A new large Cathartidae from the quaternary of Argentina, with a review of the fossil record of condors in South America

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Abstract. The fossil record of condors in South America is relatively extensive. However, fossil specimens for the late Pleistocene of Argentina are scarce. Here, we report a new genus and species of a large sized cathartid of the condor lineage. The new taxon, *Pampagyps imperator* nov. gen. et sp. is based on a right tarsometatarsus from the “Cantera Nicolás Vignogna III” fossiliferous locality, at Marcos Paz County, Buenos Aires Province, Argentina. The fossil was found in the middle levels of the outcrop assigned to the Lujanian Stage/Age (late Pleistocene). Its size is comparable to *Geronogyps* and *Gymnogyps*, being smaller than *Vultur*. Its combination of characters is unique, allowing recognizing a new taxon. An overview of fossil cathartids from Argentine lowlands indicates the existence of several condors that are not closely related to the extant *Vultur gryphus*. The presence of these large cathartids allows to review the fossil record of *V. gryphus*. The latter taxon has been recorded in the Pliocene of Buenos Aires Province (Argentina), and the Pleistocene of Estado Plurinacional de Bolivia and Brazil. A review of the Pliocene specimens from Buenos Aires Province suggests that they belong to an unnamed form not closely related to *Vultur*. Moreover, specimens from Bolivia are different from living *V. gryphus*, indicating that they belong to the extinct species “*Sarcoramphus*” *patruus*. Brazilian records are fragmentary and found near to the locality where the fossil form *Pleistovultur nevesi* was described. Thus, we restrict the record of *V. gryphus* to the late Pleistocene of Andean and Patagonian regions.

Key words. Cathartidae; Condors; Pleistocene; Buenos Aires; Argentina.

Resumen. El registro fósil de cóndores en Sudamérica es relativamente bueno. Sin embargo, especímenes del Pleistoceno tardío de Argentina son escasos. Damos aquí a conocer un nuevo género y especie de catártido de gran tamaño perteneciente al linaje de los cóndores. El nuevo taxón, *Pampagyps imperator* nov. gen. et sp. está basado en un tarsometatarso derecho, proveniente de la localidad fosilífera “Cantera Nicolás Vignogna III”, Partido de Marcos Paz, Provincia de Buenos Aires, Argentina. El especimen fue hallado en niveles asignados al Piso/Edad Lujanense (Pleistoceno tardío). Su tamaño es similar a *Geronogyps* y *Gymnogyps*, siendo más pequeño que *Vultur*. La combinación única de caracteres, permite reconocer un nuevo taxón. Una revisión de los catártidos fósiles de las pampas argentinas indica la existencia de varias especies de cóndores no vinculados estrechamente a *Vultur gryphus*. *V. gryphus* ha sido mencionado para el Plioceno de la Provincia de Buenos Aires (Argentina), y en el Pleistoceno del Bolivia y Brasil. Una revisión de los especímenes del Pleistoceno de la provincia Buenos Aires sugiere que pertenecen a una forma innominada, la cual no estaría cercanamente emparentada con *Vultur*. Asimismo, los especímenes provenientes de Bolivia difieren del actual *V. gryphus*, y en cambio pueden ser asignados a la especie extinta "*Sarcoramphus*" *patruus*. Los registros brasileños son fragmentarios y provienen de localidades cercanas a donde *Pleistovultur nevesi* fuera hallado. En este contexto, restringimos los registros de *V. gryphus* al Pleistoceno tardío de las regiones Andina y Patagónica.

Palabras claves. Cathartidae; Condors; Pleistoceno; Buenos Aires; Argentina.

INTRODUCTION

Cathartids or New World vultures are characterized by their great ability at soaring flight, scavenging habits, and, for condors, their large body size, including one of the greatest wingspans among living birds. This clade currently includes seven species in five genera, divided into two groups: condors (*Gymnogyps, Vultur*) and the smaller vultures (*Coragyps, Cathartes, Sarcoramphus*) (Fisher, 1946; Emslie, 1988; but see Johnson *et al.*, 2016). Condors include two living species: the California Condor (*Gymnogyps californianus*) and the Andean Condor (*Vultur gryphus*) that live in high mountains and arid regions of North and South America respectively.

The fossil record of condors is relatively good (Emslie, 1988; Tambussi & Noriega, 1999). In spite that they are currently restricted to the Americas, the fossil record indicates that small cathartids were present and probably diversified during the Paleogene in the Old World (Cracraft & Rich, 1972; Olson, 1985; Mourer-Chauviré, 2002; but see Mayr, 2009).

Based on this record, Emslie (1988; see also Stucchi & Emslie, 2005; Stucchi *et al.*, 2015) proposed that condors originated in North America and were able to expand southward following coastal corridors on the western side of the Andes. However, recent findings of Miocene condors in South America, as well as the large number and diversity of condors by early Pliocene in Argentina, indicate that a South American origin of the clade cannot be ruled out (Agnolin, 2016). This latter hypothesis is also sustained by the fact that stem vultures are all currently distributed in South America (i.e., *Cathartes, Coragyps*), and that Teratornithidae, the supposed sister-group of cathartids, appears to be also South American in origin (Campbell & Tonni, 1980; Olson & Alvarenga, 2002).

In contrast with the poor diversity of living taxa and their restricted geographical range, Pleistocene condors were notably diverse and widely distributed (Rich, 1983). In South America, a large number of extinct taxa (five different genera, including the living *Vultur gryphus*) have been described (Campbell, 1979; Tambussi & Noriega, 1999; Alvarenga & Olson, 2004; Alvarenga *et al.*, 2008; Stucchi & Emslie, 2009; Stucchi *et al.*, 2015).

The aim of the present paper is to describe a new genus and species of condor from the late Pleistocene of the eastern Pampean Region (Figure 1A) and review the fossil record of condors from the lowlands of South America.

