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

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ABSTRACT—Two new fossil crania of Old World vultures (Accipitridae, Aegypiinae), from the middle Pleistocene Jinniushan site of 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, Trigonocips, Torgos, and Aegypius), presently confined in Africa and Eurasia (Seibold and Helbig, 1995; Lerner and Mindell, 2005). Necrosyrtes, Trigonocips, Torgos, and three species of Gyps (G. africanus, G. rueppelli, G. coperothus) only occur in Africa. Aegypius and G. fulvus are widely distributed in the Afro-Eurasian 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 Trigonocips) 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 percnaptus (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 (Lù, 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

*Corresponding author.
TABLE 1. Fossil records of extinct Old World vultures.

<table>
<thead>
<tr>
<th>Species</th>
<th>Range</th>
<th>Age</th>
<th>Materials</th>
<th>Literature</th>
</tr>
</thead>
<tbody>
<tr>
<td>Palaeoborus rosatus</td>
<td>South Dakota</td>
<td>Lower Miocene</td>
<td>Distal tarsometatarsus</td>
<td>Miller and Compton, 1939</td>
</tr>
<tr>
<td>Palaeoborus howardae</td>
<td>Nebraska</td>
<td>Middle Miocene</td>
<td>Partial humerus</td>
<td>Brodkorb, 1964</td>
</tr>
<tr>
<td>Palaeoborus ambrosus</td>
<td>New Mexico</td>
<td>Lower Pliocene</td>
<td>Partial humerus</td>
<td>Wetmore, 1943</td>
</tr>
<tr>
<td>Neophronops venatus</td>
<td>South Dakota, Oregon</td>
<td>Lower and middle Pliocene</td>
<td>Distal tibiotarsus, mandible, and limb bones</td>
<td>Compton, 1935</td>
</tr>
<tr>
<td>Neophronops dactylopterus</td>
<td>Idaho, Florida</td>
<td>Upper Pliocene</td>
<td>Distal tarsometatarsus</td>
<td>Fedeuccia, 1974; Emslie, 1998</td>
</tr>
<tr>
<td>Neophronops vallicetoensis</td>
<td>California</td>
<td>Middle Pleistocene</td>
<td>Limb bones</td>
<td>Miller, 1916; Emslie, 1985</td>
</tr>
<tr>
<td>Neophronops americanus</td>
<td>California, New Mexico, Wyoming</td>
<td>Early Miocene to upper Pleistocene</td>
<td>Tarsometatarsus</td>
<td>Miller, 1916</td>
</tr>
<tr>
<td>Neophronops erans</td>
<td>California, Nevada, Mexico</td>
<td>Upper Pleistocene</td>
<td>Partial articulated skeleton</td>
<td>Rich, 1980</td>
</tr>
<tr>
<td>Neophronops ricardoi</td>
<td>California</td>
<td>Middle Miocene</td>
<td>Coracoid, limb bones</td>
<td>Bickart, 1990</td>
</tr>
<tr>
<td>Neophronops sp.</td>
<td>Arizona</td>
<td>Late Miocene to early Pliocene</td>
<td>Distal tibiotarsus</td>
<td>Brodkorb, 1964</td>
</tr>
<tr>
<td>Arikarornis macdonaldi</td>
<td>South Dakota</td>
<td>Lower Miocene</td>
<td>Femur, tibiotarsi, tarsometatarsi, pedal phalanges, cervical vertebrae</td>
<td>Brodkorb, 1964; Tyrberg, 1998; Marco, 2007</td>
</tr>
<tr>
<td>Palaeohierax gervaisii</td>
<td>France, Monaco, Austria, France, Malta</td>
<td>Lower Miocene</td>
<td>Nearly complete skeleton</td>
<td>Zhang et al., 2010</td>
</tr>
<tr>
<td>Trigonoceps occipitalis</td>
<td>China</td>
<td>Early Miocene</td>
<td>Ulna</td>
<td>Bernabei, 1982</td>
</tr>
<tr>
<td>Gansusgyps linxiaensis</td>
<td>China</td>
<td>Late Miocene</td>
<td>Partial tibiotarsus</td>
<td>Yang et al., 2000</td>
</tr>
<tr>
<td>Aegypius prepyrenaicus</td>
<td>Spain</td>
<td>Upper Pleistocene</td>
<td>Partial humerus</td>
<td>Compton, 1935</td>
</tr>
</tbody>
</table>

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 basioccipital plate and top of cranium; cranial width, maximum width across processus postorbitalis; temporal width, distance between fossae temporales; opisthotic width, distance across processus paroccipitalis; postcranial height, vertical distance between processus paroccipitales and midpoint of cranium; and limb bones.

