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REVIEW OF THE LATE PLEISTOCENE AVIFAUNA FROM LAKE MANIX, CENTRAL MOJAVE DESERT, CALIFORNIA

George T. Jefferson[1]

ABSTRACT. Late Pleistocene lacustrine clay, silt, and nearshore sand deposits of Lake Manix, Mojave Desert, California, have yielded 139 specimens of fossil birds, including several articulated partial skeletons. Six extinct and 19 extant taxa are represented. The avifauna includes the first recognized fossil gulls, *Larus oregonus* and *Larus* sp., from Pleistocene terrestrial deposits in the Southwest. *Gavia* cf. *G. arctica* (Arctic Loon), *Phalacrocorax macropus* (extinct cormorant), *Mergus* cf. *M. merganser* (Common Merganser), the extinct chronoclinal subspecies *Fulica americana shufeldti* (Shufeldt's American Coot), and cf. *Actitis* (sandpiper) are new to the Pleistocene record of the region. The avifauna is part of the Rancholabrean Camp Cady Local Fauna, and has most taxa in common with the assemblage from Fossil Lake, Oregon. Habitat preferences of comparative extant taxa and inferred depositional environments indicate extensive reedy marshlands, beach flats, and open water lacustrine conditions.

INTRODUCTION

Since H. Howard's description of the Lake Manix avifauna (Howard, 1955), many additional specimens of fossil birds, including articulated partial skeletons, have doubled the number of taxa known from the site. These additional materials add significantly to an understanding of the late Pleistocene avifauna of the inland Southwest. The first fossil gulls, *Larus oregonus* and *Larus* sp. and other extant and extinct taxa including *Gavia* cf. *G. arctica, Phalacrocorax macropus* (extinct), *Mergus* cf. *M. merganser, Fulica americana* cf. *shufeldti* (extinct), and cf. *Actitis* are new to the Pleistocene record of the region. The Lake Manix avifauna is taxonomically most similar, in the abundance of inland lacustrine forms, to the Wisconsinan age assemblage from Fossil Lake, Oregon. Other comparable late Pleistocene assemblages are known from China Lake, McKittrick, Rancho La Brea, and Carpintaria, California (Table 1). New radiometric dates (Bischoff, pers. comm., 1982) indicate that most of the material from Manix is older than 200 Kyr (thousand years) BP (before present).

J.P. Buwalda of the University of California, Berkeley (UCB), recovered the first bird fossils from Lake Manix during an exploratory expedition in 1913. At that time, he considered the fauna to be early Pleistocene, based on the fragmentary mammalian remains (Buwalda, 1914). L.V. Compton of UCB later published (Compton, 1934) a description of the five specimens collected by Buwalda and first noted similarities with the Fossil Lake avifauna. A relatively large assemblage of birds and mammals was collected in 1952 by H. Winters (1954). The twelve avian taxa from this collection were subsequently described by Howard (1955). The fauna was considered late Pleistocene in age, and no older than Illinoian.

Based on fieldwork performed during the middle 1960's and a review of existing collections, the Rancholabrean age assemblage from Lake Manix was designated the Camp Cady local fauna by G. Jefferson (1968). Initial radiocarbon dating by various institutions indicated the lake beds were Wisconsinan in age (Bassett and Jefferson, 1971).

Fossil vertebrates from Lake Manix are presently housed in five separate institutional collections: the Natural History Museum of Los Angeles County, Vertebrate Paleontology Section (LACM); San Bernardino County Museum, Earth Science Collection (SBCM); University of California, Berkeley, Museum of Paleontology (UCMP); the University of California, Riverside, Earth Sciences Department (UCR); and the United States Geological Survey, Denver, Colorado.

AGE AND STRATIGRAPHY

The Lake Manix avifauna ranges in age from greater than 350 Kyr to about 35 Kyr BP. The stratigraphic section is well dated by C-14 (carbon-14) (Bassett and Jefferson, 1971; Marcus, pers. comm., 1984) and U/Th (uranium-thorium equilibrium) radiometric techniques (Bischoff, pers. comm., 1982), and tephrochronologic correlation (Sarna-Wojcicki, 1980). Most taxa and the majority of specimens fall between 200 and about 300 Kyr BP (Table 2).

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Table 1. Geographic distribution of taxa. Abbreviations: FLO = Fossil Lake, Oregon; CLC = China Lake, California; RLB = Quaternary Rancho La Brea, California; MKC = McKitterick, California; CAC = Carpinteria, California; sf = subfamily; g = genus; s = species; ss = subspecies. Extinct taxon = *. Data from: Fortsch, 1978; Howard, 1946, 1962; Miller, 1925, 1931, 1935; Miller and DeMay, 1942; Stock, 1953.

Lake Manix taxa	FLO	CLC	RLB	MKC	CAC
Gavia cf. *G. arctica*					
Podiceps cf. *P. nigricollis*	s		g	g	
Aechmophorus occidentalis	s	g			
Pelecanus aff.					
P. erythrorhynchos	s				
Phalacrocorax auritus	s	g	g		
*P. macropus**	s				
*Ciconia maltha**			s	s	s
*Phoenicopterus minutus**					
*P. copei**	s				
Cygnus cf. *C. columbianus*	g	g	s	s	s
Branta canadensis	s	g	s	s	
Anas cf. *A. crecca*	s	g	s	s	
A. cf. *A. platyrhynchos*	s	g	s	s	s
Aythya sp.	g	s	g		
Mergus cf. *M. merganser*	s				
Oxyura jamaicensis	s	g		s	
Haliaeetus leucocephalus	s	g	s	s	s
Aquila chrysaetos	s	g	s	s	s
Fulica americana cf.					
*F. a. shufeldti**	ss	g	s		
cf. *Grus*		g	g	g	
cf. *Actitis*					
Phalaropodinae			sf		
Larus cf. *L. oregonus**	s				
L. sp.	g				
Bubo virginianus	s		s	s	s

