

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

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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.

Un Nuevo Cóndor (Ciconiiformes, Vulturidae) del Mioceno Tardío-Plioceno Temprano de la Formación Pisco, Perú.

Resumen. Se reporta el cóndor más antiguo de América del Sur y el primero para la Formación Pisco (14–2 Ma), y se describe como *Perugyps diazi*. De esta formación, situada en la costa sur del Perú, provienen gran cantidad de aves marinas en muy buen estado de conservación, en especial de los niveles Montemar y Sacaco Sur (Mioceno tardío/Plioceno temprano, 6.0–4.5 Ma), justamente de donde procede *Perugyps*. Este nuevo cóndor añade importante información sobre la evolución y distribución biogeográfica de estas aves, pues su edad apoya la hipótesis de que los cóndores probablemente evolucionaron en América del Norte y entraron a América del Sur entre el Mioceno tardío y el Plioceno temprano. Sugerimos que su llegada pudo realizarse por el corredor costero del lado occidental de los Andes, en donde pasaron a formar parte de la diversa fauna del sur del Perú.

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 Pleisto-

cene 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

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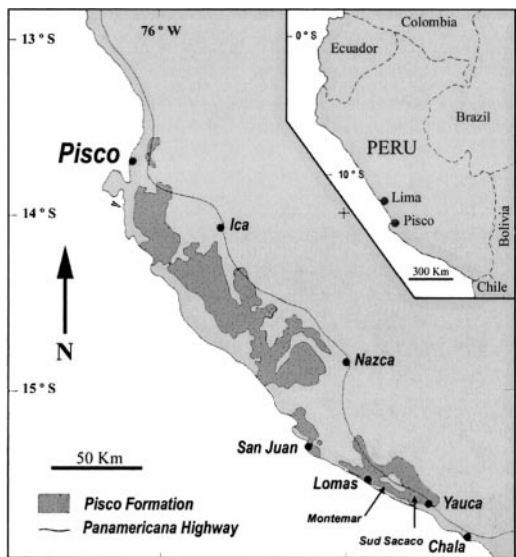


FIGURE 1. Map of the Pisco Formation in Peru showing the location of the Montemar and Sacaco Sur localities where fossils of *Perugyps diazi* new genus and species were recovered (after de Muizon and DeVries 1985). Inset map depicts the location of the Pisco Formation in relation to Lima, the capital of Peru.

of original fossil material from the country, nor could casts be made due to the fragile nature of the bones, all comparisons outside of Peru were completed with high-quality digital photographs (SONY Cyber-shot DSc-P92, 5.0 megapixels) of the fossils, in 2–3 views per element, as well as with 360° digital videos of each specimen, with modern skeletal material. Thus, we are confident that all characters that distinguish the new fossil species could be discerned from these comparisons.

Comparisons to other fossil taxa were completed using published illustrations and descriptions, and casts of Royal Ontario Museum fossils (ROM 12991, 12992, 12993, 13007) of *Geronogyps reliquus* Campbell 1979. Terminology follows that of Howard (1929) and Baumel (1993); measurements were completed with vernier calipers to the nearest 0.1 mm. All fossils described here are housed at the Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM), Lima, Peru, and are catalogued with MUSM numbers.

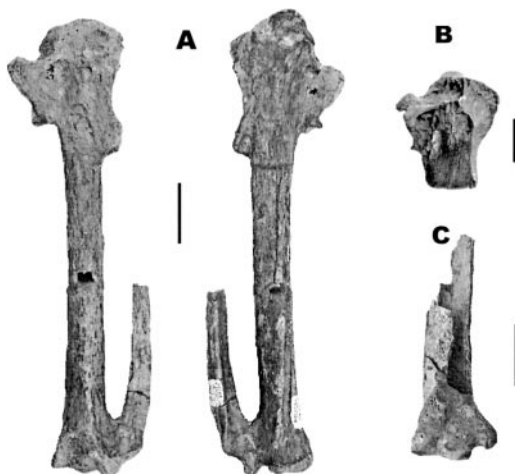


FIGURE 2. (A) Holotype right carpometacarpus (MUSM 213) of *Perugyps diazi* new genus and species in internal (left) and external (right) views. (B) Proximal right carpometacarpus (MUSM 206) of *Perugyps diazi* new genus and species in internal view. (C) Distal left ulna (MUSM 423) of *Perugyps diazi*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

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

bust, than in *Vultur* and *Gymnogyps*; postzygophyses rounder and angled more laterally than in *Vultur* and *Gymnogyps*.

3. Coracoid with deep and rounded sternocoracoidal impression that is not pneumatic (shallower and not rounded, often pneumatic in *Vultur*, *Gymnogyps*, *Sarcoramphus*, *Coragyps*, and *Cathartes*).

4. Carpometacarpus with anterior carpal fossa less pneumatic than in *Vultur*, *Gymnogyps*, *Sarcoramphus*, *Coragyps*, and *Cathartes*. Proximal symphysis short, as in *Vultur*; symphysis relatively longer in *Cathartes*, *Coragyps*, and *Gymnogyps*. MUSM 206 has a muscle scar for the flexor metacarpi short and pronounced, as in *Vultur* and *Breagyps* (L. Miller 1910); scar in less pronounced in *Gymnogyps* and more so in *Cathartes* and *Coragyps*. The scar is longer and pronounced in *Sarcoramphus*. The intermetacarpal tuberosity is low in *Perugyps*, similar to *Vultur*, *Gymnogyps californianus*, and *Breagyps*, and higher in *Sarcoramphus*, *Cathartes*, *Coragyps*, and *G. kofordi* Emslie 1988.