Comparison 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, 347579M, 19990, 320977M, 321827F; Trigoniceps occipitalis, 320859F, 347358; Aegypius monachus, 18223, 428040F, 289569; Palaeoborus umbrosus, 19354M; Gyps himalayensis, 19534M; Palaeohierax gervaisii, 1820646, 291440M, 291443F, 291441F, 620645; Gyps fulvus, 587404M, 431591F, 43016M; Neophron percnopterus, 17835, 610499; Necrosyrtes monachus, 614886, 291442F, 18894, 620646, 291440M, 291441F, 260245; Gypaetus barbatus, 345684F, 17834, 19383; Gypohierax angolensis, 224820, 291078F, 226143, 18892, 291316M.

SYSTEMATIC PALEONTOLOGY

Class AVES Linnaeus, 1758
Order ACCIPITRIFORMES Vouc, 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Cranial length</th>
<th>Cranial width</th>
<th>Cranial height</th>
<th>Opisthotic width</th>
<th>Temporal width</th>
<th>Postcranial height</th>
</tr>
</thead>
<tbody>
<tr>
<td>Torgos sp.</td>
<td>72.6</td>
<td>&gt;72.7</td>
<td>46.8</td>
<td>&gt;50.2</td>
<td>56.4</td>
<td>33.2</td>
</tr>
<tr>
<td>Aegypius jinniushanensis</td>
<td>66.2</td>
<td>79.2</td>
<td>45.9</td>
<td>51.6</td>
<td>57.8</td>
<td>38.3</td>
</tr>
<tr>
<td>Aegypius monachus (n=4)</td>
<td>70.4</td>
<td>81.0</td>
<td>46.4</td>
<td>52.2</td>
<td>57.4</td>
<td>36.8</td>
</tr>
<tr>
<td>Torgos tracheliotus (n=4)</td>
<td>63.8–72.7</td>
<td>78.8–82.6</td>
<td>44.0–47.5</td>
<td>50.4–53.9</td>
<td>54.8–59.3</td>
<td>34.3–40.7</td>
</tr>
<tr>
<td>Trigoniceps occipitalis (n=2)</td>
<td>64.5–73.4</td>
<td>76.4–83.5</td>
<td>46.5–49.7</td>
<td>50.4–55.5</td>
<td>56.4–61.0</td>
<td>35.6–39.2</td>
</tr>
<tr>
<td>Gyps coprotheres (n=1)</td>
<td>69.3</td>
<td>54.8</td>
<td>38.4</td>
<td>41.5</td>
<td>43.4</td>
<td>37.8</td>
</tr>
<tr>
<td>Gyps africanus (n=10)</td>
<td>62.6 ± 2.86</td>
<td>49.4 ± 2.62</td>
<td>35.7 ± 1.61</td>
<td>35.8 ± 2.69</td>
<td>38.9 ± 2.03</td>
<td>34.5 ± 2.58</td>
</tr>
<tr>
<td>Gyps himalayensis (n=1)</td>
<td>68.4</td>
<td>58.3</td>
<td>40.3</td>
<td>42.3</td>
<td>46.0</td>
<td>39.2</td>
</tr>
<tr>
<td>Gyps fulvus (n=1)</td>
<td>70.3</td>
<td>54.9</td>
<td>39.0</td>
<td>40.6</td>
<td>42.3</td>
<td>38.5</td>
</tr>
<tr>
<td>Neophron percnopterus (n=2)</td>
<td>53.3</td>
<td>47.9</td>
<td>34.4</td>
<td>29.1</td>
<td>39.2</td>
<td>23.3</td>
</tr>
<tr>
<td>Necrosyrtes monachus (n=8)</td>
<td>51.6, 52.9</td>
<td>47.8, 47.9</td>
<td>33.0, 35.8</td>
<td>29.1, —</td>
<td>39.1, 39.2</td>
<td>23.3, —</td>
</tr>
<tr>
<td>Gypaetus barbatus (n=3)</td>
<td>67.4, 71.2</td>
<td>66.5, 71.4</td>
<td>41.3, 41.6</td>
<td>47.4, 49.3</td>
<td>51.2, 53.3</td>
<td>29.6, 31.9</td>
</tr>
<tr>
<td>Gypohierax angolensis (n=5)</td>
<td>53.2 ± 1.23</td>
<td>44.9 ± 0.2</td>
<td>32.1 ± 1.15</td>
<td>23.1 ± 1.32</td>
<td>34.6 ± 0.24</td>
<td>22.9 ± 0.34</td>
</tr>
<tr>
<td>51.4 ± 0.6</td>
<td>44.6 ± 4.51</td>
<td>31.0 ± 3.37</td>
<td>21.8 ± 2.46</td>
<td>34.3 ± 3.49</td>
<td>22.7 ± 2.35</td>
<td></td>
</tr>
</tbody>
</table>
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)


