A NEW GENUS OF TERATORN FROM THE HUAYQUERIAN OF ARGENTINA (AVES: TERATORNITHIDAE)

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ABSTRACT: A review of the family Teratornithidae, heretofore known only from two genera and three species restricted to North America, is followed by the description of a new genus and species, *Argentavis magnificens,* from the Huayquerian (late Miocene) of Argentina. The new teratorn possessed cranial adaptations similar to those of *Teratornis merriami* L. Miller. It was approximately twice as large as *T. merriami,* with a probable wingspan of 6.5 to 7.5 m, the largest flying bird known to science. A possible second occurrence of a teratorn in late Pleistocene deposits of South America (La Carolina, Ecuador) is noted.

RESUMEN: Se realiza una revisión de la familia Teratornithidae, sólo conocida hasta el momento a través de dos géneros y tres especies restringidas a América del Norte. Se describe un nuevo género y especie, *Argentavis magnificens,* procedente de sedimentos de Edad Huayqueriense (Mioceno tardío) de la Argentina. Este nuevo teratorno poseía adaptaciones craneanas similares a aquéllas de *Teratornis merriami* L. Miller, siendo su tamano aproximadamente el doble que el de esta última especie. *Argentavis magnificens* tenía una envergadura probable de 6.5–7.5 m, por lo que representa el ave voladora de mayor tamaño conocida hasta ahora. Se hace referencia también a otro posible registro para un teratorno en el Pleistoceno tardío de América del Sur (La Carolina, Ecuador).

The teratorns are members of an extinct avian family, the Teratornithidae Miller 1925, long considered to be related to the New World vultures of the family Vulturidae. This relationship was based primarily on the raptorial appearance of the beak and certain parts of the postcranial skeleton, although it was questioned even as it was originally proposed (Miller 1909). All known species of the family were very large to gigantic birds, a fact that led many people to consider the teratorns as necessarily having a condor-like style of flying.

To date, the family Teratornithidae has been composed of only two genera, *Teratornis* and *Cathartornis*. The former contains two species, *Teratornis merriami* L. Miller 1909 and *T. incredibilis* Howard 1952. *Teratornis merriami* was the first described and is the best known species of the family, being represented by hundreds of specimens recovered from the asphalt deposits at Rancho La Brea, California, as well as specimens from other late Pleistocene localities in California, Florida, and Nuevo León, México (Brodkorb 1964).

In his original description of *Teratornis merriami,* Miller (1909:315) stated: "*Teratornis,* if it be considered raptorial, displays characters more or less distinctive of each of these groups [other families of the order Accipitriformes], though a preponderance of cathartid affinities is evident." While even then believing that *Teratornis* should be placed in its own family, he hesitated to take that step because of the lack of any hindlimb elements assignable to *T. merriami*. The following year, Miller (1910) described a new genus and species, *Pleistogyps rex,* based upon the hindlimb elements of *T. merriami,* an error he later recognized and corrected (Miller 1925:92). At that time, he established the family Teratornithidae, stating that "*Teratornis* . . . shows very bold divergence in its osteology from the closely knit family of the Cathartidae [=Vulturidae], the divergence taking a number of different pathways. The degree of divergence is in excess of those osteological differences to be noted between most families of living birds classified under one order" (Miller 1925:94).

Teratornis merriami was a very large bird, standing about 0.75 m tall, with a wingspan of 3.5 to 3.8 m. Early estimates (Fisher 1945; Stock 1956; Howard 1972) placed its weight at about 23 kg, but new data and calculations (John Anderson pers. comm.) indicate that 15 kg is a more accurate estimate. The California Condor, *Gymnogyps californianus* (Shaw), reaches a wingspan of 2.75 to 3.1 m and a weight of 9 to 10.5 kg (Koford 1953). Because of its size, it was long thought that *T. merriami* must have been a soaring bird, using wind currents and updrafts to maintain flight, much as the condors do. The tendency to equate large size with soaring flight probably played a significant role in maintaining the concept of *Teratornis* as a condor-like bird. After a study of the postcranial osteology, Fisher (1945) concluded that *T. merriami* was better adapted for flapping flight than condors. He suggested that the type of flight of *T. merriami* may have been similar to that in modern herons and pelicans, and also that it was not ca-

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pable of soaring under conditions that would keep *Gymnogyps* in the air indefinitely.

With this background, the discovery of the even larger *Teratornis incredibilis* was quite astounding. Unfortunately, *T. incredibilis* is known from only three specimens, none of which is particularly diagnostic. The species was named on the basis of a complete cuneiform bone from Smith Creek Cave, Nevada, a site that is "certainly no older than late Pleistocene" (Howard 1972:343). The second specimen referred to the species came from Irvingtonian deposits in the Vallecito Creek valley of the Anza-Borrego Desert, San Diego County, California. This specimen, a distal end of a radius, was referred to *T. incredibilis* "based on its general resemblance to that of *Teratornis merriami* and its tremendous size" (Howard 1963:16). The third specimen, the anterior portion of a beak, came from Blancan deposits in the Fish Creek beds of the Anza-Borrego Desert. This specimen was also referred to *T. incredibilis* on the basis of its general resemblance to *T. merriami* and its large size (Howard 1972).

Whether all of the three specimens referred to *T. incredibilis* are actually from the same species is problematical. As discussed by Howard (1972:343), if the three specimens are from the same species, its longevity would be in excess of three million years. However, these specimens are so undiagnostic that they may not even all belong to the same genus, much less the same species, and if they are all of the same species they may belong to a genus other than *Teratornis* (see Howard 1972:343). We hasten to add that we believe Howard's method of describing the specimens was most appropriate; she brought their existence to the attention of the scientific community, while at the same time leaving the resolution of higher level taxonomic categories until the discovery of more diagnostic material.

The three specimens referred to *T. incredibilis* are each approximately 40 percent larger than corresponding specimens of *T. merriami*. The large size of the cuneiform and radius indicates that *T. incredibilis* was a flying bird, and Howard (1952:52) has suggested that it had a wingspan of about 4.9 to 5.2 m, an estimate based upon the size of its cuneiform relative to that of *T. merriami*. *Teratornis incredibilis,* then, was rivaled only by *Osteodontornis orri* Howard 1957, a gigantic marine bird from the Miocene of California, for the title of the world's largest flying bird. Howard (1957:15) suggested that *O. orri* may have had a wingspan near 5 m.