Table 2. Stratigraphic/chronologic range of taxa in the Manix Formation. Abbreviations: m TS = meters above base type section, Kyr = approximate thousand years. Stratigraphic occurrence = X. Extinct taxon = *. Data from: Howard, 1955; Jefferson, 1968; Bassett and Jefferson, 1971; Bischoff, pers. comm., 1982.

	m TS	9	11	27	30	36
Taxon	Kyr BP	350+	300	200	100	20
Gavia cf. *G. arctica*			X			
Podiceps cf. *P. nigricollis*			X	-------X		
Aechmophorus occidentalis			XX	-X-X--X	---X	--XX
Pelecanus aff. *P. erythrorhynchos*			XX			
Phalacrocorax auritus			X	----------	X--X	---X
*P. macropus**		X	----------	----------		X
*Ciconia maltha**			X	----------	----------	X
*Phoenicopterus minutus**			XX			
*P. copei**			X			
Cygnus cf. *C. columbianus*			X			
Branta canadensis			X	---X		
Anas cf. *A. crecca*			X			
A. cf. *A. platyrhynchos*			X			
Aythya sp.			X			
Mergus cf. *M. merganser*			X			
Oxyura jamaicensis			XX			
Haliaeetus leucocephalus			X	----------	----------	X
Aquila chrysaetos			X			
Fulica americana cf. *F. a. schufeldti**					X	
cf. *Grus*						X
cf. *Actitis*			X			
Phalaropodinae			X			
Larus cf. *L. oregonus**			X			
L. sp.			X	----------	----------	X
Bubo virginianus			X			

Lacustrine, fluvial, and alluvial fan deposits of the Manix Formation (Jefferson, 1968; Jefferson et al., 1982), are well exposed in bluffs along the Mojave River, 32 km (kilometers) east of Barstow, San Bernardino County, California. Here, 39 m (meters) of exposed sediment were deposited in a large freshwater lake that occupied approximately 402 square km, including the present Coyote and Troy playa lake basins and Afton Canyon. The horizontal distribution of laterally equivalent sedimentary facies reflects fluctuations in the depositional system. Fluvial and lacustrine deposits interfinger in a transgressive/regressive sequence in response to Pleistocene climatic changes.

Buwalda (1914) recognized a lower and an upper set of lacustrine deposits within the basin. He attributed their presence to climatic change and/or tectonic activity.

Winters (1954) described eighteen distinct sedimentary units in the stratigraphic section, numbered from the top of the section downward (see columnar section in Jefferson et al., 1982). Following Buwalda (1914) and Blackwelder and Ellsworth (1936), Winters recognized two major, climatically controlled lacustrine phases. He considered the older phase (units 16 through 14) to be Illinoian in age and the younger phase (units 13 through 1) temporally correlative with the Tahoe glaciation. The stratigraphic ranges of avian taxa reported by Howard (1955) are described with reference to Winters' numbered units.

Jefferson (1968) divided the Manix Formation into four

members on the basis of lithologically distinctive lacustrine, fluvial, and lateral fluvial and alluvial facies within the basin. The lowest unit, member A, is composed of unfossiliferous alluvial conglomerates (Winters' unit 18). These rocks are poorly exposed in the type stratigraphic section (Winters, 1954; Jefferson, 1968; Jefferson et al., 1982) (located in the NE ¼, SW ¼ of section 10, T 10 N, R 4 E, U.S.G.S. 15 minute Newberry, California Quadrangle, 1955). The basal 11 m of well-exposed deposits in the type section, member B, mainly consists of fluvial sands and gravels (Winters' unit 17). A U/Th date of 350+ Kyr was obtained from a fragment of a small *Equus* sp. humerus located 9 m above the base of these deposits (Bischoff, pers. comm., 1982). The middle 16 m of exposed section, the lower part of member C, is composed primarily of lacustrine silts and clays. The base of member C is estimated to be about 290 Kyr BP. The lower part of member C is approximately equivalent to Buwalda's (1914) lower lake and units 16 through 14 of Winters (1954). The upper 12 m of the Manix Formation, the upper part of member C and member D, consists of lacustrine silts and clays overlain by fluvial sands. These deposits are roughly equivalent to the upper lake beds of Buwalda (1914) and units 13 through 1 of Winters (1954). They range in age from about 200 to 19 Kyr (Bassett and Jefferson, 1971; Sarna-Wojcicki, 1980; Bischoff, pers. comm., 1982; Marcus, pers. comm., 1984).

All but two avian taxa (Table 2) are known from the basal 1 m of member C (Jefferson, 1968), which consists of very nearshore silts and sands, and one half of the recorded taxa (13 of 26) are restricted to this level. This horizon corresponds to unit 16 of Winters (Winters, 1954; Howard, 1955) and to the base of the lower lake of Buwalda (1914) and others (Blackwelder and Ellsworth, 1936).

Generally, the more abundant taxa are longer ranging and exhibit a more continuous stratigraphic record (Table 2 and Table 3). The stratigraphic distribution of all taxa is restricted to lacustrine sedimentary facies. Considering the relatively small sample size for any single taxon, it is probable that observed biostratigraphic ranges within the Lake Manix section are determined by taphonomic factors and do not represent the temporal range of any taxon.

Other avifauna of similar taxonomic composition (Table 1) are Wisconsinan in age. The Manix avifauna shares most taxa with the assemblages from Fossil Lake, Oregon and China Lake, California. Material from Fossil Lake is stratigraphically associated with a C-14 date of 29 Kyr BP (Allison, 1966). A C-14 date of 18 Kyr (Fortsch, 1978) and a U/Th date of 42 Kyr (Davis et al., 1981) are associated with the avifauna from China Lake. The oldest C-14 dates from both McKittrick (Berger and Libby, 1966) and Rancho La Brea (Marcus and Berger, 1984) are about 38 Kyr.