**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

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**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 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 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 less 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 postorbitals. 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 dorsal is shows as a marked depression surrounded laterally and caudally by highly raised margins. There is no occurrence of the sulcus nervi olfactorii. The lamina paraparaphenoideal is more resembles a right-angled triangle in profile, with the apex directed anteriorly and the central part a little concave. The processus lateralis paraparaphenoideal 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 paraparaphenoideal 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 paraparaphenoideal; 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. VII-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 paraparaphenoideal; PC, prominentia cerebellaris; PLP, processus lateralis paraparaphenoideal; PPA, processus paroccipitalis; PPO, processus postorbitalis; PS, processus suprameaticus; TS, temporal scar. Scale bars equal 1 cm. (Color figure available online.)
and Trigonoceps Aegypius jinniushanensis. Thus, a new species is erected as processus suprameaticus are less protrudent in the new specimen from Aegypius Aegypius and 1995). The size index represented by dimensions and ratios of at least that the first two should be merged (Seibold and Helbig, A. monachus pared with cessus suprameaticus, and a less distinct crista temporalis. Com-
less depressed fossa temporalis, the least development of the pro-
processus postorbitalis, a broader fossa temporalis, a less protruding
by a shorter, more pointed, and ventrally projecting proces-
Gyps Gyps—possibly prominent caudally in aegypiins; it is best developed, result-
of the longitudinal diameter. The prominentia cerebellaris is vari-
transverse diameter of the foramen magnum is shorter than that
Aegypius Aegypius, Sarcogyps, and Trigonoceps are very closely related; they have all been con-
which is a character specifically related to the manner of feeding
the shape of the cranial base, Gyps is unique among aegyiins. The outline of the crest is a rough arc in aegyiins. 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 vari-
right in a rounded posteriorian, 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 basilar. The monotypic genera Aegypius, Torgos, Sarcogyps, and Trigonoceps are very closely related; they have all been con-
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. Com-
Torgos, 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 Ae-
thus, a new species is erected as Aegypius jinniushanensis (Table 2), and only minor mor-
Aegypius and Torgos is identical (Table 2), and only minor mor-

discernible between these two gen-
Aegypius 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 basilar. The monotypic genera Aegypius, Torgos, Sarcogyps, and Trigonoceps are very closely related; they have all been con-
As 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. adduc-
tor mandibulæ externus rostralis temporalis and M. adduc-
tor mandibulæ externus rostralis lateralis. The long, triangular, well-developed processus postorbitalis in Aegypius, Torgos, and Trigonoceps reveals the size of M. adductor mandibulæ externus rostralis temporalis that adds the mandible and probably also retracts the maxilla (Richards and Bock, 1973). The fossa temporalis and temporal scar provide extensive insertion for M. adductor mandibulæ 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-8: 50) in lateral (A), ventral (B), and dorsal (C) views. Abbreviations: CO, condyulus occi-
cipitalis; CT, crista temporalis; FAF, facies articularis fronsotalis; FM,
foramen magnum; FO, foramen opticum; FP, fossa parabasalis; FS, fossa subcondylaris; LD, lamina dorsalis; LP, lamina parabasalis; PLP,
processus lateralis parasphenoidalis; PPA, processus paroccipitalis; PPO,
processus postorbitalis; PS, processus suprameaticus; PZ, processus zygo-
maticus; TS, temporal scar. Scale bars equal 1 cm. (Color figure available online.)
and Trigonocops 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 paraphenoideal, left ala paraphenoideal, and left part of the lamina paraphenoideal.  
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 extends 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 sumeniensis, 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 Trigonocops 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 Aegypiinae reported from Pleistocene Palaearctic sites.