The genus *Cathartornis* is composed of only one species, *C. gracilis* Miller 1910, a taxon based upon two tarsometatarsi from Rancho La Brea, California. In a reevaluation of *C. gracilis,* Miller and Howard (1938) considered it to be generically distinct from *Teratornis*. They also considered *Teratornis* and *Cathartornis* to be sufficiently similar to warrant the transfer of the latter from the Vulturidae, wherein it was originally placed, to the Teratornithidae. Based upon the size of the tarsometatarsus, which is as long as but more slender than that of *Gymnogyps californianus*, *C. gracilis* is the smallest of the known teratorns.

Brodkorb (1964) reduced the Teratornithidae to subfamilial rank within the Vulturidae. On the other hand, Jollie (1977:111) considered *T. merriami* to be "the most extreme cathartid in some respects" and the teratorns to be distinct at the familial level within the Accipitriformes. Olson (1978:168), however, has suggested that the teratorns may be a pelecaniform group. This suggestion was based in part upon the shape of the sternum of *T. merriami,* about which Fisher (1945:727) noted, "There is nothing cathartid about this bony element . . . " The senior author of the present paper recently initiated detailed studies of the osteology of *T. merriami,* with the intended goal of further determining its functional morphology and phylogenetic relationships. Preliminary results indicate that *T. merriami* was condor-like in its locomotory but not its feeding behavior, and that the teratorns may not be related to any of the families of Accipitriformes. In fact, *T. merriami* does have many structural similarities to pelecaniform birds, both in its cranial (as noted below) and postcranial osteology. However, these similarities appear to be a result of convergence and probably do not reflect phylogenetic relationships.

In summary, the Teratornithidae has been comprised of three species of very large to gigantic flying birds placed in two genera, all known from North America. Two of the species, *Teratornis incredibilis* and *Cathartornis gracilis,* are known from only a few specimens, and may or may not be related to *T. merriami*. The latter is known from hundreds of specimens, but its physical characteristics and relationships with other avian groups are still poorly understood.

To the Teratornithidae we can now add a new genus and species of such staggering proportions that one can only marvel that such a bird could have existed, and at the good fortune of finding a fragmented associated skeleton of it.

SYSTEMATICS

Order Accipitriformes (Vieillot 1816)
Family Teratornithidae L. Miller 1925

DESCRIPTION: Family characters listed by Miller (1925:94) include: (1) lateral and backward extension of postauditory prominences; (2) close approximation of maxillopalatines; (3) reduction of cerebellar region; (4) compression and vaulting of beak; (5) elliptical foramen magnum; (6) broadening and shortening of sternum; (7) weakness and openness of furcula; (8) ruggedness of humeral head; (9) elongation and attenuation of ulna and metacarpus; (10) relative weakness of posterior limbs; (11) reduction of trochanter of femur; (12) reduction of tibial crests; (13) columnar character of tarsometatarsus. Additional characters not listed by Miller include (14) skull broad and dorsoventrally flattened; and (15) quadrate with an L-shaped mandibular articulation extending without break from quadratojugal socket to anteromost point of ventral surface.

Argentavis **new genus**

TYPE SPECIES: *Argentavis magnificens* new species.

DIAGNOSIS: Differs from *Teratornis* L. Miller 1909 by having skull (Fig. 1a, b) (1) broader, more flattened dorsoventrally, with greater posterolateral extension of postauditory prominences; with (2) foramen magnum lying in a plane facing more posteriad, i.e., more vertical; (3) foraminal openings immediately anterolateral to occipital condyle large, but possibly enlarged by breakage (very small in *Teratornis*); (4) occipital condyle as wide as widest portion of foramen magnum (about

Table 1. Measurements (in mm) of *Argentavis magnificens* new genus new species, *Teratornis merriami* L. Miller,[1] and *Gymnogyps californianus* (Shaw) (n = 1).

	Argentavis magnificens	*Teratornis merriami*	*Gymnogyps californianus*
Skull			
Length	435 ± 20	222.0	158.0
Maximum width through postauditory prominences	150 ± 10	86.7	50.0
Top of cranium through ventral tip of occipital condyle	66 ± 5	55.7	45.0
Maximum width of foramen magnum	15.5 ± 1	12.2	11.4
Height of foramen magnum	17.5 ± 1	13.4	12.5
Width of occipital condyle	15.0	9.5	6.1
Height of occipital condyle	11.0	6.1	5.0
Quadrate			
Maximum distance from squamosal articulation to tip of mandibular articulation	66 ± 2	36.7–39.2 38.3	27.8
Anteroposterior ventral length	46 ± 3	24.2–28.5 26.4	18.0
Center of socket for quadratojugal to anterior end of mandibular articulation	53 ± 2	25.5–28.3 26.8	15.3
Humerus			
Length	570 ± 10	310.0–330.0 318.2	271.0
Least width of shaft	49.0	22.9–26.7 24.6	21.0
Depth of shaft at point of least width	35.0	17.6–20.5 19.5	16.0
Coracoid			
Head to internal distal angle	325 (est.) (as preserved, 205)	151.3–163.5 156.5	98.0
Head to medial opening of coracoidal fenestra	125.0	70.1–77.7 74.4	53.2
Maximum width of glenoid facet	31.0	17.9–18.8 18.3	13.4
Dorsal end of glenoid facet to ventral end of procoracoid	78.0	39.1–42.6 40.5	35.7
Tarsometatarsus			
Length	240 (est.) (as preserved, 133)	130.4–145.8 139.8	121.5
Width at distal end of distal foramen	42.0	20.8–23.4 22.0	22.5

[1] Measurements for the skull were taken from specimen No. LACM HCB1381. For the other elements, measurements were taken from five complete specimens of each from the collections in the George C. Page Museum, Natural History Museum of Los Angeles County. This group of measurements is not intended to be definitive for the species, but only to demonstrate its general size.

one-third narrower than foramen magnum in *Teratornis*); (5) transverse ridge connecting the postauditory prominences absent; (6) postauditory prominence with posterolateral corner less angular, not projecting ventral to occipital condyle in posterior view; (7) quadratojugal with quadrate articulation projecting much less sharply ventrad.