MATERIALS AND METHODS

We follow the osteological nomenclature of Howard (1929) with the emendations made by Campbell (1979). The description of the tarsometatarsus follows the methodology and arrangement employed by Campbell (1979).

The clade Cathartiformes, now widely recognized by means of molecular studies (Johnson *et al.*, 2016), was recently sustained morphologically by Alvarenga (1985) with the aim to emphasize the distinctiveness of this clade.

The phylogenetic arrangement of Emslie (1988) is followed. The "condor group" as recognized by Emslie (1988) and previous authors is here termed as Vulturinae, after Campbell (1979). In spite that Johnson *et al.* (2016) proposed *Sarcoramphus* to be well-nested among condors, we discard this arrangement until new evidence sustaining such proposal become available.

Institutional Abbreviations

MACN Pv., Colección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Argentina; MLP, Colección de Paleontología de Vertebrados, Museo de La Plata, Argentina; MMCIPAS., Museo Municipal "José F. Bonaparte" Centro de Investigaciones Paleontológicas y Arqueológicas de Salto, Salto, Argentina; MPLK., Museo de Ciencias Naturales "Lucas Kraglievich", Marcos Paz, Argentina; Nordenskjöld Collection A, Nordenskjöld Collection at the Naturhistoriska Riksmuseet, Sweeden.

Locality and geological setting

The specimen MPLK-00001 was discovered by one of the authors (F.I.) in 2012 at "Cantera Nicolás Vignogna III" (34°54´42.2´´S and 58°42´12.3´´W; Marcos Paz County, Buenos Aires Province; Figure 1A). The specimen was exhumed from the middle levels of the section (Figure 1B), which is composed of continental and estuarine facies. The continental facies where the fossil was collected consist of silty fine to medium, or medium to coarse bioclastic sandstones. This facies association is interpreted as deposited in coastal creeks that experienced crevassing during high-discharge periods and the development of splays. A radiocarbon date of 31950 ± 830 YBP was obtained from the estuarine facies (Gasparini *et al.*, 2014, 2016). These levels also yielded fossils of mammals (e.g., marsupials, xenarthrans, toxodonts, equids, mastodonts, rodents), turtles, fishes, passerine birds, mollusks, diatoms, and ostracods which are currently under study.

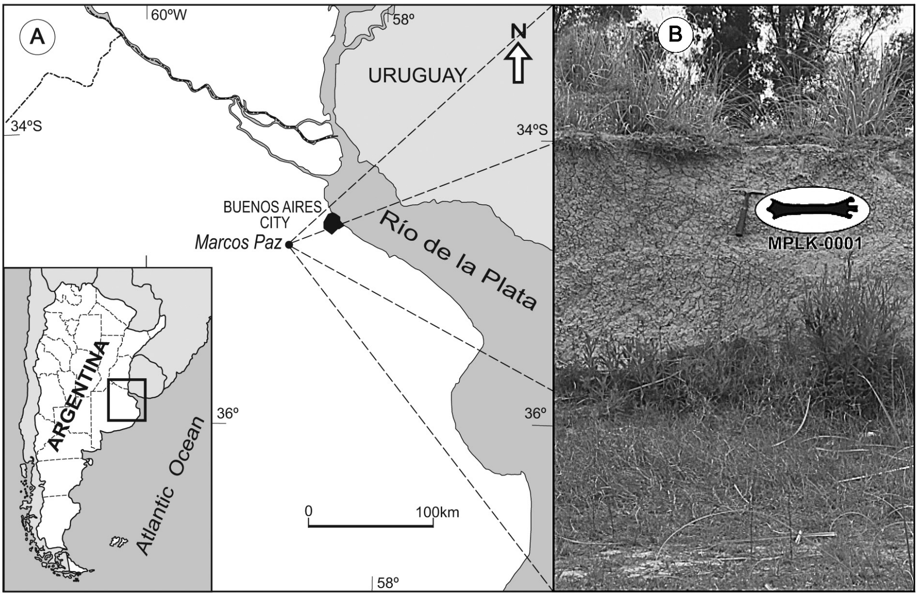

Figure 1. Map depicting the location of "Cantera Nicolás Vignogna III" fossiliferous locality (Marcos Paz County, Buenos Aires Province, Argentina) where MPLK-00001 was found in A; and B, level of the section where the fossil was exhumed.

The fossil mastofauna which was recovered at the same level of MPLK-00001 comprised taxa mainly adapted to open or semi-open and arid or semi-arid environments (e.g. *Toxodon*, *Megatherium*, *Notiomastodon* (=*Stegomastodon)*, *Doedicurus*, *Glyptodon*, *Macrauchenia*). This faunal assemblage supports the paleoenvironmental scenario that appears to have been extended over the Lujanian in the Pampean Region and north-central Argentina, Paraguay and part of Bolivia, whereas, in the Argentinean Mesopotamia, western Uruguay and southern Brazil, the conditions were mainly warm and more humid at the same age (Carlini *et al.*, 2004).

Other new records of Cathartidae include a left proximal end of ulna (MMCIPAS, unnumbered specimen) found in the cliff of the Salto-Arrecifes River on the shores of Salto city. It comes from a unit of 1 m of thickness constituted by massive limolites, lens of fine sand and gravels, deposited on riverbeds or floodplains and referred to the Lower Lujanian "Green Beds" *sensu* Toledo (2011) (early late Pleistocene; 50/55-30 ka AP). This stratigraphic unit corresponds to the Jáuregui Member of the Luján Formation as defined by Toledo (2008).

SYSTEMATIC PALEONTOLOGY

CATHARTIFORMES Coues, 1884

CATHARTIDAE Lafresnaye, 1839
VULTURINAE (Iliger, 1811)
Pampagyps imperator nov. gen. et sp.