<table>
<thead>
<tr>
<th>Range</th>
<th>Age</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Binagady, Azerbaijan</td>
<td>MP</td>
<td>Gyps fulvus, Aegypius monachus, Neophron percnopterus</td>
</tr>
<tr>
<td>Sandalja, Croatia</td>
<td>LP</td>
<td>Gyps fulvus, Aegypius monachus, Neophron percnopterus</td>
</tr>
<tr>
<td>Cueva de Zafarraya, Spain</td>
<td>LP</td>
<td>Gyps fulvus, Neophron percnopterus</td>
</tr>
<tr>
<td>Grotte de la Vache, France</td>
<td>LP</td>
<td>Gyps fulvus, Aegypius monachus</td>
</tr>
<tr>
<td>Grotte de l’Observatoire, France</td>
<td>LP</td>
<td>Gyps fulvus, Aegypius monachus</td>
</tr>
<tr>
<td>Liko cave (Crete), Greece</td>
<td>LP</td>
<td>Gyps fulvus, Gyps meliensis</td>
</tr>
<tr>
<td>Hayonim cave (Galilee), Israel</td>
<td>LP</td>
<td>Gyps fulvus, Aegypius monachus, Neophron percnopterus</td>
</tr>
<tr>
<td>Kebara + Qafzeh (Galilee), Israel</td>
<td>LP</td>
<td>Gyps fulvus, Aegypius monachus</td>
</tr>
<tr>
<td>Grotta del rincipe (Liguria), Italy</td>
<td>LP</td>
<td>Gyps fulvus, Aegypius monachus, Gyps meliensis</td>
</tr>
<tr>
<td>Ksár’Akil, Lebanon</td>
<td>LP</td>
<td>Gyps meliensis, Gyps sp.</td>
</tr>
<tr>
<td>Gandia fissure, Malta</td>
<td>?</td>
<td>Gyps meliensis, Gyps sp.</td>
</tr>
<tr>
<td>“Malta,” Malta</td>
<td></td>
<td>Aegypius prepyrenaicus, Aegypius monachus</td>
</tr>
<tr>
<td>Gabasa, Spain</td>
<td>LP</td>
<td>Aegypius jinniushanensis, Torgos sp.</td>
</tr>
<tr>
<td>Jinniushan, China</td>
<td>MP</td>
<td></td>
</tr>
</tbody>
</table>

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

We are grateful to personnel of the field group from the School of Archaeology and Museology at Peking University and the Cultural Relics and Archaeology Institute of Liaoning Province for discovering the specimens, H. Meijer and M. Spitzer for discussion, S. Emslie, F. Hertel, and T. Worthy for valuable comments. This work was supported partly by the National Natural Science Foundation of China (30870263, 31071877), and performed during a residency in the Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

LITERATURE CITED


We thank E. R. S. Lambe (now Baas-Becking) for collectings and for providing us with photographs of the holotype. We also thank J. A. Thomas, Jr. for providing photographs of the syntypes. 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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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 Donázár, 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: Neophron tops americanus and Neogyps errans, Neogyps vallectoenis and Neophron tops 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 Mlókóvy (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 (Breagoeps 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 three Middle Miocene species of Neogyps are not known from any area except the Afrotropical savannas, and the Middle Miocene Neogyps from China and the Middle Miocene Neogyps from Africa might be the result of the loss of inland California Condor populations (Emslie, 1987; Fox-Dobbs et al., 2006).


Wetmore, A. 1943. Two more fossil hawks from the Miocene of Nebraska. Condor 45:229–231.


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