Tarsometatarsus (Fig. 4l–m) with (1) center of shaft in anterior view distinctly elevated above those portions of shaft leading to internal and external trochleae, resulting in the distal foramen lying well below the elevation of the center of the shaft (in *Teratornis* the shaft is well rounded in this area, with opening for distal foramen lying at same level as anterior edge of center of shaft); (2) distal foramen of uniform width throughout its length, with outer extensor groove leading to it restricted in width by elevated center of shaft (distal foramen wider proximally than distally in *Teratornis,* with outer extensor groove wide proximally, narrowing significantly at distal foramen); (3) shaft with anterior half at most proximal preserved point quite convex, with medial side extending farthest anteriad (in *Teratornis,* anterior metatarsal groove extends distad to become outer extensor groove, so anterior half of shaft is not convex at any point proximal to distal foramen); (4) shaft appears elliptical in cross section at most proximal point preserved, with long axis of ellipse running anteromedially-posterolaterally (roughly rectangular in *Teratornis,* being wider than deep); (5) shaft edge external to distal foramen more convex.

Differs from *Catharthornis* Miller 1910 by having tarsometatarsus with anterior surface of shaft convex (strongly grooved, or channeled, throughout length in *Cathartornis*).

ETYMOLOGY: Latin, *argentum,* silver; *avis,* feminine, bird. In reference to Argentina, the country of origin.

MEASUREMENTS: For measurements of the holotype see Table 1.

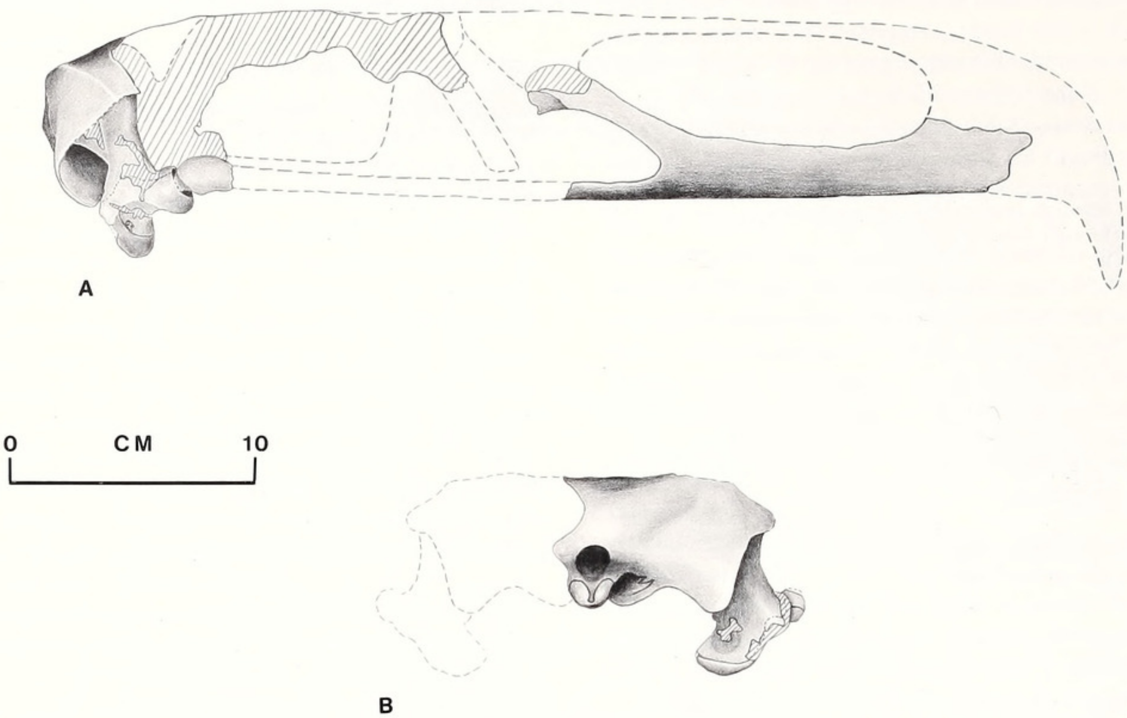

Figure 1. Holotype (Museo de la Plata No. 65-VII-29-49) skull of *Argentavis magnificens* new genus new species in lateral (a) and posterior (b) view. ×0.30. In this and all other figures the hatched areas represent portions of the specimen where the bone has flaked away, but the matrix remains to show form; the dotted lines show estimated outline of bone where missing, based upon corresponding bones of *Teratornis merriami*.

Argentavis magnificens new species

Figures 1, 2a–c, 3, 4

HOLOTYPE: Associated partial skeleton, consisting of portions of skull, right quadrate, humeral end and shaft of right coracoid, left humerus with badly damaged proximal and distal ends, portion of shaft of left(?) ulna, portion of shaft of right radius, distal end of left metacarpal II, midportion of left metacarpal III, shaft of right tibiotarsus, shaft of right tarsometatarsus. Original in the División Paleontología Vertebrados del Museo de La Plata, No. 65-VII-29-49; cast in Natural History Museum of Los Angeles County, LACM 120074. Collected by Rosendo Pascual and Eduardo Tonni.

TYPE LOCALITY: Salinas Grandes de Hidalgo, Departamento Atreucó, La Pampa Province, Argentina. Located about 15 km south of the Hidalgo station on the railroad connecting Carhué (Buenos Aires Province) with Doblas (La Pampa Province), approximately 37°14′S, 63°36′W; see Figure 5.

HORIZON AND AGE: Epecuén Formation (fide Pascual 1961) (lowest level outcropping at locality). Huayquerian (late Miocene).

DIAGNOSIS: As for genus. For measurements see Table 1.

ETYMOLOGY: Latin, *magnificens,* magnificent.

DESCRIPTION: All of the bones have been severely fractured, but, except for the skull, crushing has been minimal. The fracture lines have been omitted from the illustrations. In some places the bone has flaked away, leaving only a replica in matrix to indicate its general form. Where this has happened in areas without diagnostic characters, the illustrations were prepared as if the bone were still present. Hatching indicates where bone has broken away in diagnostic areas, leaving only the general form. Unfortunately, all the bones of the postcranial skeleton lack their most diagnostic portions. Were it not for the partial skull and quadrate, the specimen would have to be considered indeterminate; but these two elements provide strong evidence that relates *Argentavis* to *Teratornis*.