SYSTEMATIC DESCRIPTIONS

Most fossil specimens assigned to extant species are morphologically indistinguishable from the modern birds. The identifications are based primarily on the extensive recent osteological collections at LACM, and all measurements are from LACM specimens, unless otherwise noted.

Table 3. Faunal composition. Abbreviations: Extinct taxon = *.

Taxon	Identified specimens	Relative percentage
Gavia cf. *G. arctica*	1	0.7
Podiceps cf. *P. nigricollis*	4	2.8
Aechmophorus occidentalis	41	29.5
Pelecanus aff. *erythrorhynchos*	12	8.6
Phalacrocorax auritus	15	10.8
*P. macropus**	2	1.4
*Ciconia maltha**	6	4.3
*Phoenicopterus minutus**	14	10.1
*P. copei**	4	2.8
Cygnus cf. *C. columbianus*	3	2.1
Branta canadensis	11	7.9
Anas cf. *A. crecca*	1	0.7
A. cf. *A. platyrhynchos*	2	1.4
Aythya sp.	4	2.8
Mergus cf. *M. merganser*	2	1.4
Oxyura jamaicensis	3	2.1
Haliaeetus leucocephalus	2	1.4
Aquila chrysaetos	2	1.4
Fulica americana cf. *F. a. shufeldti**	1	0.7
cf. *Grus*	1	0.7
cf. *Actitis*	1	0.7
Phalaropodinae	1	0.7
Larus cf. *L. oregonus**	3	2.1
L. sp.	2	1.4
Bubo virginianus	1	0.7
Total	139	99.5

The use of trinominal names for extinct and extant subspecies follows Howard (1946). Subspecific names have been employed by Howard (1946) to distinguish morphologically and/or proportionally distinct fossil forms from modern species of the same size range. She considers the extinct subspecies chronoclinal ancestors to the modern forms. Although the application of subspecific names is noted in the discussions, they are not applied to fossil populations that may be larger or smaller than the modern species or fall within the range of modern subspecies.

Class Aves

Order Gaviiformes

Family Gaviidae

Genus *Gavia* Foster, 1788

Gavia cf. *G. arctica* (Linnaeus, 1758) (Arctic Loon)

REFERRED MATERIAL. SBCM A 500-1506, left and right angular and dentary.

DISCUSSION. The fragmentary mandible, SBCM A 500-1506, compares favorably with modern specimens of *G. arctica.* It is more slender and not as deep as in *G. immer* (Common Loon). Although incomplete, the dorsal margin of the dentary is straight in lateral view as in *G. arctica,* not concave as in *G. stellata* (Red-throated Loon).

Order Podicipediformes

Family Podicipedidae

Genus *Podiceps* Brehm, 1831

Podiceps cf. *P. nigricollis* Brehm, 1831 (Eared Grebe)

REFERRED MATERIAL. UCR 10555, sternum; UCR 10509 and UCR 10576, distal ends of left humeri; UCR 10556, distal right tibiotarsus.

DISCUSSION. Both distal left humeri, UCR 10509 and 10576, are morphologically indistinguishable from modern specimens of *Podiceps.* The humeri are distinctly smaller than the extinct species *P. parvus* (Shufeldt, 1913) from Fossil Lake, Oregon.

P. nigricollis and *P. auritus* (Horned Grebe) are similar in size and osteologically inseparable. The width of the distal end of the humerus of *P. auritus* is generally larger, but overlaps that of *P. nigricollis.* A sample of seven humeri of *P. auritus* (LACM Ornithology 86335, 86336, 86337, 86339, 86340, and 86341) have a mean width of 7.5 mm (millimeters) and the mean of six *P. nigricollis* (LACM Ornithology 1691, 86329, 86330, 86331, 86332, 86333, and 86334) is 6.9 mm. UCR 10509 and 10576 are closest in size to *P. nigricollis,* measuring 7.2 mm and 6.8 mm in width, respectively.

Genus *Aechmophorus* Coues, 1862

Aechmophorus occidentalis (Lawrence, 1858) Western Grebe

REFERRED MATERIAL. LACM 2457, partial skeleton including left and right femora, tibiotarsi, tarsometartarsi, and other elements (Howard, 1955); LACM 123458, nearly complete postcranial skeleton; UCR 10542, maxilla, mandible, and 4th cervical vertebra; LACM 2466, cervical vertebra (Howard, 1955); LACM 112445, cervical vertebra; UCR 14546, cervical vertebra and first tarsal phalanx; LACM 112459, costal margin of sternum; LACM 112414, synsacrum; LACM 2465, right coracoid (Howard, 1955); UCR 10538 and 10613, right coracoids; UCR 10882, proximal right coracoid; LACM 112401, distal left humerus; UCR 10553, proximal left humerus; LACM 2469, right humerus (Howard, 1955); LACM 123443, proximal left humerus; UCR 14580, 10615, and 10616, right humeri; UCR 10893, proximal right humerus; LACM 1515, fragment humerus; UCR 10612 and 10874, left femora; UCR 10602, distal left femur; LACM 123448, proximal right femur; UCR 10610 and 10611, right femora; UCR 10552, distal right femur; UCR 13955, left tibiotarsus and first tarsal phalanx; UCR 10618, right tibiotarsus; UCR 10617, distal right tibiotarsus; UCR 10554, 10609 and 10769, proximal left tarsometatarsi; LACM 2458, proximal right tarsometatarsus (Howard, 1955); UCR 10767, proximal and distal ends of right tarsometatarsus; UCR 10507, distal right tarsometarsus; UCMP 12859, right tarsometatarsus (Compton, 1934); UCR 10614, proximal tarsometatarsus; LACM 2459, fragment tarsometatarsus (Howard, 1955); UCR 10619, first tarsal phalanx.