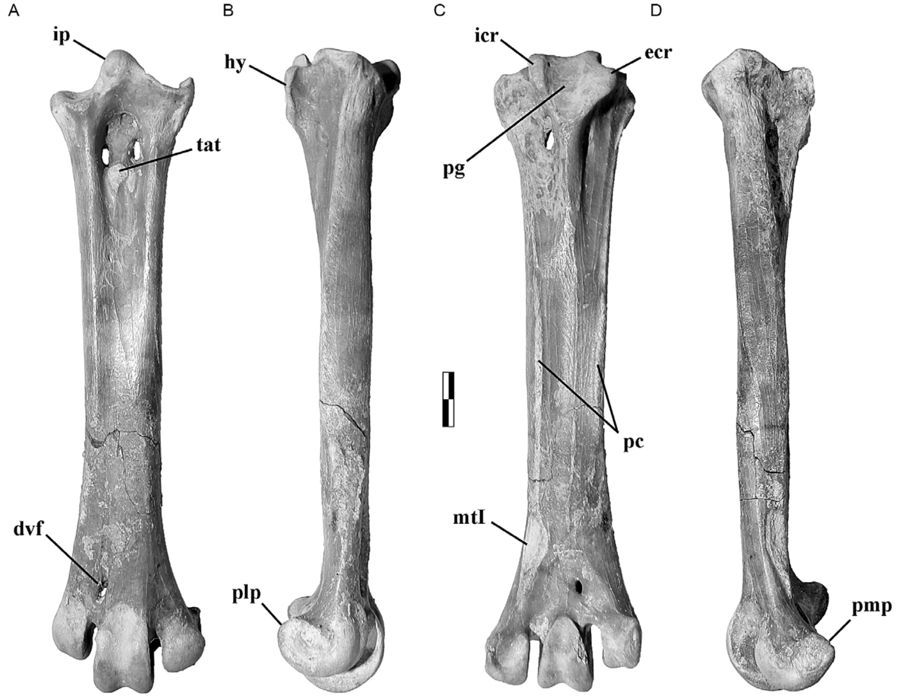

Figure 2. *Pampagyps imperator* nov. (MPLK-00001; holotype) right tarsometatarsus in A, anterior; B, lateral; C, posterior; and D, medial views. References: dvf, distal vascular foramen; ecr, external calcaneal ridge; icr, inner calcaneal ridge; ip, intercotylar prominence; pc, palmar crests; pg, posterior groove; plp, posterolateral process; pmp, posteromedial process; tat, tibialis antiquus tubercle. Scale bar: 1 cm.

Holotype. MPLK-00001, a complete right tarsometatarsus (Figs. 2, 3).

Diagnosis. Medium-sized condor (Table 1) diagnosable on the basis of the following combination of characters (autapomorphies marked by an asterisk*): 1) metatarsal shaft relatively stout, with subvertically oriented and subparallel medial and lateral margins; 2) high and subtriangular-shaped intercotylar prominence; 3) notably wide and deeply excavated anterior metatarsal groove; 4) rounded and mound-like tibialis antiquus tubercle; 5) small distal vascular foramen, with poorly defined outer extensor groove; 6) trochlea IV relatively small, subquadrangular in contour when viewed anteriorly, and with well-defined trochlear groove*; 7) hypotarsus proximally located and subtriangular in contour when viewed posteriorly*; 8) hypotarsus

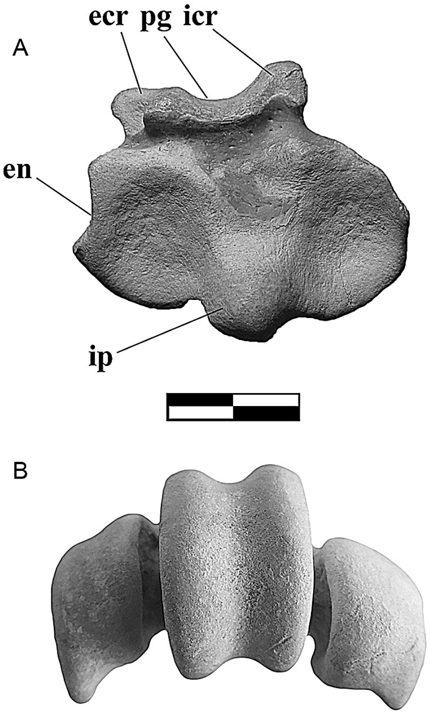

Figure 3 *Pampagyps imperator* nov. (MPLK-00001; holotype) right tarsometatarsus in A, proximal; and B, distal views. References: ecr, external calcaneal ridge; en, external notch; icr, inner calcaneal ridge; ip, intercotylar prominence; pg, posterior groove. Scale bar: 1 cm.

Table 1. Main measurements of tarsometatarsus of *Pampagyps imperator* nov., compared with some recent and extinct condors (modified from Campbell, 1979).

Measurements/Taxon	*Gymnogyps howardae*	*Gymnogyps californianus*	*Vultur gryphus*	*Geronogyps reliquus*	*Pampagyps imperator*
Total length	118.5-122	117.8	118.8-134.7	121.8-124.5	110.2
Proximal width	25.8-29.9	26.7	27.5-29.8	25.4-26.3	27.3
Distal width	29.5-34.0	29.8	30.7-33.6	29.0-30.0	28.7
Minimum width of shaft	13.4-13.5	14.0	13.7-14.7	13.8	14.0
Maximum width of trochlea III	10.6-12.1	11.1	12.1-12.9	10.6-11.6	9.2

separated from internal proximal cotyle by a wide and deep concavity; 9) external calcaneal ridge with a well-developed posterior longitudinal groove*; 10) external proximal cotyle with a deep notch on its lateral surface; and 11) well-developed and prominent posterior plantar crests.

Type and only included species. *Pampagyps imperator* nov. sp.
Age. Lujanian (Late Pleistocene to early Holocene).
Etymology. *"Pampa"* from the Pampa Region where the holotype was found, and *"gyps"*, masculine, vulture. "*Imperator"* from the Latin, which means Commander.