The quadrate (Fig. 2a–c) of *Argentavis* differs from that of *Teratornis* by having (1) quadratojugal socket positioned farther from main body of quadrate, i.e., with short leg of L-shape proportionately longer, giving appearance of having a "neck;" (2) mandibular articulation extending farther anteroventrad, but not as far anteriad proportionately, giving greater degree of curvature to ventral edge in medial view; (3) pterygoid articulation positioned more laterally; (4) squamosal articulation with medial portion hemispheric, mounted on columnar-like structure (medial portion elongated, positioned on more massive extension of main body of quadrate in *Teratornis*); (5) mandibular articulation with anterior one-half of medial portion, i.e., its long leg, proportionately much larger, lying at less of an angle to horizontal.

The coracoid of *Argentavis* (Fig. 4a–d) is characterized by having (1) shaft laterally compressed at humeral end, nearly flat anterior to glenoid facet (not compressed, and well rounded anterior to glenoid facet in *Teratornis*); (2) procoracoid reduced, with ventral margin lying at about 45 degrees to main axis of shaft (not reduced, with ventral margin straight and lying at 90 degrees to main axis of shaft in *Teratornis*); (3) glenoid facet deeply concave in lateral view, with deepest point lying just ventral to horizontal midline of facet (slightly concave in lateral view, with deepest point lying near ventral end in *Teratornis*); (4) glenoid facet in posterior view with medial edge roughly vertical and in line with coracoidal fenestra, and parallel to main axis of shaft (sloping significantly mediad from dorsal to ventral points in posterior view, not in line with

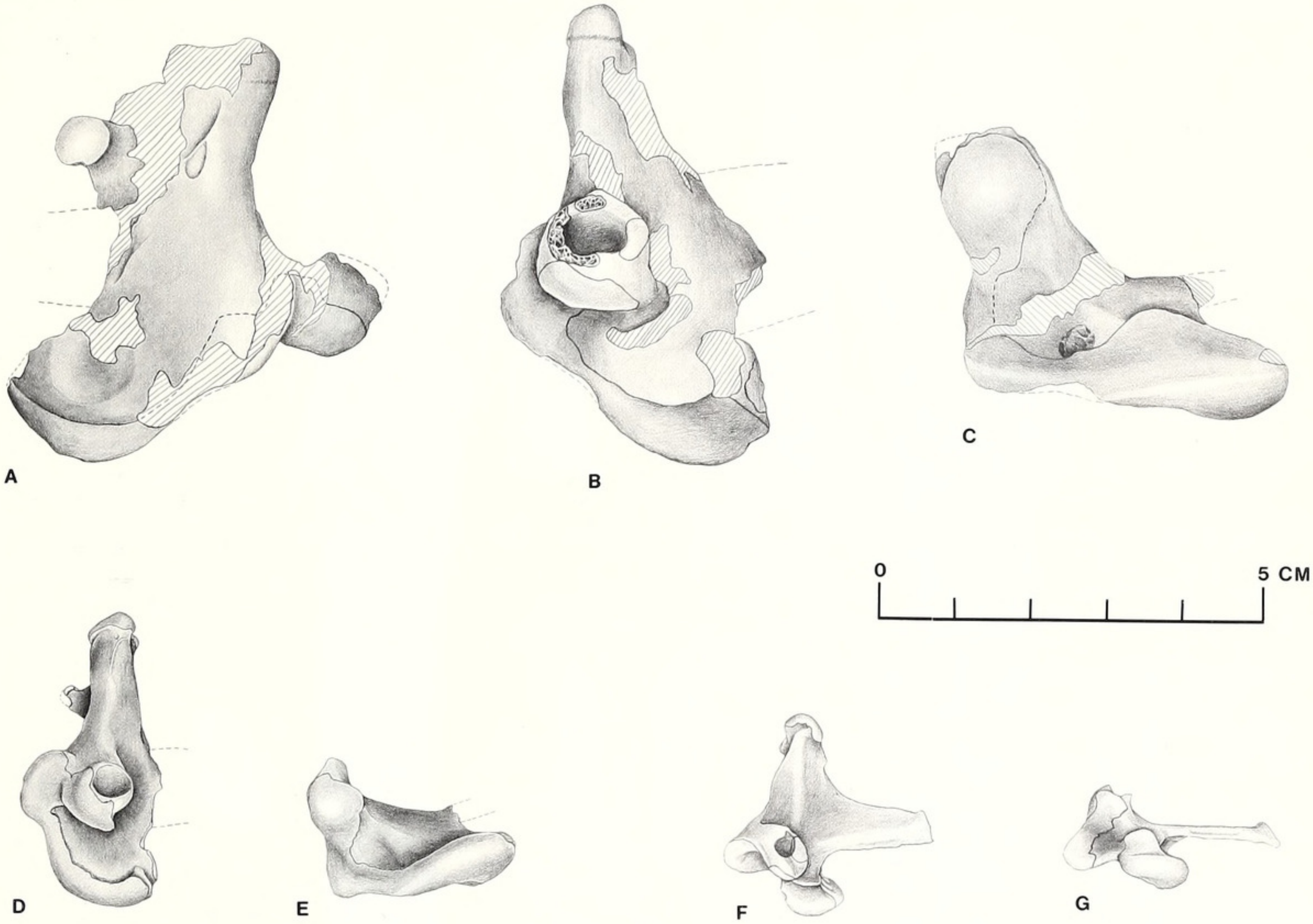

Figure 2. Holotype (Museo de la Plata No. 65-VII-29-49) right quadrate of *Argentavis magnificens* new genus new species in posterolateral (a), lateral (b), and ventral (c) view; quadrate of *Teratornis merriami* L. Miller (LACM HCB747) in lateral (d) and ventral (e) view; quadrate of *Gymnogyps californianus* (Shaw) (LACM Bi1800) in lateral (f) and ventral (g) view. All ×1.

coracoidal fenestra or main axis of shaft in *Teratornis*); (5) coracoidal fenestra lying much nearer procoracoid, and opening mediad more posteriorly; (6) ridge leading ventrad from procoracoid toward internal distal angle small, but distinct (absent in *Teratornis*).

The humerus of *Argentavis* (Fig. 3a–b) differs from that of *Teratornis* by having (1) shaft in anterior view with proximal two-thirds relatively straighter and distal one-third curving more sharply dorsad; (2) shaft in dorsal view appearing more strongly sigmoid; (3) external tricipital groove appearing to extend proximad to ectepicondylar prominence, which is broken away (does not extend proximad to ectepicondylar prominence in *Teratornis*); (4) deltoid crest with very pronounced knob, the distal portion of which is broken away (similar, but with knob less elevated above and less sharply demarcated from shaft proximally in *Teratornis*); (5) shaft slightly less but still deeply convex between deltoid crest and bicipital crest.