DISCUSSION. Miller (1911a) described the extinct subspecies *A. o. lucasi* based on the collections from Fossil Lake, Oregon. Howard (1955:201) described the size of the leg bones of LACM 2457 as falling "in the zone of overlap of the Fossil Lake and Recent specimens, although equal to or greater than the average for *A. o. lucasi.*" Likewise, the skeleton, LACM 123458, is osteologically inseparable from the ranges exhibited by modern specimens of *A. occidentalis* and ancestral *A. o. lucasi.* The femora in LACM 123458 and LACM 2457 are relatively short compared to the type femur (UCMP 12605) for *A. o. lucasi.* The measurements and proportions of the remaining elements, however, are most similar to this extinct subspecies. The complete postcranial skeleton, LACM 123458, is significant in allowing the description of the proportions of limb elements relative to isolated elements. *A. o. lucasi* is only represented by isolated elements from Fossil Lake.

In the forelimb of LACM 123458, the lengths of the coracoid, humerus and ulna (Table 4) are very close to the means of *A. o. lucasi* from Fossil Lake and modern specimens (Howard, 1946). The coracoid falls between the two means, and the humerus and ulna fall on the mean of *A. o. lucasi.*

The femur of the Lake Manix specimen, LACM 123458, measures 42.0 mm in length, which is the same as the smallest of 63 specimens of *A. o. lucasi* and well below the mean of 44.3 mm for eight modern specimens (Howard, 1946). The type of *A. o. lucasi* (Miller, 1911a), a femur (UCMP 12605), measures 48 mm in length. Measurements of femoral length in the Fossil Lake sample are greater than the largest modern specimens and overlap with all but the smallest modern specimens.

The length of the tibiotarsi in LACM 123458, 124 mm measured to the proximal articular surface, falls very near the mean of *A. o. lucasi* reported from Fossil Lake, which is 124.9 mm (Howard, 1946). The total length of this element ranges from 135 to 147 mm in seven modern specimens (Gilbert et al., 1981) compared to 146 mm for LACM 123458. The widths of the proximal and distal ends of the tibiotarsi measure 11.3 mm and 13.3 mm, respectively, compared to a range of 10 to 14 mm for the proximal end of seven modern specimens (Gilbert et al., 1981).

Tarsometatarsal measurements and ratios (Table 4) of LACM 123458 are essentially identical to those for *A. o. lucasi* listed by Howard (1946, 1955). As with the femora from Fossil Lake, tarsometatarsi of *A. o. lucasi* are generally longer than the modern species and heavier-shafted with a narrow proximal end (Howard, 1947).

Where comparable measurements are possible, the size and proportions of isolated skeletal elements from Lake Ma-

Table 4. Measurements for *Aechmophorus occidentalis*, LACM 123458. Means of comparable measurements for Recent specimens are from Howard (1946). Abbreviations: M = mean of Recent specimens; prox. = proximal; dist. = distal; max. = maximum; dia. = diameter; int. = internal; est. = estimated plus or minus 1 mm; intcot. = intercotylar tubercle.

	LACM 123458	M
Coracoid		
Length	44.8	44.3
Humerus		
Length	118.0	116.1
Prox. width	19.4	
Dist. width	11.6	
Mid-shaft max. dia.	6.4	
Radius		
Length	103.4	
Prox. max. dia.	4.8	
Dist. max. dia.	5.4	
Mid-shaft max. dia.	3.3	
Ulna		
Length	107.1	106.1
Prox. width	8.8	
Dist. width	6.0	
Mid-shaft dia.	5.3	
Femur		
Int. length	42.0	44.3
Max. length	46.1	
Width dist. condyles	15.1	
Tibiotarsus		
Length	146 est.	
Length to articular surface	124 est.	119.0
Width prox. articular surface	11.3	
Width dist. condyles	13.3	
Tarsometatarsus		
Length	77.6	74.5
Shaft width	4.2	
Shaft max. depth	7.5	
Prox. width	13.7	
Width intcot.	5.2	
Shaft width/length	5.4%	
Shaft max. depth/length	9.7%	
Prox. width/length	17.6%	
Width intcot./breadth	123.8%	

nix are more similar to LACM 123458 than to *A. occidentalis* and *A. o. lucasi*. Coracoids, UCR 10538 and 10613, are greater than 43 (estimated) and 46.0 mm in length, and fall between the means of the two taxa. Femora UCR 10610, 10611, and 10612, which measure approximately 44 (estimated), 42.6 and 46.6 mm in length, are relatively small. The breadth of the intercotylar tubercle relative to the width of the shaft in tarsometatarsi UCR 10609 and 10767, is 128 and 142 mm (mean 135). This falls below the range for the Recent form (146–170 mm, mean 154) and close to the mean (140) of *A. o. lucasi* (Howard, 1946, 1955).

A. o. lucasi is defined on the basis of a femur larger than the largest Lake Manix specimen. Only one isolated femur from Fossil Lake is as small as those from Lake Manix. LACM 2457 and LACM 123458 have small femora, and although close to *A. o. lucasi* in all other skeletal dimensions, cannot be assigned to the late Pleistocene extinct subspecies from Fossil Lake, Oregon. The assemblage from Fossil Lake is significantly younger than the Lake Manix assemblage which may account for these minor proportional differences.

