos* sp. was more aggressive than the other sympatric fossil species *A. jinniushanensis*. The finding of sympatric fossil aegypiins is not unusual, and is most frequently reported in Pleistocene sites of the Palaearctic (Table 3), with only two reported pairs in the New World: *Neophrontops americanus* and *Neogyps errans*, *Neophrontops vallecitoensis* and *Neophrontops americanus*, both in California (Table 1). Most of the sympatric fossil aegypiins were composed of members of different feeding groups (Table 3), which is also what one finds for modern scavenger guilds. The guild in five sites from Greece, Spain, Malta, and China consisted of only one feeding group, either pulling or tearing. We can expect that each pair in these guilds was able to reduce competition by behavioral, ecological, and/or temporal differentiation.

The cranium referred to *Torgos* is the second fossil report of this modern genus; however, the first report, *Torgos tracheliotus todei* Kleinschmidt, 1953, from the late Pleistocene of Germany, was regarded as a synonym of *Aegypius monachus* by Mlíkovský (1998). Although *Torgos* is now confined to the Afrotropical savannas, our finding suggests that it had a wider distribution in the Pleistocene. The evolution and radiation of Old World vultures are thought to be closely related to the appearance and abundance of ungulates and grassland (Houston, 1983; Mundy et al., 1992; Zhang et al., 2010). The disappearance of *Torgos* from northeast China might be the result of the loss of grassland and savannah from the region, and the Pleistocene extinction of a suite of large mammalian herbivores, as occurred with the New World vultures. It has been reported that at the end of the Pleistocene, many vultures became extinct (*Breagyps clarki, Neogyps errans, Neophrontops americanus*) or range-restricted (*Gymnogyps californianus*) in North America, coinciding with a 72% reduction in the generic diversity of the mammalian megafauna (Emslie, 1987; Koch and Barnosky, 2006). Radiocarbon and stable isotope data suggest that dependence upon carrion of terrestrial megafauna underlies the extinction of inland California Condor populations (Emslie, 1987; Fox-Dobbs et al., 2006).

The evolutionary history of Old World vultures can probably be traced back before the Miocene. The two middle Pleistocene

crania from northeastern China add precious material to the poor collections of the Old World vulture fossils from the Old World, and are valuable for reconstructing the radiation and distribution of aegypiins, although it is too early at the present, without older and more complete fossils, to outline the subfamily's deeper evolutionary history (Rich, 1983).

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