AN EARLY CONDOR-LIKE VULTURE FROM NORTH AMERICA

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ABSTRACT.—A new genus and species of condor-like vulture (Ciconiiformes: Vulturidae) is described from the middle Miocene (Barstovian) of North America and is the earliest condor now known in the New World. The fossil record at present indicates that the Vulturidae originated in the Old World, but diversified in the New World. Large body size in vultures developed in North America at least 4 million years (Ma) earlier than thought previously, and the condors probably evolved in North America. Condors were most diverse in the late Pleistocene but are now near extinction. *Received 16 October 1987, accepted 22 March 1988.*

THE family Vulturidae (Ciconiiformes), the New World vultures, consists of seven living species in North and South America. The fossil record indicates that this family was once more diverse and probably originated in Europe or Asia (Olson 1985). No fossils of vulturids younger than the early Miocene [25 million years ago (Ma)] are known in the Old World (Cracraft and Rich 1972). The family has since become restricted to the New World where the earliest record is from the late Oligocene/early Miocene (Alvarenga 1985). Condors are large, distinct vultures whose fossil history has been traced to the late Miocene of North America (Becker 1986), where they probably originated. Extant species include the Andean Condor (*Vultur gryphus*) and the California Condor (*Gymnogyps californianus*); the King Vulture (*Sarcoramphus papa*) is intermediate in characters between the condors and the smaller vulturids (*Cathartes, Coragyps*) (Fisher 1946; Emslie in press).

Recently, two discoveries have increased our knowledge of the fossil history and evolution of the condors. The first was a partial skeleton of a condor closely related to the living California Condor, *Gymnogyps californianus*, from the early Pleistocene (1–1.5 Ma) of Florida (Emslie in press). The second is a single complete tarsometatarsus from the middle Miocene of California. This specimen has characters typical of Vulturidae, including a moderately developed intercotylar prominence, rectangular hypotarsus without a bony canal, deep and long anterior metatarsal groove, and trochleae with only a slight curvature when viewed distally (Cracraft and Rich 1972). It represents a new genus and species of condor-like vulture.

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MATERIAL AND METHODS

Specimens of fossil and Recent vultures were examined at the National Museum of Natural History, Smithsonian Institution, Washington, D.C.; the Natural History Museum of Los Angeles County (LACM); the University of California Museum of Paleontology, Berkeley; and, the Florida State Museum and the collections of Pierce Brodkorb, Gainesville, Florida. Skeletons of Recent vultures examined include *Cathartes aura* (3), *C. burrovianus* (2), *C. melambrotus* (1), *Coragyps atratus* (3), *Sarcoramphus papa* (8), *Vultur gryphus* (12) and *Gymnogyps californianus* (15). Fossil specimens examined are discussed below; all comparisons are from original material except for *Plesiocathartes europaeus* Gaillard 1908, *Diatropornis ellioti* (Milne-Edwards 1892) and *Pliogyps fisheri* Tordoff 1959 for which only casts were available. A cast of *Brasilogyps faustoi* Alvarenga 1985 was not available, and published description and illustrations of this fossil were used in comparison here. All measurements were taken with Vernier calipers to the nearest 0.1 mm.

SYSTEMATICS

Order Ciconiiformes
Family Vulturidae (Illiger 1811)
Hadrogyps n. gen.

Type species:—***Hadrogyps aigialeus*** n. sp.

Generic diagnosis.—Tarsometatarsus with intercotylar prominence moderately high and robust and divides internal and external cotylae nearly completely, as in *Vultur* and *Sarcoramphus* (prominence is low and blunt in *Diatropornis*,

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TABLE 1. Comparative measurements (mm) of the tarsometatarsus of *Sarcoramphus papa* (n = 8; 1 male, 5 female, 2?), *Pliogyps* and LACM 123996. Column headings are TL = total length; PB = proximal breadth; PD = proximal depth; LBS = least breadth shaft; LDS = least depth shaft; DB = distal breadth; BMT = breadth middle trochlea; DMT = depth middle trochlea. Measurements of *P. fisheri* are from Tordoff (1959).