Order Pelecaniformes

Family Pelecanidae

Genus *Pelecanus* Linnaeus, 1758

Pelecanus aff. *P. erythrorhynchos* Gmelin, 1789 (American White Pelican)

REFERRED MATERIAL. UCR 14724, anterior sternum; UCR 10633, proximal left scapula; LACM 2460, left coracoid (Howard, 1955); UCR 20991, proximal right coracoid; LACM 123445, right humerus; UCR 15669, proximal humerus fragment; LACM 2462, proximal right radius (Howard, 1955); LACM 123447, proximal left carpometacarpus; LACM 2461, distal right femur (Howard, 1955); UCMP 21855, left femur (Compton, 1934); UCMP 12857, first tarsal phalanx left second digit (Compton, 1934); UCMP 12858, first tarsal phalanx, left third digit (Compton, 1934).

DISCUSSION. As noted by Howard (1955) and confirmed by additional specimens, the Lake Manix pelican is morphologically the same, but larger than the extant American White Pelican. No fossils are smaller than the largest modern specimens examined. The complete right humerus, LACM 123445, measures 336 mm in length compared to five modern specimens which range from 284 to 321 mm (Gilbert et al., 1981).

The Lake Manix material apparently represents a robust population of *P. erythrorhynchos*. Although criteria such as size alone have been used previously by others to define fossil avian subspecies or chronoclinal races, I do not concur with the practice. Proportional differences in limb measurements between the modern and fossil specimens cannot be demonstrated on the basis of the small Lake Manix sample.

Family Phalacrocoracidae

Genus *Phalacrocorax* Brisson, 1760

Phalacrocorax auritus (Lesson, 1831) Double-crested Comorant

REFERRED MATERIAL. LACM 123457, nearly complete postcranial skeleton; UCR 10577, premaxilla fragment;

Table 5. Measurements for *Phalacrocorax auritus*, LACM 123457. Abbreviations: M = mean of four large Recent specimens (LACM Ornithology 100734, 100831, 100832, and 101213); prox. = proximal; dist. = distal; dia. = diameter; max. = maximum; est. = estimated plus or minus 1 mm; proc. = process; int. = internal.

	LACM 123457	M
Scapula		
Length	89.2	85.0
Prox. width	18.9	18.0
Humerus		
Length	161.2	154.8
Prox. width	25.0	22.9
Dist. width	17.7	16.6
Mid-shaft dia.	8.8	8.2
Radius		
Length	168.1	160.0
Prox. max. dia.	8.9	8.6
Dist. max. dia.	9.3	9.5
Mid-shaft dia.	4.5	4.6
Ulna		
Length	168 est.	164.5
Prox. width	13.4	12.9
Dist. width	10.0	10.1
Mid-shaft dia.	6.6	6.3
Carpometacarpus		
External length	77.4	74.9
Prox. depth	15.0	13.9
Height proc. metacarpal 1	11.7	11.1
Femur		
Int. length	61.7	57.9
Max. length	64.0	60.4
Dist. width	18.9	16.9
Tibiotarsus		
Length to prox. articular surface	113.7	107.8
Width dist. condyles	14.1	13.1

UCR 10635, left quadrate; UCR 15667, right scapula; UCR 10637, left coracoid; SBCM A 1768-1, distal right coracoid and proximal right femur fragment; UCR 10627, left humerus; UCR 14684, distal right humerus; LACM 2468, distal left ulna; UCR 10557, proximal right carpometacarpus; UCR 10623, distal right carpometacarpus; UCR 14666, proximal and distal ends of tibiotarsus; SBCM A 500-1500, proximal left tarsometatarsus; UCR 10630, distal right tarsometatarsus; UCR 14547, first tarsal phalanx.

DISCUSSION. Lake Manix material compares very favorably with the largest modern specimens of *P. a. albociliatus* (Table 5) from the Pacific coast. Measurements of the principal limb elements of LACM 123457 (Table 5) are distinctly smaller than those given for extinct *P. macropus* (Cope, 1878) (Howard, 1946), and are slightly larger than the largest modern specimens examined or listed by Gilbert et al. (1981). Large size is also evident in all isolated limb elements.

Howard (1932) placed subgeneric value on the ratio of the distance from the anterior intermuscular line to the internal edge of the coracoid compared to the length of the coracoid measured to the internal sternal lip. The subgenus *Phalacrocorax* (*P. auritus, P. carbo,* and *P. olivaceus*) has a ratio of 15 percent, compared to 19–21 percent in the subgenus *Compsohalieus* (*P. pencillatus*) and 21–22 percent in the subgenus *Urile* (*P. pelagicus* and *P. perspicillatus*) (Howard, 1946). *P. macropus* yields a ratio of 17–19 percent. This ratio for LACM 123457 (11.7 mm, 71.9 mm) is 16.3 percent. The isolated left coracoid, UCR 10637, measures 65.2 and 11.0 mm and yields a ratio of 16.9 percent.

Measurements of isolated elements are also larger than the largest *P. auritus* examined, although smaller than *P. macropus*. Width of the distal end of humerus UCR 10627 is 17.5 mm and mid-shaft diameter is 9.8 mm. Distal humerus, UCR 14684 measures 15.6 mm in width. In UCR 14666, the width of the distal end of the tibiotarsus measured across the proximal edge of the supratendinal bridge is 13.1 mm. The proximal end of the specimen is 14.2 mm in width. The left proximal tarsometatarsus, SBCM A 500-1500, measures 14.0 mm in width, 19.1 mm in depth, and has a mid-shaft width of 7.3 mm and depth of 7.1 mm. The ridge supporting the external cotyle in this specimen is thickened and more prominent than in modern specimens.

The Lake Manix material apparently represents a robust population of *P. auritus* larger than the living west coast form (Table 5). No intermediate-sized individuals are present in the sample. Relative limb proportions of LACM 123457 and in modern specimens are essentially identical.