The preserved portion of the ulna of *Argentavis* (Fig. 4i) has no diagnostic characters, displaying only three papillae of the secondaries spaced about 30 mm apart (spaced about 15 to 18 mm apart in *Teratornis merriami*).

The carpometacarpus of *Argentavis* (Fig. 4e–h) differs from that of *Teratornis* by having metacarpal II with (1) tendinal groove deeper, bordered by more pronounced ridges, and lying more anteriorly on external side of shaft; (2) shaft with posterior half more rounded, with a small ridge lying on posterior side and extending a short distance proximad to most proximal point preserved (ridge absent in *Teratornis*); (3) distal metacarpal symphysis lies closer to center of shaft proximally; (4) facet for digit II with that portion preserved having anterior end extending farther posteriad at a greater angle. Metacarpal III has (1) shaft more triangular in cross section; (2) anterior surface more excavated, bordered externally by more pronounced ridge).

The tibiotarsus of *Argentavis* (Fig. 4j–k) lacks any diagnostic characters, but can be seen to differ from that of *Teratornis* by having (1) shaft slightly curved in anterior view, although some curvature seen in Figure 4j–k may be a result of breakage (essentially straight in *Teratornis*); (2) fibular crest much less developed, although this may be a result of breakage; (3) tendinal groove with proximal end more symmetrical and lying near center of shaft rather than near internal edge of shaft.

AGE AND ASSOCIATED FAUNA

The holotype of *Argentavis magnificens* was collected from the brownish to reddish terrestrial sediments of the late Miocene Epecuén Formation (fide Pascual 1961). This formation

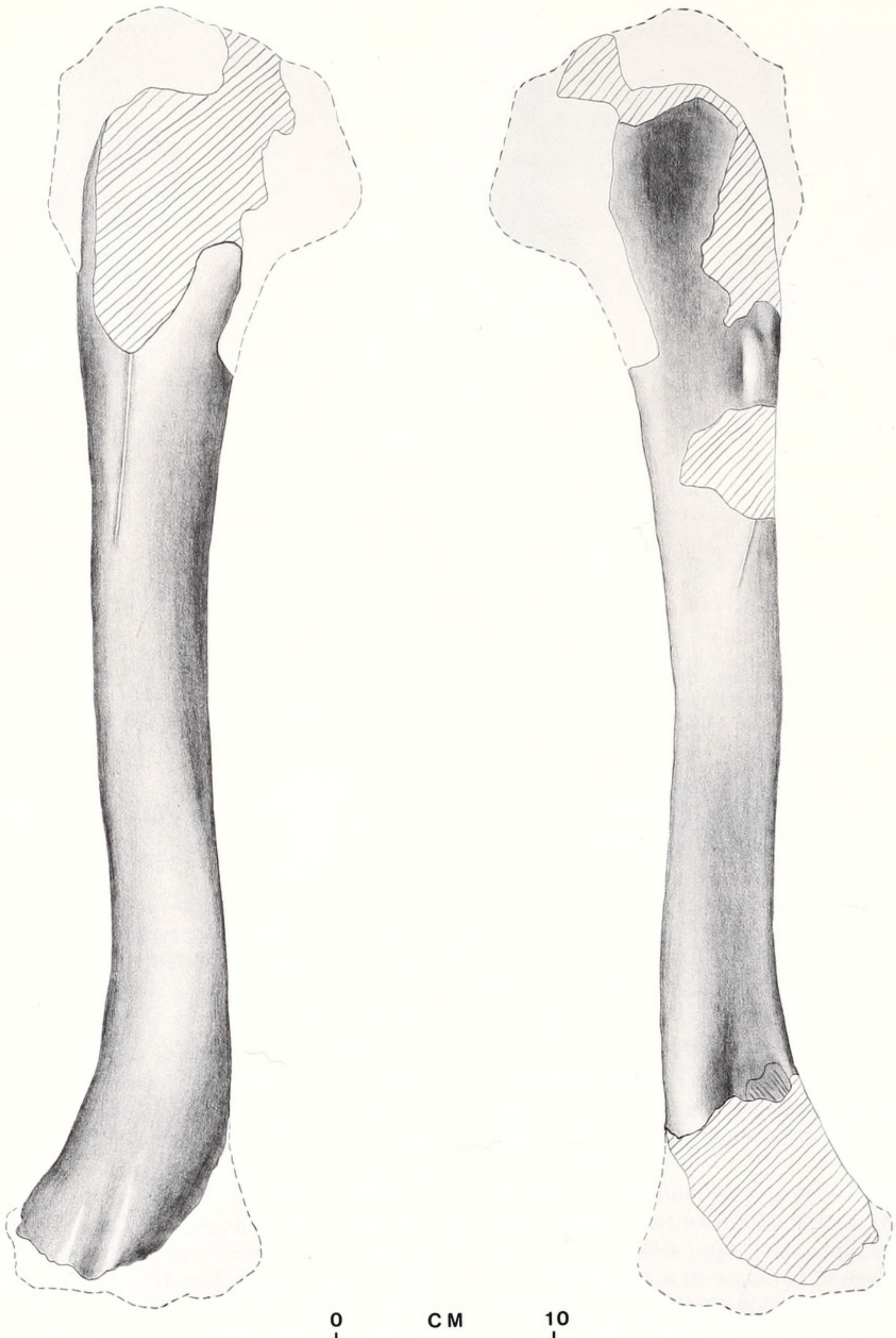

Figure 3. **Holotype (Museo de la Plata No. 65-VII-29-49) left humerus of** *Argentavis magnificens* **new genus new species in anconal (a) and palmar (b) view.** ×0.30.

is composed primarily of fine sand with minor amounts of silt and rare lenses of clay. Irregular thicknesses of caliche-like concretions occur at several levels; isolated concretions may also occur.