Taxon	TL	PB	PD	LBS	LDS	DB	BMT	DMT
S. papa								
Mean ± SD	97.3 ± 1.8	20.3 ± 0.6	14.9 ± 0.6	10.1 ± 0.4	5.6 ± 0.1	23.3 ± 0.6	8.5 ± 0.2	11.0 ± 0.4
Range	94–99.6	19.3–21.3	14.1–16	9.6–10.5	5.5–5.9	22.5–24	8.3–8.8	10.3–11.6
Pliogyps fisheri (UMMP 38319)	94.0	21.9	—	11.4	7.7	—	9.6	15.2
Pliogyps charon (UF 25952)	86.6	21.1	16.0	10.1	6.3	24.0	9.2	13.5
LACM 123996	93.4	20.7	16.4	11.6	6.7	23.5	9.0	13.8

unknown in *Plesiocathartes,* and moderately high, less robust and only partly divides the cotylae in *Brasilogyps, Cathartes, Coragyps, Breagyps, Gymnogyps* and *Geronogyps*); shaft straight and columnar to ends (shaft flares gradually to steeply towards ends in all other genera of vulturids); anterior metatarsal groove distinct for ⅔ length of shaft (groove extends from ½ to nearly total length of shaft in *Diatropornis, Plesiocathartes, Brasilogyps, Pliogyps, Vultur, Gymnogyps, Geronogyps, Cathartes* and *Coragyps,* and ¼ to ½ length of shaft in *Breagyps*); two large proximal foramina (foramina vary from 2–4 and remain relatively small in all other vulturids); posterior shaft distinctly concave, as in *Sarcoramphus* and *Geronogyps* (shaft flat in *Diatropornis, Pliogyps fisheri, Vultur* and *Breagyps,* and slightly concave in *Plesiocathartes, Gymnogyps, Cathartes, Coragyps* and *Pliogyps charon*); anterior distal foramen large, as in *Sarcoramphus* (relatively small in all other vulturids); ridge below hypotarsus short, broad and rounded, as in *Pliogyps fisheri, Coragyps* and *Breagyps* (ridge relatively narrower and longer in all other vulturids); middle trochlea relatively long and narrow, as in *Diatropornis, Vultur, Breagyps* and *Coragyps* (trochlea shorter and more robust in *Pliogyps, Geronogyps, Gymnogyps, Sarcoramphus* and *Cathartes*).

Etymology.—From Greek *hadros,* for stout or thick, and *gyps,* masculine, vulture.

Description.—Size larger and relatively more robust than *Diatropornis, Plesiocathartes, Brasilogyps, Cathartes* and *Coragyps,* and smaller and relatively less robust than *Gymnogyps, Geronogyps, Vultur* and *Breagyps;* size nearly equal to *Pliogyps* and *Sarcoramphus.* Nearest in size and proportions to the living King Vulture, *S. papa,* but slightly shorter in length and has a more robust shaft and middle trochlea (Table 1). The tarsometatarsus of *Pliogyps charon* is shorter than LACM 123996, has greater breadth at the ends and is less robust in the shaft, while that of *P. fisheri* has a shaft with greater depth and proportionally larger middle trochlea (Table 1).

This taxon differs from all other living and fossil genera of vulturids by its stout, columnar shaft and relatively large proximal and distal foramina. The large proximal foramina are suggestive of an immature individual. The bone, however, is well ossified and only slightly porous at the ends indicating it is from a nearly full-grown adult. In modern vultures of this age, the proximal foramina are at adult size and

