A NEW CONDOR (CICONIIFORMES, VULTURIDAE) FROM THE LATE MIOCENE/EARLY PLIOCENE PISCO FORMATION, PERU

MARCELO STUCCHI1,3 AND STEVEN D. EMSLIE2,4
1Asociación Ucumari, Jr. Los Agrólogos 220, Lima 12, Peru
2Department of Biological Sciences, University of North Carolina, Wilmington, NC 28403

Abstract. We report the oldest fossil condor (Vulturidae) from South America and the first from the Pisco Formation (14.0–2.0 Ma) of Peru, described herein as Perugyps diazi new genus and species. The Pisco Formation, exposed on the southern coast of Peru, has produced well-preserved and abundant marine and terrestrial vertebrate fossils from the late Miocene/early Pliocene (6.0–4.5 Ma) Montemar and Sacaco Sur localities, from where P. diazi was recovered. The new condor adds to our knowledge on the evolution and biogeographic distribution of New World vultures. The age of this new species supports the hypothesis that condors probably evolved in North America and entered South America by the late Miocene/early Pliocene. We believe it is likely that the first condors to reach South America probably did so via a coastal corridor along the western side of the Andes where they became part of the diverse coastal fauna in southern Peru.

Key words: condor, Miocene, Peru, Perugyps diazi, Pisco Formation, Pliocene, Vulturidae.

INTRODUCTION

The oldest record of the family Vulturidae in the Americas is the early Oligocene genus Phasmagyps Wetmore 1927 from the United States (see Emslie 1988a), though the validity of this taxon has been questioned (Olson 1985). New World vultures appeared in South America by the late Oligocene/early Miocene in Brazil with Brasilogyps Alvarenga 1985, a species very similar in size and features to the living Coragyps (Emslie 1988a). In Peru, fossils of five modern genera (Vultur, Gymnogyps, Sarcoramphus, Coragyps, and Cathartes) and one extinct genus (Geronogyps Campbell 1979) have been identified and described, all from late Pleistocene tar seeps at Talara on the northern coast (Campbell 1979). Recently, eight disassociated bones of a new species of condor were found in deposits of the Montemar (6–4.5 Ma) and Sacaco Sur (5 Ma), vertebrate-bearing levels of the Pisco Formation on the south-central coast of Peru (Fig. 1). These fossils are assumed to represent a single genus and species of condor described herein.

METHODS

All fossils were compared with skeletal material of living genera of condors and vultures (Vultur Linnaeus 1758, Sarcoramphus Duméril 1806, Cathartes Illiger 1811, Gymnogyps Lesson 1842, Coragyps Saint-Hilaire 1853) at the U. S. National Museum of Natural History, Smithsonian Institution (USNM), and the Field Museum of Natural History (FMNH), Chicago. Because current Peruvian law does not allow the removal...
FIGURE 1. Map of the Pisco Formation in Peru showing the location of the Montemar and Sacaco Sur localities where fossils of *Perugyps diazi* new genus and species were recovered (after de Muizon and DeVries 1985). Inset map depicts the location of the Pisco Formation in relation to Lima, the capital of Peru.

FIGURE 2. (A) Holotype right carpometacarpus (MUSM 213) of *Perugyps diazi* new genus and species in internal (left) and external (right) views. (B) Proximal right carpometacarpus (MUSM 206) of *Perugyps diazi* new genus and species in internal view. (C) Distal left ulna (MUSM 423) of *Perugyps diazi* new genus and species in internal view. Scale bar = 2 cm.

RESULTS

SYSTEMATIC PALEONTOLOGY

Order Ciconiiformes (Bonaparte 1854)
Family Vulturidae (Illiger 1811)

*Perugyps* gen. nov.

*Perugyps diazi* sp. nov. (Fig. 2–4)

**Holotype.** Right carpometacarpus missing proximal portion of os metacarpale minus (MUSM 213; Fig. 2A), collected by M. Stucchi, July 2000.

**Locality/horizon.** Pisco Formation, Montemar vertebrate-bearing locality (late Miocene/early Pliocene; 6.0–4.5 Ma; de Muizon and DeVries 1985; DeVries, pers. comm.).

**Diagnosis.** *Perugyps* is diagnosed as a condor by the following characters:

1. Mandible with symphysis proportionately larger than in *Coragyps*, *Cathartes melambrotus* Wetmore 1964, and *Gymnogyps*; smaller than in *Sarcoramphus* and *Vultur*, and similar in proportions to *Cathartes aura* (Linnaeus 1758). Symphysis is proportionately broader and the dentary has a relatively higher coronoid process than in all living Vulturidae. Mandible longer than in *Vultur gryphus* Linnaeus 1758 and *Gymnogyps californianus* (Shaw 1798, Table 1).
2. Sixth cervical vertebra with prezygopophyses angled more anteriorly, rounder and more ro-
TABLE 1. Mandibular measurements (mm) of living Vulturidae in comparison with Perugyps diazi new genus and species. Measurement codes are: (1) symphysis length, (2) symphysis width at proximal end, (3) coronoid process height, (4) coronoid process-articular length, and (5) total length of mandible. All measurements are mean ± SD.