Phalacrocorax macropus Cope, 1878

REFERRED MATERIAL. SBCM A 500-1382, premaxilla; LACM 123442, proximal right humerus.

DISCUSSION. The nearly complete premaxilla, SBCM A 500-1382 (Fig. 1), is damaged along the proximal edge and is missing about 2–3 mm of bone tissue. Its dorsal margin in lateral view is more concave than in *P. auritus*. The specimen is more robust than the premaxilla of either *P. auritus* or *P. pencillatus* relative to its comparatively short length of 62 mm. It measures 16.8 mm in width at the distal margin of the nasal aperture and 13.3 mm in dorsal–ventral height, exceeding the size of both large modern species. These features closely conform to Shufeldt's (1892) description of the upper mandible of *P. macropus* from Fossil Lake, Oregon.

Although the proximal ends of the humeri are not known for *P. macropus*, the size and thickness of the mid-shaft of LACM 123442 support its placement here. The humerus measures 26.1 mm across the proximal end and has a mid-shaft diameter of 10.4 mm. A large modern specimen of *P. auritus* (LACM Ornithology 100734) measures 24.2 mm in proximal width, 16.2 mm across the distal end, and has a mid-shaft diameter of only 8.4 mm. Gilbert et al. (1981) give

the range for the proximal width of six modern specimens as 23 to 24 mm. The width of the distal humerus of *P. macropus* ranges from 18.6 to 19.8 mm (Howard, 1946).

Order Ciconiiformes

Family Ciconiidae

Genus *Ciconia* Linnaeus, 1758

Ciconia maltha Miller, 1910

REFERRED MATERIAL. LACM 2463, right humerus (Howard, 1955); UCR 13637, proximal right femur; UCR 14732, proximal right tibiotarsus; UCR 10629, proximal and distal right tarsometatarsus; UCR 10628 and 10759, first tarsal phalanges.

DISCUSSION. All fossil *Ciconia* material from California has been referred to *C. maltha* (Howard, 1942). The Lake Manix specimens are indistinguishable from equivalent elements in the Rancho La Brea sample.

Order Phoenicopteriformes

Family Phoenicopteridae

Genus *Phoenicopterus* Linnaeus, 1758

Phoenicopterus minutus Howard, 1955

REFERRED MATERIAL. LACM 2446, left scapula (Howard, 1955); SBCM A 500-1507, proximal left scapula; UCR 14669, right scapula; LACM 2474, right coracoid fragment and scapula (Howard, 1955); UCR 10578, proximal right coracoid; UCR 10631, left coracoid; UCR 10636, proximal first carpal phalanx; SBCM A 500-1504, proximal left femur; UCR 14544, proximal right femur; LACM 2445 (type specimen), right tibiotarsus and proximal tarsometatarsus (Howard, 1955); LACM 112438, distal left tibiotarsus; LACM 2473, proximal left tarsometatarsus (Howard, 1955); UCR 10875, proximal right tarsometarsus.

DISCUSSION. Howard (1955) described *P. minutus* as a very small flamingo, smaller than extinct *P. stocki* (Miller, 1944) from the Pliocene of Mexico. It differs from *P. stocki*, the larger extinct *P. copei* (Shufeldt, 1892) and the modern *P. chiliensis* (Chilean Flamingo), and *P. ruber* (Greater Flamingo) in minor, but distinctive, morphologic characters. Howard (1955) provisionally referred a left scapula, LACM 2446, and a right coracoid fragment and scapula, LACM 2474, to this taxon. Comparable additional specimens of these elements, SBCM A 500-1507, UCR 14669, 10578, and 10631, now support the assignment of this material to *P. minutus*.

Femora were not previously known for *P. minutus*. SBCM A 500-1504 and UCR 14544 are closely comparable to, but distinctly smaller than, modern species of *Phoenicopterus* as well as the extinct *P. copei* (Shufeldt, 1892). A narrow shallow groove common to all the species of *Phoenicopterus* is present

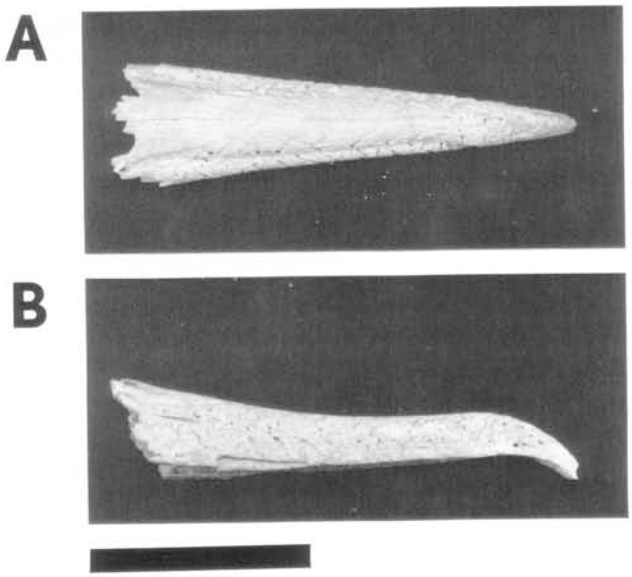

Figure 1. *Phalacrocorax macropus* premaxilla, SBCM A 500-1382. A, right lateral view. B, dorsal view. Scale bar is 30 mm.

on the lateral margin of the crest in both specimens. The width of SBCM A 1500-1504 is 16.8 mm. The trochanteric ridge visible in this specimen swings medially towards the head of the femur, as in *P. ruber*. UCR 14544, although incomplete and abraded along the dorsal edge of the trochanter, measures 16.1 mm in width.