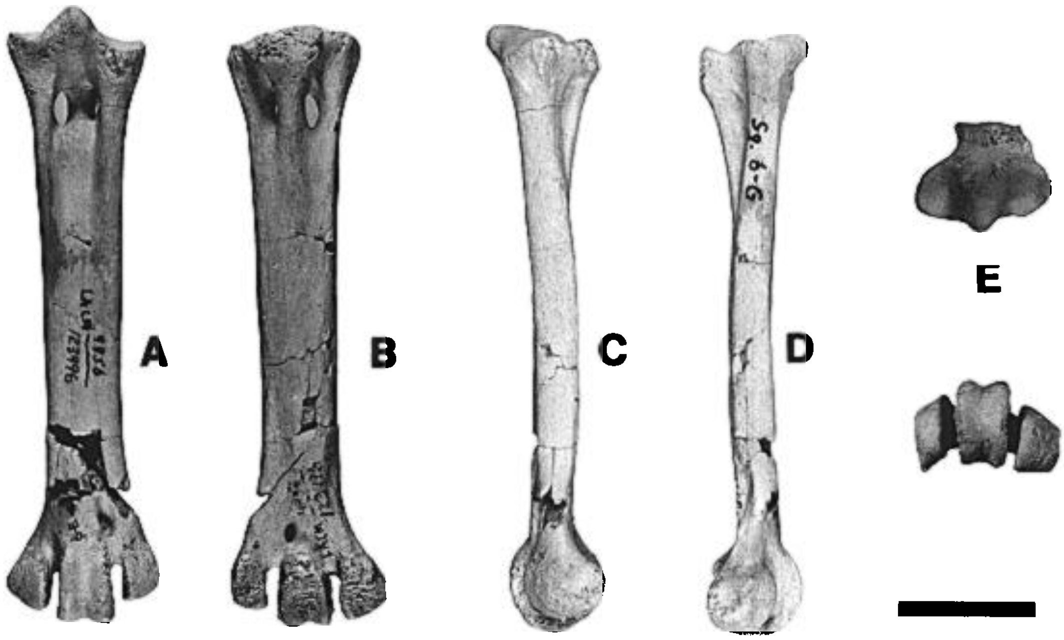

Fig. 1. Left tarsometatarsus, LACM 123996, of *Hadrogyps aigialeus* n. sp. from Sharktooth Hill, Kern Co., California, in (A) anterior, (B) posterior, (C) lateral, (D) internal, (E) proximal and (F) distal views. Scale 1×, bar = 2 cm.

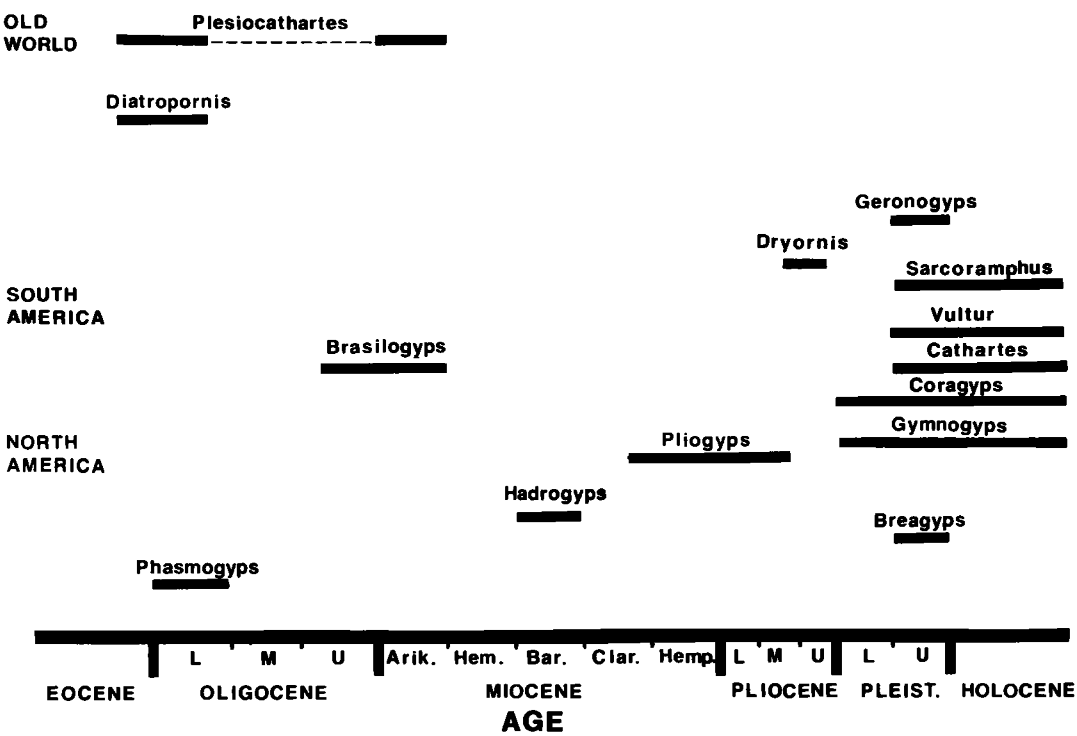

Fig. 2. Geologic and geographic distribution of all valid genera of Vulturidae (Ciconiiformes). Epochs (not to scale) are divided into lower (L), middle (M) and upper (U) periods, or by Land Mammal Ages (Miocene only). Specimens of uncertain geologic distribution are indicated with a dashed line; horizontal alignment of taxa does not reflect phylogenetic relationship. Note genera *Cathartes*, *Coragyps* and *Gymnogyps* have occurred or do occur in both South and North America.

TABLE 2. Fossil taxa referred to Vulturidae with their age, locality, and systematic status. Taxa no longer considered vulturid are indicated by an asterisk (*).