Referred material. MMCIPAS, unnumbered specimen; right proximal end of ulna (Fig. 4). This specimen is referred to *Pampagyps imperator* on the basis of similar size, and because it comes from a near locality and coeval beds.

DESCRIPTION AND COMPARISONS

Intercotylar prominence very high and wide at its base, resulting in a subtriangular contour (wider and broader in *Vultur* and *Breagyps*). Internal proximal cotyle deep, narrow, with high inner margin that is slightly laterally curved. External cotyle rounded, with a notably concave notch on its lateral surface (similar to *Gymnogyps,* straight in *Geronogyps, Hadrogyps, Breagyps*, and *Vultur*). Hypotarsus proximally located, being slightly more proximally extended than proximal cotyla when viewed posteriorly. Hypotarsus relatively narrow (similar to *Geronogyps* and *Sarcoramphus*; wider in *Vultur* and *Gymnogyps*), with a deep and narrow posterior groove, moderately notched externally, with narrow central ridge that narrows distally (more deeply grooved, with a broad central ridge in *Vultur*; slightly grooved, moderately externally notched, and broad central ridge in *Gymnogyps*; slightly grooved, moderately externally notched, and with a narrow central ridge in *Geronogyps* and *Breagyps*). Hypotarsus separated from internal proximal cotyle by a wide and deep concavity (similar to *Geronogyps*; smaller and shallower in *Gymnogyps, Breagyps*, and *Vultur*). External calcaneal ridge with a well developed posterior longitudinal groove (poorly excavated in *Vultur, Gymnogyps, Hadrogyps, Breagyps*, and *Geronogyps*).

Proximal foramina small (expanded in *Hadrogyps*). Anterior metatarsal groove notably transversely wide and greatly excavated, poorly pneumatized proximal to the attachment of *M. tibialis antiquus* (narrower, shallower, and poorly pneumatized in *Gymnogyps, Breagyps*, and *Geronogyps*; wide but notably pneumatic in *Vultur*; transversely wide but proximodistally short in *Hadrogyps*). Attachment for the *M. tibialis antiquus* very large, conforming a mound-like tubercle (notably wider in *Geronogyps*; smaller in *Vultur, Gymnogyps, Breagyps*, and *Hadrogyps*). Attachment of the *M. extensor hallucis longus* located halfway between the base of the anterior metatarsal groove and the inner metatarsal ridge (similar to *Geronogyps*; near the inner metatarsal groove in *Vultur* and *Gymnogyps*). Internal and external anterior metatarsal ridges rounded and narrow (broad external and narrow internal ridges in *Vultur*; both broad and rounded in *Gymnogyps*; external broad and rounded and internal with sharp proximal edge in *Geronogyps*). In posterior view the plantar crests of the tarsometatarsus are very prominent and acute, contrasting with the condition of *Vultur* and *Geronogyps*, whereas in this aspect, *Pampagyps* is similar to smaller cathartids as *Sarcoramphus* and *Coragyps*.

Tarsometatarsus relatively robust, with subparallel medial and lateral margins, being only slightly concave proximally to distal trochleae (lateral margin straight in *Aizenogyps* and *Hadrogyps*). Shaft moderately depressed lateral to the hypotarsus (deeply depressed in *Gymnogyps*). Shaft transversely flat posterior to midpoint (flat

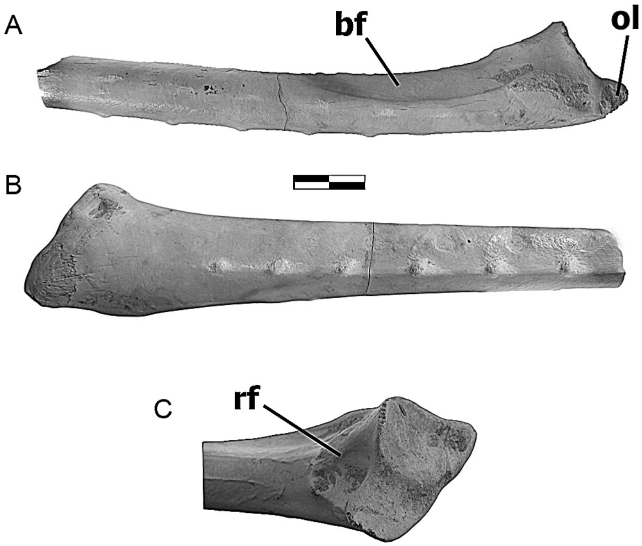

Figure 4. *Pampagyps imperator* nov. (MMCIPAS, unnumbered specimen) left proximal end of ulna in A, lateral; B, posterior; and C, anterior. References: bf, brachial fossa; ol, olecranal fossa; rf, radial fossa. Scale bar: 1 cm.

to gently convex in *Vultur*; flat to concave in *Gymnogyps*; concave in *Geronogyps* and strongly concave in *Hadrogyps*). Shaft widens abruptly to meet internal and external proximal cotylae. Shaft widens subequally to meet distal trochleae II and IV, placing trochlea III near midline of the shaft (similar to *Vultur, Breagyps*, and *Gymnogyps*; in *Geronogyps* it widens much more to meet trochlea II, displacing trochlea III from middle of the shaft).

Anterior surface of trochlea II small (relatively larger in *Vultur, Breagyps*, *Geronogyps,* and *Gymnogyps*) and subquadrangular in contour (notably rounded in *Geronogyps, Breagyps*, and *Gymnogyps*). Trochlea II with a well-developed trochlear groove (flat in *Vultur, Geronogyps,* and *Gymnogyps*). Trochlea II does not extend distally to reach the distal end of trochlea III (similar to *Vultur*, *Breagyps*, and *Gymnogyps*; reaching the level of the distal end of trochlea III in *Geronogyps* and *Pliogyps*). Trochlea III relatively short (similar to *Geronogyps* and *Breagyps*; long in *Vultur, Gymnogyps, Pliogyps,* and *Hadrogyps*). Anterior surface of trochlea IV small, poorly delimited proximally (larger and strongly delimited proximally in *Vultur* and *Hadrogyps*; notably large but poorly delimited proximally in *Gymnogyps* and *Geronogyps*). Trochlea IV with prominent proximal projection on its proximolateral corner in posterior view (similar to *Geronogyps* and *Gymnogyps*; rounded in *Vultur*). Wide external trochlear notch (similar to *Vultur*; relatively narrow in *Gymnogyps* and *Geronogyps*). Notably small distal vascular foramen in anterior view, with poorly defined outer extensor groove (large with well-defined outer extensor groove in *Vultur, Gymnogyps, Geronogyps*; enlarged in *Hadrogyps*).