A proximal carpal first phalanx, UCR 10636, although morphologically comparable, is smaller than specimens of *P. ruber* and tentatively referred to *P. minutus*.

Phoenicopterus copei Shufeldt, 1892

REFERRED MATERIAL. LACM 112410, cervical vertebra; LACM 2448, left tarsometatarsus (Howard, 1955); UCR 10879, right tarsometarsus and three associated phalanges; LACM 123440 and UCR 14693, medial first tarsal phalanges.

DISCUSSION. Howard (1955) placed the immature left tarsometatarsus, LACM 2448, in the extinct species *P. copei* based on comparison with measurements of the distal condyles of tibiotarsi from Fossil Lake, Oregon. Tarsometatarsi are not present in the Fossil Lake sample. The widths of the fossil tarsometatarsi are greater than that of modern species of *Phoenicopterus* (Howard, 1946).

Measurements of the right tarsometatarsus, UCR 10879, are very close to LACM 2448, which measures 328 mm in length, 19 mm in width across the proximal articular surface, 12 mm in intercotylar width, and 6.8 mm in height of intercotylar tubercle. UCR 10879 measures 333.6 mm in length, 18.6 mm in width across the proximal articular surface, 12.1 mm in width across the intercotylar tubercle, and the height of the intercotylar tubercle is 6.8 mm (Jefferson, 1968).

The two medial tarsal first phalanges, LACM 123440 and UCR 14693, are large but otherwise comparable to *P. ruber.*

Order Anseriformes

Family Anitidae

Genus *Cygnus* Linnaeus, 1758

Cygnus cf. *C. columbianus* (Ord, 1815) (Whistling Swan)

REFERRED MATERIAL. UCR 10634, scapula; UCR 14725, distal left tibiotarsus; UCR 13953, lateral first tarsal phalanx.

DISCUSSION. The scapula, UCR 10634, is not separable from modern specimens of *C. columbianus.* UCR 14725, a distal left tibiotarsus, measures 18.9 mm in width, which is slightly smaller but otherwise closely comparable to a sample of four modern specimens (LACM Ornithology 86547, 86548, 86552, and 86553 that range from 20.5 to 24.7 mm in width). It is clearly separable from similar-sized specimens of *Branta* where the tendinal groove is distinct and extends to the midshaft. The distal margin of the supra-tendinal bridge is concave in *Cygnus* and straight in *Branta.* The lateral tarsal phalanx, UCR 13953, is morphologically comparable to *C. columbianus* although more slender.

C. buccinator (Trumpeter Swan) and the extinct species *C. paloregonus* (Cope, 1878) are present in the Fossil Lake, Oregon, fauna. Both taxa exceed the dimensions of *C. columbianus,* which is not found at Fossil Lake.

Genus *Branta* Scapoli, 1769

Branta canadensis Linnaeus, 1758 Canada Goose

REFERRED MATERIAL. UCR 10621, maxilla; LACM 123450 and UCR 10622, left scapula; LACM 123449, left coracoid; LACM 112409 and UCR 10625, fragment right coracoid; UCR 10624, right coracoid; UCR 10894, proximal and distal left humerus; UCR 10626, partial right humerus; UCR 10620, distal left ulna; LACM 2464, proximal and distal right femur (Howard, 1955).

DISCUSSION. The Lake Manix specimens are separable into large and small forms that do not overlap in size. The larger specimens (UCR 10621, maxilla; LACM 123450 and UCR 10622, left scapula; LACM 123449, left coracoid; LACM 112409 and UCR 10625, fragment right coracoid; UCR 10624, right coracoid; UCR 10894, proximal and distal left humerus; LACM 2464, proximal and distal right femur) are closely comparable in morphology and size to modern specimens of the largest subspecies of *B. canadensis, B. c. canadensis.*

The relatively small distal left ulna, UCR 10620, is identical in size and morphology to specimens of the Recent *B. c. minima,* smallest subspecies of *B. canadensis.*

Although clearly assignable to Anserini, both ends of the humerus, UCR 10626, are badly damaged. This specimen is tentatively considered a small *B. canadensis* based on an approximate length of 160 mm.

The largest and smallest (nominal) subspecies of *B. canadensis* are also represented at Fossil Lake, Oregon (Howard, 1955). In this respect, the limited Lake Manix sample appears to parallel the Fossil Lake avifauna. However, the material does not warrant subspecific assignment.

Genus *Anas* Linnaeus, 1758

Anas cf. *A. crecca* Linnaeus, 1758 (Green-winged Teal)

REFERRED MATERIAL. LACM 112415, right humerus.

DISCUSSION. Approximately 1 to 2 mm of bone tissue have been abraded from the head and entepicondyle of the right humerus, and the external tuberosity and pectoral attachment are missing. Although the specimen is incomplete, a total length of 56 mm is comparable with the size of *A. crecca.*

Anas cf. *A. platyrhynchos* Linnaeus, 1758 (Mallard)

REFERRED MATERIAL. UCR 10551, partial right humerus; UCR 13956, proximal right humerus.

DISCUSSION. The end of right humerus UCR 10551 proximal to the bicipital crest is missing. The preserved portion is 82 mm in length. A total estimated length of 103–104 mm is slightly larger than the largest modern *A. platyrhynchos* examined.

The proximal humerus, UCR 13956, is inseparable from equivalent elements in the Rancho La Brea sample of *A. platyrhynchos.* It is distinguished from similar-sized small members of the Anserini by a more laterally directed median crest and deeper ligamental furrow.

Genus *Aythya* Boie, 1822

Aythya sp. Greater Scaup or Canvasback

REFERRED MATERIAL. UCR 14545, left coracoid; LACM 2472, right scapula (Howard, 1955); LACM 2475, distal left humerus (Howard, 1955); SBCM AE 873-2, left femur.