Taxon	Age	Locality	Status
**Lithornis vulturinus* Owen 1842	Early Eocene	Sheppey Isle, England, London Clay	specimen lost; referred as a volant, palaeognathous bird (Olson 1985)
**Paracathartes howardae* Harrison 1979	Early Eocene	Willwood Formation, Wyoming	possibly Gruiformes (Rich 1983 citing K. Campbell, pers. comm.)
**Eocathartes robustus* Lambrecht 1935	Middle Eocene	Coal deposits, Geiseltales, Germany	not vulturid (Olson 1985 citing P. Houde, pers. comm.)
**Neocathartes grallator* Wetmore 1944	Late Eocene	Washakie Formation, Wyoming	now referred to Gruiformes, Bathornithidae (Olson 1985)
Diatropornis ellioti (Milne-Edwards 1892)	Late Eocene/Early Oligocene	Phosphorites du Quercy and Boussac, France	
Plesiocathartes europaeus Gaillard 1908	Late Eocene/Early Oligocene	Phosphorites du Quercy France	
**Amphiserpenterius schlosseri* Gaillard 1908	Late Eocene/Early Miocene	Phosphorites du Quercy, San Gerand-le-Puy France	originally in Sagittariidae, moved to Vulturidae by Cracraft and Rich (1972), and back to Sagittariidae by Mourer-Chauvire and Cheneval (1983)
**Teracus littoralis* Milne-Edwards 1871	Early Oligocene	Puy-en-Velay, France	removed from Vulturidae by Cracraft and Rich (1972); Incertae Sedis (Olson 1985)
Phasmagyps patritus Wetmore 1927	Early Oligocene	Chadron Formation, Colorado	status uncertain (Olson 1985)
**Palaeogyps prodromus* Wetmore 1927	Early Oligocene	Chadron Formation, Colorado	referred to Gruiformes, Bathornithidae (Olson 1985)
Undescribed genus and species	Late Oligocene	Mongolia	currently under study by E. N. Kurochkin (Olson 1985)
Brasilogyps faustoi Alvarenga 1985	Late Oligocene/Early Miocene	Taubate sediments, Brazil	
**Amphiserpentarius robustus* (Milne-Edwards 1871)	Late Oligocene/Early Miocene	Langy, France	referred to *Amynoptilon robustum* (Sagittariidae) by Cracraft and Rich (1972) and to *Pelargoppapus magnus* by Mourer-Chauvire and Cheneval (1983)
Plesiocathartes (?) *gaillardi* Crusafont and Villalta 1955	Early Miocene	Burdigalian, Spain	needs additional study (Olson 1985)
Hadrogyps aigialeus n. gen. n. sp.	Middle Miocene	Sharktooth Hill, California	discussed here
Pliogyps charon Becker 1986	Late Miocene	Love Bone Bed, Florida	
Pliogyps fisheri Tordoff 1959	Middle Pliocene	Rexroad, Kansas	
Sarcoramphus kernense (L. Miller 1931)	Middle Pliocene	Pozo Creek, Kern Co., California	considered a *nomen dubium* (Emslie in press)
Dryornis pampeanus Moreno and Mercerat 1891	Early–Middle Pliocene(?)	Monte Hermosa Form., Argentina	originally assigned to Gruiformes, referred to Vulturidae by Brodkorb (1967)
Gymnogyps n. sp. Emslie in press	Early Pleistocene	Leisey Shell Pit 1A, Hillsborough Co., Florida	

Table 2. Continued.

Taxon	Age	Locality	Status
Vultur fossilis (Moreno and Mercerat 1891)	Late Pleistocene	Canada de Rocha, Lujan, Argentina	junior synonym of *Vultur gryphus* (Fisher 1944, Campbell 1979)
Vultur pratruus (Lonnberg 1902)	Late Pleistocene	Tarija, Bolivia	junior synonym of *Vultur gryphus* (Fisher 1944, Campbell 1979)
Cathartidarum Winge 1888	Pleistocene	Lagoa Santa, Brazil	referred to *Coragyps atratus* by Brodkorb (1964)
Sarcoramphus? fisheri Campbell 1979	Late Pleistocene	Talara, Peru	
Geronogyps reliquus Campbell 1979	Late Pleistocene	Talara, Peru	
Gymnogyps howardae Campbell 1979	Late Pleistocene	Talara, Peru	
Gymnogyps amplus L. Miller 1911	Late Pleistocene	Samwel Cave, California	junior synonym of *G. californianus* (Emslie in press)
Antillovultur varonai Arredondo 1976	Late Pleistocene	Cueva de Paredones, Cuba	considered congeneric with *Gymnogyps* (Olson 1978, Emslie in press)
Breagyps clarki (L. Miller 1910)	Late Pleistsocene	Rancho La Brea, California	
Coragyps occidentalis (L. Miller 1909)	Late Pleistocene	Potter Creek Cave, California	

are not large as in younger birds (pers. obs. of all specimens examined for this study; Emslie in press). The large size of the foramina in *Hadrogyps* therefore is considered an adult character for the genus. The specimen is well-preserved, is not water-worn, and does not appear to have been transported over a great distance prior to deposition.