Ulna (Fig. 4) with relatively small olecranon (similar to *Gymnogyps*; larger in *Vultur* and *Geronogyps*). Attachment of anterior articular ligament small, not extending far distally (similar to *Geronogyps*; large and extending relatively farther in *Vultur* and *Gymnogyps*). Proximal radial depression notably wide and subtriangular in contour (similar to *Gymnogyps*; smaller and rounded in *Vultur* and *Geronogyps*). Poor pneumaticity of the area distal to proximal cotylae (similar to *Gymnogyps*; strongly pneumatic in *Vultur* and *Geronogyps*).

DISCUSSION

Based on these comparisons, it is clear that *Pampagyps* differs from previously described condors from South America. Size definitely distinguishes *Pampagyps* from the minute *Wingegyps* (Alvarenga & Olson, 2004) and the extinct "*Sarcoramphus*" *fisheri* (Campbell, 1979). Comparisons with *Pleistovultur nevesi* (Alvarenga *et al*., 2008) and *Dryornis pampeanus* (Tambussi & Noriega, 1999) are not possible due to the lack of overlapping material. Comparisons with the Miocene genera *Kuntur* and *Perugyps* indicate major differences on trochlear morphology and hypotarsal conformation (Stucchi & Emslie, 2005; Stucchi *et al*., 2015). The same applies to the columnar and robust tarsometatarsus of *Aizenogyps* that shows very short and robust trochleae (Emslie, 1998). Likewise, the very distinct *Pliogyps* differs from *Pampagyps* in having strongly concave medial and lateral margins above distal trochleae, strongly spreading distal trochleae, and very large and wide metatarsal trochlea III (Tordoff, 1959; Becker, 1986).

Because of the poor knowledge about the phylogenetic relationships among fossil condors, the position of *Pampagyps* within vulturines is uncertain. However, general similarities noted in the description, together with similar size and general proportions, suggest that this genus is more closely related to *Gymnogyps* and *Geronogyps*, being notably different in most characters from *Vultur*. However, a detailed analysis of the relationships among condor genera is beyond the scope of the present contribution, and we regard the phylogenetic position of *Pampagyps* among condors as uncertain.

The fossil record of condors in Lowlands of South America

As expressed by Tonni & Noriega (1998), Cenizo *et al.* (2015), and Jones *et al.* (2015) it is possible that diversification in predatory birds and scavengers was initiated by the development and evolutionary history of giant South American mammals comprising the megafauna. In fact, Pleistocene Cathartidae and Caracarini falconids underwent a high diversification probably linked to the abundance of carcasses of megamammals (body mass over 1000 kg). Later, by the latest Pleistocene-early Holocene, the massive extinction of all megafauna (44 from 44 taxa, and 80% of those large mammals over 44 kg) (Cione *et al.*, 2003; 2015) was probably the primary factor that prompted the extinction of several genera and species of cathartids. The same was proposed for the California Condor by Emslie (1987). Tyrberg (2008) also recognized a correlation between fossil avian extinctions and mammalian megafaunal extinctions.

The description of *Pampagyps imperator* adds to this hypothesis further evidence on the diversity of condors in the late Neogene and elevates to six the number of condors in the fossil record of South American lowlands, which also includes *Dryornis pampeanus* (Moreno & Mercerat, 1891; Tambussi & Noriega, 1999) and *Geronogyps reliquus* from Argentina (Tonni & Noriega, 1998; Noriega & Tonni, 2007; Tambussi & Noriega, 1999), *Wingegyps cartellei* (Alvarenga & Olson, 2004) and *Pleistovultur nevesi* (Alvarenga *et al.*, 2008) from Brazil. Possible new unnamed condors have been recently reported: a gigantic specimen from Pleistocene deposits at Uruguay (Rinderknecht *et al.*, 2016), other condors were briefly described by Alvarenga *et al.* (2008) from the late Pleistocene of Brazil and by Fernández Osuna *et al.* (2015) from the late Pleistocene of Santa Fe Province, Argentina. Further, in the collections of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN Pv-13717) there is an incomplete right radius belonging to a large cathartid that was found in late Pleistocene deposits (Carcarañá Formation?) at the Carcarañá river, near the National Route 9, Santa Fe province, Argentina (Figure 5). The specimen differs from *Vultur gryphus* and other vultures in anatomical details, suggesting that it belongs to an undescribed new taxon. In addition to these taxa, the living species *Vultur gryphus* has been identified from several Pliocene and Pleistocene sites in Perú, Estado Plurinacional de Bolivia, Argentina, and Brazil (Tambussi & Noriega, 1999; Alvarenga, 1998; Lönnberg, 1902; Campbell, 1979) (see below).

The new record of *Pampagyps* indicates that the diversity of condors in lowlands of South America was even higher than previously thought. This high Pleistocene diversity of fossil vulturines in the lowlands, and the fact that living *Vultur gryphus* is mostly restricted to the Andean Region, prompts the possibility that the purported lowland *Vultur* fossil records might really belong to other taxa of vulturines.