The late Miocene age assignment of the Epecuén Formation is based on the following mammalian fauna reported for the deposits of Salinas Grandes de Hidalgo by Zetti (1972): Order Marsupialia, Family Borhyaenidae: *Borhyaenidium musteloides* Pascual and Bocchino, *Thylacosmilus* aff. *atrox* Riggs; Order Carnivora, Family Procyonidae: *Cyonasua brevirostris* Moreno and Mercerat; Order Notoungulata, Family Toxodontidae: *Pisanodon* n. sp.; Family Hegetotheriidae: *Hemihegetotherium* n. sp., *Paedotherium borrelloi* Zetti; Order Litopterna, Family Macraucheniidae: ?*Promacrauchenia* sp.; Order Edentata, Family Mylodontidae: *Elassotherium altirostre* Cabrera; Family Dasypodidae: *Proeuphractus* sp., *Macroeuphractus* sp.; Family Glyptodontidae: Sclerocalyptinae gen. et sp. indet.; Order Rodentia, Family Caviidae: *Orthomyctera*

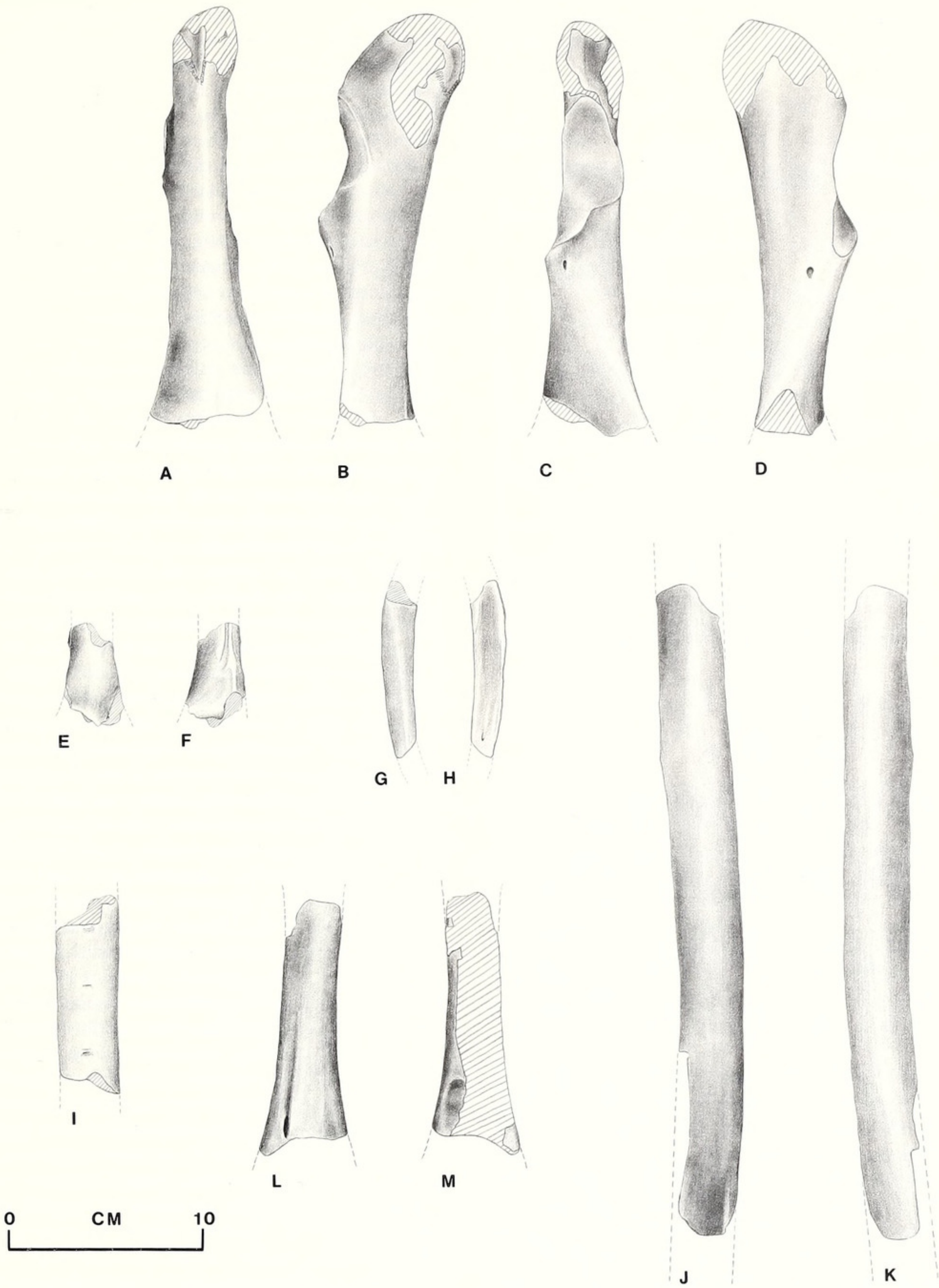

Figure 4. Holotype (Museo de la Plata No. 65-VII-29-49) of *Argentavis magnificens* new genus new species: right coracoid in anterior (a), lateral (b), posterior (c), and medial (d) view; distal end of left metacarpal II in internal (e) and external (f) view; medial portion of left metacarpal III in lateral (g) and medial (h) view; portion of shaft of left(?) ulna in anconal (i) view; shaft of right tibiotarsus in anterior (j) and posterior (k) view; shaft of right tarsometatarsus in anterior (l) and posterior (m) view. ×0.30.

sp., *Paleocavia* sp.; Family Hydrochoeridae: ?Protohydrochoerinae gen. et sp. indet.; Family Chinchillidae: *Lagostomopsis* sp.; Family Octodontidae: *Phtoramys* sp., *Pseudoplataeomys* sp.; Family Echimyidae: ?*Eumysops* sp.

This assemblage of mammalian taxa is characteristic of the Huayquerian (*sensu* Pascual et al. 1965), a South American land mammal age conventionally referred to the late Miocene (Marshall et al. 1979). In addition to *Argentavis magnificens* and the mammalian fauna, reptiles and other birds are known from the deposits, but have yet to be described.