Hadrogyps aigialeus n. sp.

Holotype.—Left tarsometatarsus missing portion of distal shaft and with ends moderately eroded, LACM 123996, collected by S. A. McLeod, 19 April 1982.

Locality/horizon.—Middle Miocene, Round Mountain Silt, Sharktooth Hill, Kern Co., California, LACM Loc. 4956. The biostratigraphy of this locality was discussed in detail by Barnes (1976) and Barnes and Mitchell (1984). The vertebrate fauna is dominated by marine taxa, particularly cetaceans and pelagic birds (Savage and Barnes 1972; Barnes 1976; Wetmore 1930; Miller 1961, 1962; Howard 1966, 1984; Barnes and Mitchell 1984). Land mammals represented include a tapir, camel, fissiped carnivore and the horse *Merychippus brevidontus* (Mitchell 1965; Savage and Barnes 1972). Savage and Barnes (1972) place this locality within the Barstovian Land Mammal Age (LMA), or 13–15 Ma. Based on the associated fauna, this vulture is presumed to have lived in a coastal or shoreline habitat.

Diagnosis.—As for the genus.

Etymology.—From Greek *aigialeus,* of the shore.

Discussion

The fossil history of the Vulturidae was once thought to have begun in the early Eocene. Systematic revisions now place the first records of this family in the late Eocene/early Oligocene with the small *Diatropornis ellioti* and *Plesiocathartes europaeus* (tarsometatarsi 25–50% smaller than *Cathartes aura,* see Cracraft and Rich 1972), and an undescribed taxon from Mongolia. All fossils previously assigned to the Vulturidae are summarized in Table 2, with their current systematic status.

In North America, four species of Vulturidae have been described from the Eocene and Oligocene but of these only one, *Phasmagyps patritus* Wetmore 1927, may be vulturid (Table 2). Except for *Hadrogyps,* no other fossil vulturids are known in North America until the late Miocene. In South America, the earliest vulturid known is *Brasilogyps faustoi* (Deseadan LMA, 28–21 Ma; see MacFadden et al. 1985 for a discussion on the age of this LMA which corresponds in part with the Arikarean LMA of North America). This vulture is remarkedly similar to *Coragyps* in size and characters, as noted by Alvarenga (1985), evincing the advanced state of the family at this early stage. No other vultures are known from South America until the early to middle Pliocene (Table 2). The largest was *Dryornis pampeanus* from the Montehermosan LMA (Tonni 1980); all other South American condors are late Pleistocene (Table 2).

Prior to now, the fossil record of condors in North America began in the late Miocene (9 Ma) with the appearance of *Pliogyps charon* (Table 2). This robust vulture was closely related to *P. fisheri* from the late Pliocene (Tordoff 1959; 3.3 Ma) and apparently represents part of a radiation of short-legged, robust condor-like vultures in North America (Becker 1986). Only one other pre-Pleistocene condor is known in North America, *Sarcoramphus kernense* (Miller 1931) from the early Pliocene, but it is too poorly known for systematic diagnosis (Table 2). No other condors are known until the early Pleistocene, when a newly described species of *Gymnogyps* appears (Emslie in press), and the late Pleistocene *Breagyps clarki*. The phylogenetic relationships of these condors with living taxa are discussed by Emslie (in press). Only one character of the tarsometatarsus, a more lateral position of the metatarsal facet (position more posterior in other vulturids), is diagnostic for condors (including *Sarcoramphus*) and is present in *Hadrogyps*. Without other elements, the phylogenetic relationship of *Hadrogyps* with other condors cannot be determined.

The geologic and geographic distribution of all valid genera of Vulturidae are summarized in Fig. 2. Greatest diversity occurred in the late Pleistocene, although this may be biased by the more complete fossil record for this period. The discovery of a condor-like vulture in the middle Miocene of California represents the earliest definite vulturid now known in North America, and indicates that large body size in vultures developed much earlier than previously thought. Its probable relationship to condors suggests that this group evolved in North America. In the late Pleistocene, five genera and seven species (including *Sarcoramphus* and living taxa) of condors existed in North and South America. Only three genera and three species survive today and one (*Gymnogyps*) is near extinction in North America. If condors evolved in North America, additional fossils may be expected from other Miocene localities.

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