<table>
<thead>
<tr>
<th>Species</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perugyps diazi (MUSM 261)</td>
<td>22.5</td>
<td>25.7</td>
<td>23.2</td>
<td>35.1</td>
<td>140.0</td>
</tr>
<tr>
<td>Coragyps atratus (n = 5)</td>
<td>13.4 ± 1.3</td>
<td>9.3 ± 0.9</td>
<td>10.6 ± 0.7</td>
<td>18.5 ± 0.7</td>
<td>87.3 ± 3.4</td>
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<tr>
<td>Cathartes melambrotus (n = 2)</td>
<td>10.6 ± 0.5</td>
<td>9.5 ± 0.3</td>
<td>10.0 ± 0.0</td>
<td>14.6 ± 1.3</td>
<td>75.0 ± 1.9</td>
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<tr>
<td>Cathartes aura (n = 5)</td>
<td>11.2 ± 1.1</td>
<td>8.3 ± 0.9</td>
<td>9.1 ± 0.2</td>
<td>14.3 ± 0.8</td>
<td>70.2 ± 1.7</td>
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<tr>
<td>Sarcoramphus papa (n = 5)</td>
<td>17.0 ± 0.7</td>
<td>13.8 ± 0.4</td>
<td>13.6 ± 0.4</td>
<td>23.8 ± 0.6</td>
<td>90.7 ± 1.8</td>
</tr>
<tr>
<td>Vultur gryphus (n = 2)</td>
<td>24.0 ± 0.8</td>
<td>18.9 ± 0.4</td>
<td>18.8 ± 1.3</td>
<td>38.3 ± 1.7</td>
<td>131.2 ± 4.2</td>
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<tr>
<td>Gymnogyps californianus (n = 4)</td>
<td>18.6 ± 1.5</td>
<td>17.4 ± 0.6</td>
<td>16.2 ± 0.9</td>
<td>37.5 ± 0.9</td>
<td>129.5 ± 6.3</td>
</tr>
</tbody>
</table>

FIGURE 3. (A) Right mandible with distal symphysis (MUSM 261) of Perugyps diazi new genus and species in dorsal (top) and lateral (bottom) views. (B) Sternal end of right coracoid (MUSM 205) of Perugyps diazi new genus and species in ventral (left) and dorsal (right) views. Scale bar = 1 cm.
FIGURE 4. (A) Distal left tibiotarsus (MUSM 260) of Perugyps diazi new genus and species in anterior view. (B) Right tarsometatarsus (MUSM 204) of Perugyps diazi new genus and species in anterior (left) and posterior (right) views. Scale bar = 2 cm.

distal left tibiotarsus, MUSM 260 (Fig. 4A); right tarsometatarsus, MUSM 204 (Fig. 4B).

Measurements. See Table 1 for mandibular measurements. Measurements that are approximate due to erosion on the bone are indicated by the ~ symbol. Holotype right carpometacarpus (MUSM 213): total length, 147.2 mm; proximal breadth, 38.4 mm; least breadth and depth of shaft, 26.9 and 23.1 mm, respectively. Proximal right carpometacarpus (MUSM 206): proximal breadth, 40.2 mm. Distal left ulna (MUSM 423): distal breadth and depth, 17.8 mm and 24.9 mm, respectively. Distal left tibiotarsus (MUSM 260): distal breadth and depth, 27.6 mm and 26.2 mm, respectively. Right tarsometatarsus (MUSM 204): total length, ~141 mm; proximal breadth, 28.7 mm; least breadth 15.7 mm and depth of shaft 8 mm; middle trochlea breadth ~11.3 mm and depth ~14.7 mm; distal breadth, ~40 mm.

DESCRIPTION

The Family Vulturidae is characterized by the presence of a deep and often pneumatic anterior carpal fossa in the carpometacarpus, which is not present or shallow in Ciconiidae and Teratornithidae (Emslie 1988b). Other characteristics for Vulturidae are a massive os metacarpale minus and majus with a broad distal symphysis, a long and proximally curved os metacarpalis alulare, with a rounded extensor process; a broad contour of the carpal trochlea, and rounded facets on the distal articular surface. The carpometacarpus of Perugyps (MUSM 206, 213) presents at least three clear condor characteristics including (1) a proximally curved process extensorius, (2) low intermetacarpal tuberosity, and (3) large size (Hertel 1992).

In addition to characters above in the generic diagnosis, further characters distinguish Perugyps diazi.