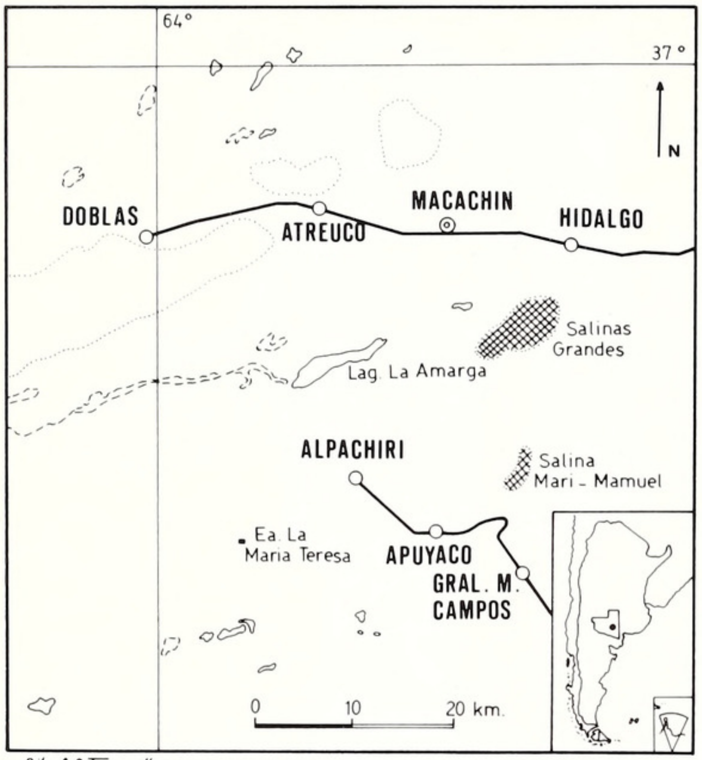

Figure 5. Map showing location of type locality, Salinas Grandes, in Argentina.

DISCUSSION

The similarities of the skull and quadrate of *Argentavis* to those of *Teratornis* are very striking when characters of these two genera are contrasted with those of genera of the other accipitriform families. Although the unique structure of the teratorn skull has been commented on since its description (Miller 1909), there has been no attempt to analyze it as there has been for its postcranial skeleton (Fisher 1945). The studies now in progress on *Teratornis merriami* will attempt to fill this void. A few preliminary comments about functional morphology that apply to both *Argentavis* and *Teratornis* are presented here.

Teratornis appears to be more specialized than *Argentavis*, e.g., by having the postauditory prominences ending in a more angular corner that projects ventral to the occipital condyle and a prominent transverse ridge connecting the postauditory prominences. *Teratornis* also has the posterior portion of the skull much more rounded, in both lateral and posterior view (for illustrations of *T. merriami* see Miller 1909, 1925; Jollie 1978). It is not possible to make additional cranial comparisons because of the damaged nature of the holotype skull of *Argentavis magnificens*.

The posterior extension of the postauditory prominences is an adaptation to increase the gape of the mouth by moving the hinge line of the jaw posteriad. In both *Argentavis* and *Teratornis* the quadrate articulates with the squamosal posterior to the occipital condyle, giving the maximum possible gape without actually having the squamosal lying farther posteriad than the parietal or supraoccipital.

The articulation of the quadrate with the squamosal is such that, when the ventral end is swung through its arc, it moves posterolaterally at an angle of about 45 degrees to the long axis of the skull. This contrasts with the condition found in other accipitriform families where the quadrate movement is almost parallel to the long axis of the skull, and is far more restricted. By rotating the quadrate so that the ventral end moves laterad as much as it moves posteriad, pressure is exerted on the articular of the lower jaw, forcing the rami of the lower jaws apart posteriorly. A similar, but less developed, condition is found in pelicans (Pelecaniformes: Pelecanidae), and the pelican quadrate bears a strong superficial resemblance to the teratorn quadrate. The Frigatebird, *Fregata magnificens* (Pelecaniformes: Fregatidae), and albatrosses (Procellariidae: Diomedeidae) also have a similar condition.

As illustrated by *Gymnogyps* (Fig. 2f–g), in the family Vulturidae the mandibular articulation is not "L-shaped" or continuous, and the two portions do not lie perpendicular to each other. All genera of vulturids have a distinct shelf on the medial side of the anterior portion of the mandibular articulation, a character limited to that family within the Accipitriformes. The lateral component of the articular movement on the quadrate, and of the quadrate on the squamosal, in *Gymnogyps* and other vulturids is minimal.

In the teratorn quadrate, the quadratojugal socket is much less restrictive than in vulturids, an adaptation that assists the lateral movement of the quadrate. A similar condition exists in frigatebirds and albatrosses; in the pelicans there is no socket present, only a flat or convex articular surface.

The lower jaw of *Argentavis* is unknown, which is perhaps to be expected if it resembled that of *Teratornis*. The lower jaw of *Teratornis merriami* is very weak, as noted by Howard (1950), and even at Rancho La Brea no complete specimens are known; the portion immediately anterior to the mandibular foramen was apparently such a thin sheet of bone that it was never preserved, or it was lost in collection and preparation. This character is also an adaptation for lateral movement of the posterior portion of the lower jaw; it provides a weak spot where the jaw can flex without having a weak symphysis. This condition is also present in frigatebirds and albatrosses. The exact function of this character complex in feeding remains to be worked out, but it appears very unlikely that teratorns fed in a manner similar to any other accipitriform.

A comparison of the measurements of *Argentavis magnificens* and *Teratornis merriami* reveals that the former is almost twice the size of the latter in almost all measurements. If we were to assume that it is reasonable to extrapolate directly from the estimated size of *T. merriami* (isometric scaling), we could say that *A. magnificens* had a wingspan of 7 to 7.6 m, a height of 1.5 m, and a weight of 120 kg. Of course, there is the possibility that isometric scaling may not be applicable in this case. Also, because the size of *T. merriami* was calculated with the consideration in mind that it was a condor-like bird, its estimated wingspan may be quite erroneous; and the estimate may as well be too small as too large. The estimate of the height and the new weight estimate of *T. merriami* are probably much more accurate. In spite of these qualifications, *A. magnificens* is certainly the largest flying bird known to have existed.

The question as to how such a tremendously large bird like *Argentavis magnificens* could fly remains unanswered. It is often believed that very large flying birds must depend on wind currents to become airborne and remain aloft, and that "the maximum size attainable by flying birds is limited by surface-volume ratio and the speed of flight" (Storer 1971:152). Or, "The larger the bird, the faster it must fly to stay airborne" (Pettingill 1970:2). As noted above, however, Fisher (1945) suggested that *T. merriami* was capable of flapping flight, possibly similar to that of herons and pelicans, both of which may fly at speeds considerably slower than that observed for many smaller species. Storer (1971:153) commented that "Under present conditions, the larger albatrosses, pelicans, storks, swans, condors, turkeys, and bustards must represent about the largest size to which flying birds can evolve." While it is certainly true that environmental conditions in La Pampa Province of Argentina were very different in the Huayquerian than they are today, it is questionable whether the mechanics of avian flight have changed. Rather, there is a greater probability that our understanding of avian flight is still very incomplete.