The fossil record and history of living South American condor (*Vultur gryphus*)

Vultur gryphus was reported from Pliocene and Pleistocene deposits from Argentina (Tambussi & Noriega, 1999), Pleistocene-Holocene of Brazil (Alvarenga, 1998), Bolivia (Lönnberg, 1902; Campbell, 1979), and Perú (Campbell, 1979) (Fig. 6). Most of the fossil records of the living *Vultur gryphus* are outside the current distribution and range of this taxon, and its current distribution in the Andean Region was considered by Tonni & Noriega (1998) the result of the retraction of its range due to climatic change and megafaunal extinction.

The Pliocene record of *Vultur gryphus* is from the Farola de Monte Hermoso and from the Middle Pliocene of Quequén Salado River, at the Buenos Aires Province, Argentina (Tambussi & Noriega, 1999). These records consist of the distorted proximal end of a humerus and an ulnar shaft. However, the assignment to *Vultur gryphus* was not sustained by the authors based on formal features. The analysis of the proximal humerus (MLP 48-XII-16-225) differs from *Vultur* in the orientation and morphology of dorsal and ventral tubercles. Regarding the ulnar shaft (MLP 63-VI-10-15), this element lacks enough diagnostic characters preventing its referral to *V. gryphus*. On this basis, these specimens cannot be confidently referred to *V. gryphus* or even to *Vultur*. In this regard, we consider these specimens as Cathartidae indet.

Another possible record of *Vultur gryphus* that is near the outer limit of its current distribution is from the Pleistocene *s.l.* (exact stratigraphical position unknown) of Tarija, Bolivia. This record corresponds to the holotype on which Lönnberg (1902) based the species *Sarcoramphus patruus*. This taxon was based on a nearly complete left tarsometatarsus with slightly eroded hypotarsus (Nordenskjöld Collection A 50; holotype; Figure 7), and an incomplete right femur (Nordenskjöld

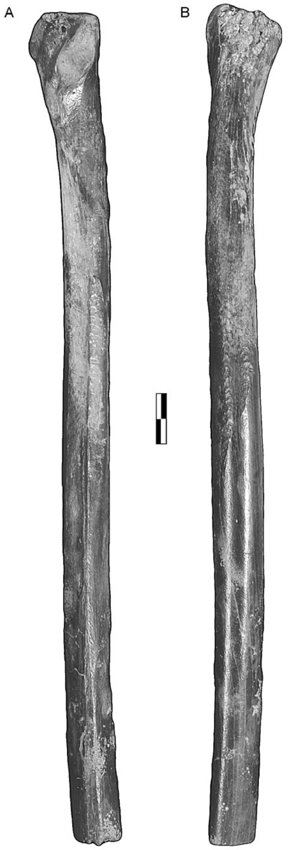

Figure 5. Cathartidae indet. (MACN Pv-13717), incomplete right radius in A, anterior; B, posterior views. Scale bar: 1 cm.