Mandible. In dorsal view, the distal symphysis of MUSM 261 (Fig. 3A) is distinctly longer than in Coragyps, Sarcoramus, or Gymnogyps, exceeded in length only by Vultur; the symphysis is relatively broader in Perugyps compared to all living Vulturidae. The symphysis in Cathartes aura is proportionally the same length as in Perugyps. Vultur and Gymnogyps also have a longer and more pronounced (higher) proximal end and articular (Table 1). In addition, the ventral surface of the mandible in lateral view curves downward more sharply towards the distal end in Gymnogyps compared to Perugyps (Fig. 3A) and Vultur.

Cervical vertebra. MUSM 263 is more similar to Vultur than Gymnogyps in size, shape, and robustness. MUSM 263 also is similar in characters to Cathartes, though much larger. In anterior view, Perugyps has external borders of the prezygopophyses positioned at the same height as the diapophyses, similar to Sarcoramus and Cathartes; these borders are relatively higher in Coragyps. No vertebrae of Bregyps or Geronogyps were available for comparison.

Coracoid. MUSM 205 (Fig. 3B) has an internal distal angle that is more robust, curved, and with a lower-hanging rim and the line for muscle attachment that is more distinct and extends farther up the shaft in Perugyps, compared to all living genera of Vulturidae. Geronogyps (ROM 12991, 12992, 12993) is more like Vultur in the sterno-coracoidal impression, pneumatization, and shaft of internal distal angle.

Ulna. MUSM 423 (Fig. 2C) has a very pronounced and robust process lateral to the internal condyle with a small pneumatic area at the base, similar to Vultur and Gymnogyps (less robust with no or little pneumatic area in Sarcoramus, relatively robust with larger pneumatic area in Coragyps and Cathartes). The external condyle in internal view extends relatively far-
ther up the shaft, and is narrower, in Gymnogyps
than in Perugyps and Vultur. This condyle also is
relatively narrower in Perugyps than in Breagyps and the internal condyle is more prom-
inent in the latter.

Tibiotalus. MUSM 260 (Fig. 4A) is more
similar to Gymnogyps than Vultur in the mor-
phology of the distal condyles; the tendinal
opening is relatively higher (more proximal) on
the shaft in Perugyps than in these two species
or Coragyps, Cathartes, and Sarcoramphus. In
anterior view, the intercondylar area is deeply
grooved and symmetrical in Perugyps (area is
shallow and asymmetrical in Vultur and
Gymnogyps, very shallow in Cathartes). There
is a distinct bony shelf on the internal side of
the tendinal opening in Perugyps, similar to
Gymnogyps (this shelf is small in Vultur and
nearly absent in Coragyps). The external con-
dyle is relatively more robust in Perugyps com-
pared to Gymnogyps or Vultur. The tendinal
 groove passing below the suprartendinal bridge
is straight in Perugyps, Cathartes, and Sarco-
ramphus, but curved internally and proximally in
Coragyps, Gymnogyps, and Vultur (see Camp-
bell 1979). Gerontogyps (ROM 13007) has
a higher tendinal opening on the shaft, similar
to Perugyps, as well as a large shelf on the in-
ternal side. The intercondylar area is deeper in
Gerontogyps than in all living vultures, but not
as deep as in Perugyps. Perugyps does not have
any obvious features that differ from Breagyps
in this element.

Tarsometatarsus. MUSM 204 (Fig. 4B) has
an anterior metatarsal groove that is deep and
distinct, extending half way down the shaft (ex-
tends farther down the shaft in Vultur, Gymnogyps, Gerontogyps, Hadrogyps Emshie
1988, and Pliogyps Tordoff 1959). The external
border of this groove also is slightly larger than
the internal in Perugyps, Vultur, and Coragyps;
these borders are similar in size in Cathartes,
Sarcoramphus, and Gymnogyps. The shaft is rel-
atively robust as in Gymnogyps and Vultur, nar-
rrower in Coragyps, Cathartes and Sarcoram-
phus. The shaft also flares only slightly outward
at the proximal and distal ends in Perugyps
(shaft flares distinctly outward at ends in Vultur,
Gymnogyps, Gerontogyps, Breagyps, Hadrogyps,
and Pliogyps; more columnar in Hadrogyps and
Aizenogyps Emshie 1998). The tarsometatarsus
of Aizenogyps toomeyae is relatively larger and
more robust, with broader and deeper distal
trochlea, than in Perugyps.