5. Tibiotarsus with tendinal furrow more centered than in *Vultur*, *Gymnogyps*, *Sarcoramphus*, *Coragyps*, and *Cathartes*.

6. Tarsometatarsus robust with distal external trochlea placed as low or lower than middle trochlea (external trochlea higher than middle in *Vultur*, *Gymnogyps*, *Sarcoramphus*, *Coragyps*, and *Cathartes*).

Genus etymology. From Peru, where the fossils were found, and gyps from Greek, masculine, vulture.

Species etymology. Named for Mr. Eusebio Díaz, in recognition of his contributions to Peruvian vertebrate paleontology.

Referred material. MUSM 205, 206, and 260 are from the Sacaco Sur locale while MUSM 204, 261, 263, and 423 are from the Montemar locale of the Pisco Formation (Fig. 1). Right mandible with distal symphysis, MUSM 261 (Fig. 3A); cervical vertebra, MUSM 263; sternal end of right coracoid, MUSM 205 (Fig. 3B); distal left ulna, MUSM 423 (Fig. 2C); proximal right carpometacarpus, MUSM 206 (Fig. 2B),



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.

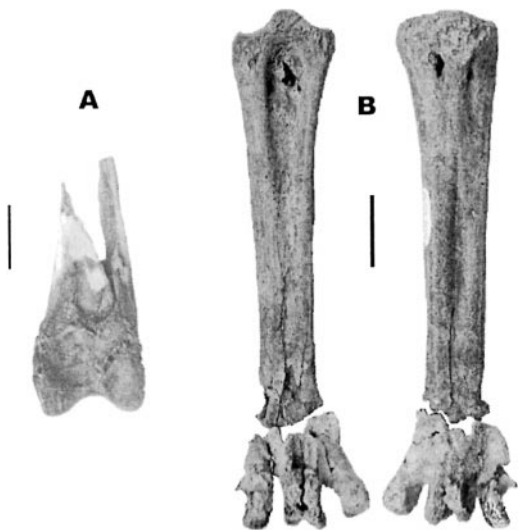


FIGURE 4. (A) Distal left tibiotarsus (MUSM 260) of *Perugyps diazi* new genus and species in anterior view. (B) Right tarsometatarsus (MUSM 204) of *Perugyps diazi* new genus and species in anterior (left) and posterior (right) views. Scale bar = 2 cm.

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*, *Sarcoramphus*, 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 *Sarcoramphus* and *Cathartes*; these borders are relatively higher in *Coragyps*. No vertebrae of *Breagyps* 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 *Sarcoramphus*, 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 prominent in the latter.

Tibiotarsus. MUSM 260 (Fig. 4A) is more similar to *Gymnogyps* than *Vultur* in the morphology 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 condyle is relatively more robust in *Perugyps* compared to *Gymnogyps* or *Vultur*. The tendinal groove passing below the supratendinal bridge is straight in *Perugyps*, *Cathartes*, and *Sarcoramphus*, but curved internally and proximally in *Coragyps*, *Gymnogyps*, and *Vultur* (see Campbell 1979). *Geronogyps* (ROM 13007) has a higher tendinal opening on the shaft, similar to *Perugyps*, as well as a large shelf on the internal side. The intercondylar area is deeper in *Geronogyps* 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 (extends farther down the shaft in *Vultur*, *Gymnogyps*, *Geronogyps*, *Hadrogyps* Emslie 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 relatively robust as in *Gymnogyps* and *Vultur*, narrower in *Coragyps*, *Cathartes* and *Sarcoramphus*. The shaft also flares only slightly outward at the proximal and distal ends in *Perugyps* (shaft flares distinctly outward at ends in *Vultur*, *Gymnogyps*, *Geronogyps*, *Breagyps*, *Hadrogyps*, and *Pliogyps*; more columnar in *Hadrogyps* and *Aizenogyps* Emslie 1998). The tarsometatarsus of *Aizenogyps toomeyae* is relatively larger and

more robust, with broader and deeper distal trochleae, than in *Perugyps*.

DISCUSSION

The Pisco Formation consists of tuffaceous sandy siltstones, medium and coarse-grained sandstones, shelly sandstones, and to a lesser extent, conglomerates, bedded tuffs, and coquinas that represent littoral environments that were partially protected and close to shore (de Muizon 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, Pelagornithidae, Laridae, Scolopacidae, Procellariidae and Diomedidae (de Muizon 1981, de Muizon 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*, *Geronogyps*, and *Wingegyps*) are known from South America (Brodkorb 1967, Campbell 1979, Alvarenga and Olson 2004). *Wingegyps cartellei* is a small enigmatic condor from the late Pleistocene of Brazil, no larger than a raven, but with characters strikingly similar to *Gymnogyps* (Alvarenga and Olson 2004). *Dryornis pampeanus* Moreno and Mercerat 1891 (early to middle Pliocene, Argentina) is not known by any elements shared with *Perugyps* and cannot be compared (Moreno and Mercerat 1891). In addition, an undescribed 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 aigaleus* from the middle Miocene, California (Emslie 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 vultures to the larger condors. *Aizenogyps toomeyae* was a large, robust condor from the Pliocene of Florida (Emslie 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 intercondylar 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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