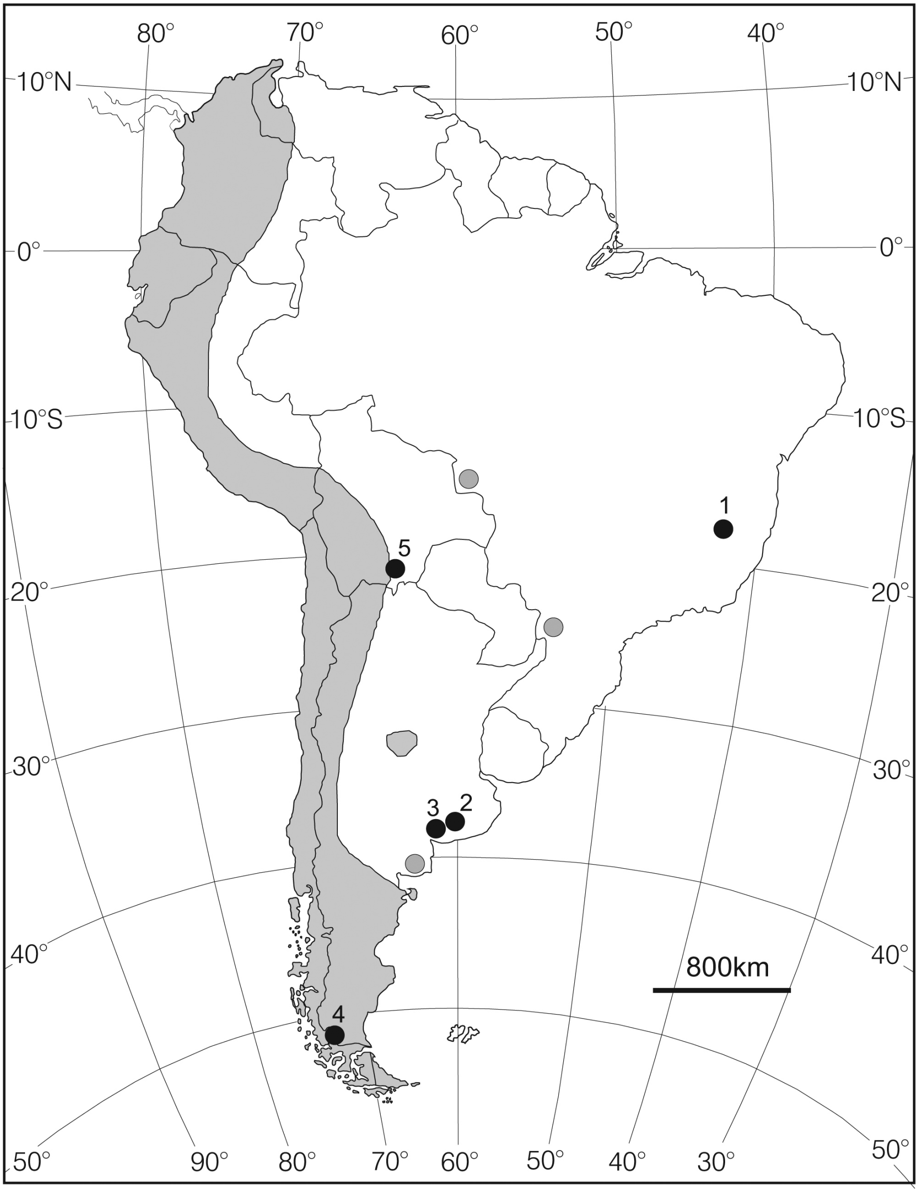

Figure 6. Map showing current and historical distribution of *Vultur gryphus* (in grey) with paleontological records (black circles). References: 1, Late Pleistocene/Holocene Minas Gerais region, Brazil (Alvarenga, 1998); 2, Late Pleistocene, “Playa del Barco”, Argentina (Tonni, 1984); 3, Pliocene, Farola de Monte Hermoso, Argentina (Tambussi & Noriega, 1999); 4, Late Pleistocene, Caverna de la Última Esperanza, Chile (present contribution); 5, Tarija, fossil locality of “*Sarcoramphus*” *patruus*. Distribution of *Vultur gryphus* modified from Ferguson-Lees & Christie, 2001 and Lambertucci, 2007).

Collection A 42a; Figure 7). Later, Fischer (1944) and Campbell (1979) considered *Sarcoramphus patruus* as synonym of *Vultur gryphus*, and noted that characters used by Lönnberg to erect the species were explained by intraspecific variation in *V.*

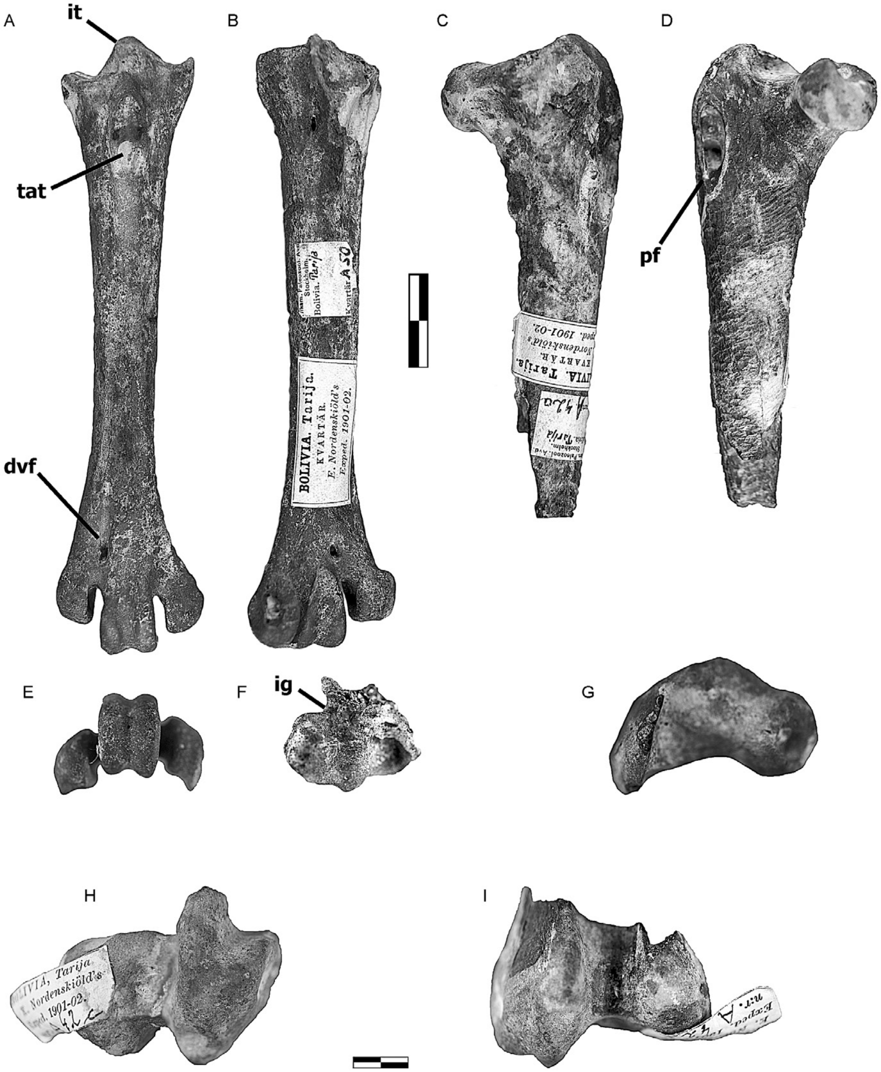

Figure 7. "*Sarcoramphus*" *patruus* Lönnberg, 1902. A, B, E, F, complete left tarsometatarsus with slightly eroded hypotarsus (Nordenskjöld Collection A 50; holotype), in A, anterior; B, posterior; E, distal; and F, proximal views. C, D, G, H, I, incomplete right femur (Nordenskjöld Collection A 42a); C, D, G, proximal end in C, posterior; D, anterior; and G, proximal; H, I, distal end in H, distal; and I, anterior views. References: dvf, distal vascular foramen; ig, inner groove separating the hypotarsus from the rest of the proximal end of the bone; it, intercotylar prominence; pf, pneumatic fossa; tat, tibialis antiquus tubercle. Scale bar: 1 cm.

gryphus. Campbell (1979) considered that although *V. patruus* was within the lower size range of the living species, there were several characters sustaining his taxonomic decision. In spite that characters enumerated by Campbell indicate that *S. patruus* is related to *V. gryphus*, there are some features that indicate that *S. patruus* is a valid taxon. For example, *S. patruus* has metatarsal shaft that widens much more to meet trochlea II, displacing trochlea III from middle of the shaft (widens subequally to meet distal trochleae II and IV, placing trochlea III near midline of the shaft in *Vultur gryphus*), proximal end of tarsometatarsus with hypotarsus separated from internal proximal cotyle by a notably wide and deep concavity (much narrower and shallower in *Vultur gryphus*), and femur with expanded proximal pneumatic foramen and with proximal end notably anteroposteriorly compressed (these two femoral features were early noted by Lönnberg in the original description). The anteroposteriorly compressed proximal femur of *S. patruus* is different from the condition of *Vultur, Gymnogyps,* and *Geronogyps*, and may constitute an autapomorphy of the species. In these features, *S. patruus* is more similar to *Geronogyps*, indicating that referral to *V. gryphus*, and even to *Vultur* is not certain.