DISCUSSION

The Pisco Formation consists of tuffaceous
sandy siltstones, medium and coarse-grained
sandstones, shelly sandstones, and to a lesser ex-
tent, conglomerates, bedded tuffs, and coquinas
that represent littoral environments that were
partially protected and close to shore (de Muiz-
zon and DeVries 1985). Six vertebrate-bearing
levels were identified by de Muizon and DeVries
(1985), including those at Montemar and Sacaco
Sur where fossils of Perugyps were recovered.
The sediments at these two localities reflect a
littoral paleoenvironment with protected beaches
and reefs exposed to marine currents (Marocco
and de Muizon 1988). Other avian families so
far identified from the Pisco Formation include
Spheniscidae, Sulidae, Phalacrocoracidae, Pela-
gornithidae, Laridae, Scolopacidae, Procellarii-
dae and Diomedea (de Muizon 1981, de Muiz-
zon and DeVries 1985, Cheneval 1993, Stucchi
2003).

Perugyps is the eighth genus of fossil condors
and condor-like vultures to be described. Of the
other seven genera, three (Dryornis, Ger-
notogyps, and Wingegyps) are known from South
America (Brodkorb 1967, Campbell 1979, Al-
varenga and Olson 2004). Wingegyps cartellei
is a small enigmatic condor from the late Pleisto-
cene of Brazil, no larger than a raven, but with
characters strikingly similar to Gymnogyps (Al-
varenga and Olson 2004). Dryornis panameus
Moreno and Mercera 1891 (early to middle Pli-
ocene, Argentina) is not known by any elements
shared with Perugyps and cannot be compared
(Moreno and Mercera 1891). In addition, an un-
described condor also from the middle Pliocene
of Argentina is known by only a proximal ulna
and radius (Tambussi and Noriega 1999) and is
not comparable to Perugyps.

Other fossil condors include Hadrogyps aig-
galeus from the middle Miocene, California
(Emshie 1988a), and Pliogyps charon Tordoff
1959 and P. fisheri Becker 1986 from the late
Miocene and middle Pliocene, respectively, of
Florida and Kansas (Tordoff 1959, Becker
1986). These two genera are smaller, condor-like
vultures that represent a parallel lineage of vul-
tures to the larger condors. Aizenogyps toomeyae
was a large, robust condor from the Pliocene of
Florida (Emshie 1998). Breagyps clarki is well
represented by fossils from the late Pleistocene Rancho la Brea, and it is distinct in morphology from all other genera (Miller 1910, Miller and Howard 1938, Howard 1974, Emslie 1988b). One other fossil genus, Antillovultur Arredondo 1976 from the late Pleistocene of Cuba, is now considered to be congeneric with Gymnogyps (Emslie 1988b, Suárez 2000, Suárez and Emslie 2003). An indeterminate genus and species of large condor from the early Pliocene Lee Creek Mine, North Carolina, is known by a humeral end of a coracoid, distal tibiotarsus, and pedal phalanx (Olson and Rasmussen 2001). This material is too fragmentary to provide diagnostic characters in comparison to other condors, though the distal tibiotarsus (USNM 430883) has a relatively shallower intercondylyar fossa compared with Perugyps (MUSM 260).

Perugyps diazi indicates that condors were present in South America by the late Miocene, at least 2.0 Ma earlier than suggested by Emslie (1988b), who proposed that condors may have arrived by the middle Pliocene and near the beginning of the Great American Biotic Interchange. In addition, Tonni and Noriega (1998) report a fossil of the living Andean Condor from the early Chapadmalalan (4 Ma), Río Quequén Salado (Buenos Aires), Argentina. Thus, it is now apparent that condors reached South America by the late Miocene to early Pliocene.

If condors did evolve in North America, then they were able to reach South America early in the evolution of this group. We hypothesize that an ancestral condor was able to expand southward following coastal corridors on the western side of the Andes. The California Condor can range hundreds of kilometers in a single day, at ground speeds up to 70–95 kph (Snyder and Snyder 2000), while the Andean Condor can reach speeds averaging 65 kph (McGahan 1971) and can fly 200 km across deserts from the Andean foothills to the coast to forage in a single day. Moreover, Pennycuick and Scholer (1984) found that the latter species is almost entirely dependent on slope uplifts to sustain prolonged soaring flight. We believe these flight capabilities of condors, along with coastal winds and updrafts common along the western slope of the Andes, may have allowed an ancestral condor to cross the marine barrier that existed between North and South America (the submerged Panamanian land bridge) in the late Miocene and early Pliocene.

During the late Miocene/early Pliocene, the Peruvian coast was characterized by a diverse assemblage of marine mammals and birds (de Muizon and DeVries 1985, Cheneval 1993, Stucchi 2003). This fauna is associated with remains of Perugyps and we believe that this condor fed on coastal carcasses of marine mammals, and perhaps took live chicks of seabirds, similar to the Andean Condor’s habits along the north coast of Peru today (Pennycuick and Scholer 1984, Wallace and Temple 1987). As no other scavenging species are known among the fauna of the Pisco Formation, it is reasonable to assume that Perugyps filled this niche. We expect that additional material of this condor will be recovered from vertebrate-bearing units of the Pisco Formation.

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LITERATURE CITED