The presence of a teratorn in South America should not be considered too surprising. Campbell (1979), in a study of the late Pleistocene avifauna of the Talara Tar Seeps of northwestern Peru, described a new species of *Gymnogyps* and a new genus and species of large eagle, *Amplibuteo hibbardi*; both genera were previously known only from North America (*G. amplus* and *G. californianus*; *Amplibuteo* (=*Morphnus*) *woodwardi*). Many Recent species previously reported as fossils only from North America were also reported from the Talara Tar Seeps. Earlier, Campbell (1976) reported an indeterminate fragmentary vulturid tarsometatarsus from La Carolina, Ecuador, that differed markedly from the three genera of condors later reported from the Talara Tar Seeps. A recent comparison of this specimen with tarsometatarsi of *T. merriami* from Rancho La Brea, California, shows that although it is not referable to *Teratornis merriami,* there is a very good possibility that it is from a different species of *Teratornis*. As collections of avian fossils, particularly those from South America, increase, we can expect to find many more examples of what have been considered North American groups appearing in South America, and vice versa (e.g., see Campbell this vol.).

Although there is a good possibility that the Teratornithidae should not be placed within the Accipitriformes, it is prudent at the present time to leave it there pending completion of more detailed studies. It can be stated that there are almost no points of similarity between the cranial osteology of teratorns and that of the members of the Falconidae, Accipitridae, Serpentariidae, or Vulturidae. And, although there are similarities between the postcranial skeleton of teratorns and those of the other families of Accipitriformes, there are many more striking differences.

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LITERATURE CITED

BRODKORB, P. 1964. Catalogue of Fossil Birds. Part 2 (Anseriformes through Galliformes). Bull. Florida State Mus., Biol. Sci. 8(3):195–335.

CAMPBELL, K.E., JR. 1976. The Late Pleistocene Avifauna of La Carolina, Ecuador. Smith. Contrib. Paleobiology 27:155–168.

———. 1979. The Non-Passerine Pleistocene Avifauna of the Talara Tar Seeps, Northwestern Peru. Royal Ontario Mus., Life Sci. Contrib. 118:1–203.

———. 1980. A Review of the Rancholabrean Itchtucknee River Avifauna, Florida. (this vol.)

FISHER, H. 1945. Locomotion in the Fossil Vulture *Teratornis*. Amer. Mid. Nat. 33:725–742.

HOWARD, H. 1950. Wonder Bird of the Ice Age. Los Angeles County Museum Leaflet Series. Science No. 3:1–3.

———. 1952. The prehistoric avifauna of Smith Creek Cave, Nevada, with a description of a new gigantic raptor. Bull. So. Calif. Acad. Sci. 51:50–54.

———. 1957. A Gigantic "toothed" Marine Bird from the Miocene of California. Santa Barbara Mus. Nat. Hist., Bull. Dept. Geol. 1:1–23.

———. 1963. Fossil birds from the Anza-Borrego Desert. Nat. Hist. Mus. Los Angeles Co., Contrib. Sci. 75:1–33.

———. 1972. The incredible teratorn again. Condor 74(3):341–344.

JOLLIE, M. 1977. A Contribution to the morphology and phylogeny of the Falconiformes (Parts 2, 3). Evol. Theory 2(4,5):115–300.

———. 1978. A Contribution to the morphology and phylogeny of the Falconiformes (Part 4). Evol. Theory 3(1):1–142.

KOFORD, C. 1953. The California Condor. National Audubon Society. Reprinted by Dover Publ., New York. 154 pp.

MARSHALL, L.G., R.F. BUTLER, R.E. DRAKE, G.H. CURTIS, AND R.H. CURTIS. 1979. Calibration of the great American interchange. Science 204(4390):272–279.

MILLER, L. 1909. *Teratornis,* a new avian genus from Rancho La Brea. Univ. Calif. Publ., Bull. Dept. Geol. 5(21):305–317.

———. 1910. The Condor-like Vultures of Rancho La Brea. Univ. Calif. Publ., Bull. Dept. Geol. 6(1):1–19.

———. 1925. The Birds of Rancho La Brea. Carnegie Instn. Washington Publ. 349:63–106.

MILLER, L., AND H. HOWARD. 1938. The status of the extinct Condor-like birds of the Rancho La Brea Pleistocene. Publ. Univ. Calif. Los Angeles, Biol. Sci. 1:169–176.

OLSON, S.L. 1978. Multiple origins of the Ciconiiformes. Proc. Colonial Waterbird Group 1978:165–170.

PASCUAL, R. 1961. Un nuevo Cardiomyinae (Rodentia, Caviidae) de la Formación Arroyo Chasicó (Plioceno inferior) de la provincia de Buenos Aires. Ameghiniana 2(4):101–132.

PASCUAL, R., AND A. BOCCHINO. 1963. Un nuevo Borhyaeninae (Marsupialia) del Plioceno medio de Hidalgo (La Pampa). Ameghiniana 3(4):97–107.

Pascual, R., E.J. Ortega, D. Gondar, and E. Tonni. 1965. Las Edades del Cenozoico mamalífero de la Argentina con especial atención a aquéllas del territorio bonaerense. An. Com. Inv. Cient. Prov. Buenos Aires 6:165–193.

Pettingill, O.S. 1970. Ornithology in Laboratory and Field. 4th ed. Burgess Publ. Co., Minneapolis. 524 pp.

Stock, C. 1956. Rancho La Brea. A Record of Pleistocene Life in California. 6th ed. Nat. Hist. Mus. of Los Angeles County, Sci. Series No. 20; Paleontology, No. 11:1–81.

Storer, R.W. 1971. Adaptive Radiation of Birds. Pp. 150–188 *in* Avian Biology (D.S. Farner and J.R. King, Eds.). Vol. 1. Academic Press, New York.

Zetti, J. 1972. Los mamíferos fósiles de Edad Huayqueriense (Plioceno medio) de la Región Pampeana. Thesis No. 240, Fac. Cs. Nat. and Museo de la Plata. 86 pp. (unpublished)