Thus, we consider *Sarcoramphus patruus* to be a valid taxon, clearly distinct from other fossil species and *V. gryphus*. In our view, the generic position of "*Sarcoramphus*" *patruus* is still regarded as uncertain.

Recently, Alvarenga (1998) reported a beak of *Vultur gryphus* from late Pleistocene-Holocene deposits at Lapa Vermelha Cave, Minas Gerais, Brazil. Although the specimen is similar to *Vultur gryphus*, its fragmentary nature, and the lack of knowledge of beak morphology in most fossil condors of South America (e.g., *Dryornis, Geronogyps, Gymnogyps reliquus, Pleistovultur, Pampagyps*) prevents the determination of the specimen. Further, it is not improbable that this isolated beak may belong to *Pleistovultur nevesi* which comes from a nearby fossil site (Alvarenga *et al.*, 2008).

Tonni (1984) described the distal end of a femur that was referred to cf. *Vultur* sp., coming from late Pleistocene beds of Monte Hermoso City, southern Buenos Aires Province, Argentina. This specimen was considered referable to *Vultur gryphus* by some authors (Ferguson-Lees & Christie, 2001). However, as indicated by Tonni (1984), the specimen is very fragmentary, preventing a determination beyond the familiar level.

Analysis of collections at MACN resulted in the discovery of a right complete carpometacarpus (MACN Pv 6860; Fig. 8) from late Pleistocene deposits at "Caverna de la Última Esperanza" (or also named "Cueva del *Mylodon*"), Chile (see Humphrey *et al.*, 1993), and belonging to the species *Vultur gryphus*. In fact, the material may be

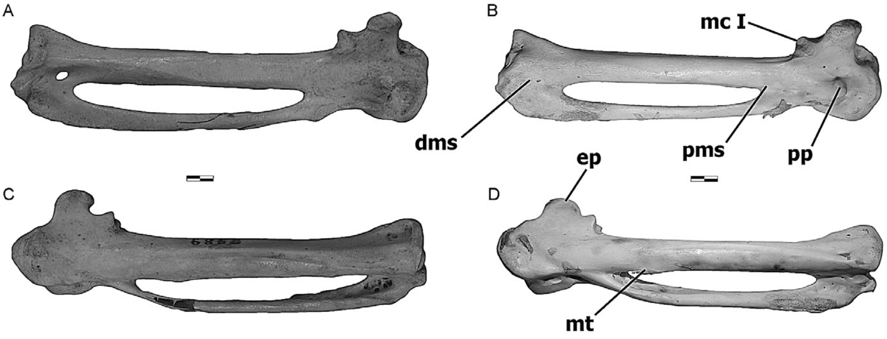

Figure 8. Right carpometacarpus of fossil (A, B; MACN Pv 6860) and recent (C, D) specimens of *Vultur gryphus* in A, C, medial; and B, D, lateral views. References: dms, distal metacarpal symphysis; ep, extensor process; mc I, metacarpal I articular surface; mt, metacarpal tubercle; pms, proximal metacarpal symphysis; pp, pisiform process. Scale bar: 1 cm.

referred to the living South American condor by the following unique combination of characters: poorly dorsally oriented extensor process, anterior carpal fossa strongly pneumatized and notably shallow, proximodistally short proximal metacarpal symphysis (shared with *Breagyps*), relatively low distal metacarpal tuberosity, notably elongate distal metacarpal symphysis (considered as synapomorphic character of *Vultur* by Emslie, 1988), and surface for attachment of external ligament notably wide, lacking a flattened anterior surface (shared with *Gymnogyps*; Howard, 1974; Campbell, 1979; Emslie, 1988; Noriega & Areta, 2005; Stucchi & Emslie, 2005).

Some authors (Emslie, 1988; Tonni & Noriega, 1998; Alvarenga, 1998; Tambussi & Noriega, 1999) suggested that the distribution of the living condor *V. gryphus* is more bounded today than by pre-Holocene times. Although this hypothesis is in accordance with paleoclimatological evidence and the fossil record of other scavenger birds, our study partially contradicts such proposal. The meager fossil record indicates that *Vultur gryphus* was probably restricted during late Pleistocene times to the same geographical area than present (Ferguson-Lees & Christie, 2001). Further, as noted by previous authors (Greenwalt, 1975; Wallace & Temple, 1987; Hertel, 1992), *V. gryphus* is a taxon specialized in living in mountain ranges and arid environments (see Lambuertucci, 2007). In fact, the Andean Condor is almost entirely dependent on slope uplifts to sustain prolonged soaring flight (Greenwalt, 1975; Pennycuick & Scholer, 1984). This evidence may indicate that the distribution of the Andean Condor may have always been intimately linked to the Andes.

In sum, the fossil record of *Vultur gryphus* in the lowlands of South America outside its current geographical range lacks empirical support. Consequently, based on the above evidence, the fossil record of *Vultur gryphus* is restricted to the report of several bones from late Pleistocene deposits at Talara Tar Seeps, northwestern Perú (Campbell, 1979) and southern Chile as reported here.

CONCLUSIONS

The new genus and species *Pampagyps imperator* is described from the late Pleistocene of Buenos Aires Province, Argentina. The size of this taxon is comparable to *Geronogyps* and *Gymnogyps*, being smaller than *Vultur*. It exhibits a unique combination of characters that clearly distinguishes it from other extant and extinct condors. Our review of fossil cathartids from the South American lowlands indicates that several specimens previously referred to the extant *Vultur gryphus* are not certainly assignable to this taxon and further review of this record is warranted. Indubitable fossil records fall within the recent geographical range of the species.

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