DISCUSSION. *A. marila* (Greater Scaup) and *A. valisineria* (Canvasback) are not easily separated osteologically. The lack of diagnostic specimens precludes a specific assignment. Howard (1955) tentatively referred LACM 2472 and 2475 to *A. valisineria.*

Genus *Mergus* Linnaeus, 1758

Mergus cf. *M. merganser* Linneaus, 1758 (Common Merganser)

REFERRED MATERIAL. UCR 10895 and 14581, left coracoids.

DISCUSSION. Of the numerous modern coracoids examined, those of *M. merganser* are generally larger than, but show considerable size overlap with the coracoids of *M. serrator* (Red-breasted Merganser). The fossil coracoids fall within the size range of *M. merganser* and *M. serrator.* However, an excavated area posterior to the brachial tuberosity and antero-ventral to the scapular facet is consistently deeper in *M. merganser* compared to *M. serrator.* Both UCR 10895 and 14581 clearly exhibit this character.

Genus *Oxyura* Bonaparte, 1828

Oxyura jamaicensis (Gmelin, 1789)
Ruddy Duck

REFERRED MATERIAL. LACM 2476, anterior sternum (Howard, 1955); LACM 112433, distal left humerus.

DISCUSSION. Lake Manix specimens are indistinguishable from modern specimens of Ruddy Duck. Although the width (8.8 mm) of the distal left humerus, LACM 112433, is close to that of *Anas crecca,* it is distinguished by having a larger anterior articular ligamental attachment and straighter shaft.

Order Accipitriformes

Family Accipitridae

Genus *Haliaeetus* Savigny, 1809

Haliaeetus leucocephalus Linnaeus, 1758
Bald Eagle

REFERRED MATERIAL. UCR 10638, distal right coracoid; UCR 14739, distal humerus.

DISCUSSION. These specimens compare closely with the Rancho La Brea sample of *H. leucocephalus.* The lateral flange on the posterior margin of the coracoid, UCR 10638, is wide and moderately hooked proximally. This condition is present on a minority of the Rancho La Brea specimens and absent from all available Recent material (Jefferson, 1968). The more laterally positioned scar for *M. coracobrachialis* in UCR 10638 clearly separates it from similar-sized coracoids of the extinct hawk, *Amplibuteo woodwardi* (Miller, 1911b).

Genus *Aquila* Brisson, 1760

Aquila chrysaetos (Linnaeus, 1758)
Golden Eagle

REFERRED MATERIAL. LACM 2470, distal right tibiotarsus (Howard, 1955); UCR 10632, fused first and second tarsal phalanges of left second digit.

DISCUSSION. The Lake Manix specimens are inseparable from the Rancho La Brea sample of *Aquila chrysaetos.* AMNH (American Museum of Natural History) 3467B, a second tarsal phalanx of digit two from Fossil Lake, Oregon, was first assigned to *A. chrysaetos* by Shufeldt (1892). This specimen, which was later referred to *Spizaetus pliogryps* by Howard (1946), is more slender than UCR 10632 and specimens of *A. chrysaetos* from Rancho La Brea. UCR 10632 measures 37.8 mm in length, 14.1 mm in proximal width, and 12.0 mm in proximal dorso-ventral height.

Order Gruiformes

Family Rallidae

Genus *Fulica* Gmelin, 1789

Fulica americana Gmelin, 1789
American Coot

Fulica americana cf. *shufeldti* Brodkorb, 1964

REFERRED MATERIAL. LACM 123446, left ulna.

DISCUSSION. Howard (1946, 1947) considered the relatively small, extinct coot, *F. minor* (Shufeldt, 1892) from Fossil Lake, Oregon, to be an ancestral subspecies (chronocline) of the modern form, *F. americana,* for which she erected subspecies *F. a. minor.* Subsequently Wetmore (1956) elevated "*minor*" to specific level following Shufeldt's original designation. Brodkorb (1964), recognizing that the name *minor* was previously occupied in the genus, renamed the taxon after Shufeldt, calling the form *F. shufeldti.*

The measurements given by Howard (1946) clearly show an overlap in the size of the specimens from Fossil Lake, Oregon, and modern specimens. There is no question that a single species is represented. Following Howard, the extinct form is considered a subspecies of *F. americana,* and is referable to *F. a. shufeldti.*

The ancestral subspecies differs from the modern American Coot in having shorter wings and relatively long legs (Howard, 1946, 1947). Mean length of three Fossil Lake ulnae is 56.9 mm, compared to 61.1 mm for 39 modern specimens (Howard, 1946). The Lake Manix ulna, LACM 123446, measures 56.8 mm.

Genus *Grus* Pallas, 1766

cf. *Grus* sp.
Crane

REFERRED MATERIAL. LACM 2467, fragmentary distal right humerus (Howard, 1955).

DISCUSSION. Howard (1955) questionably assigned this specimen to *Grus.* No additional crane specimens have been recovered.

Order Charadriiformes

Family Scolopacidae

Subfamily Scolopacinae

Genus *Actitis* Illiger, 1811

cf. *Actitis* sp.
(Sandpiper)

REFERRED MATERIAL. LACM 123451, proximal left humerus.

DISCUSSION. Various tribes within the subfamily Scolopacinae cannot be readily separated. LACM 123451 best compares with *Actitis hypoleucos* (Common Sandpiper) in size and approaches the smallest species of *Tringa* (sandpipers and yellowlegs). It differs from humeri of *Phalaropus lobatus* (Red-necked Phalarope, subfamily Phalaropodinae), which are almost identical in size, in having a deeper and more enclosed pneumatic fossa and a more rounded lateral margin of the bicipital crest.

Subfamily Phalaropodinae

Genus and species indet.

REFERRED MATERIAL. LACM 2471, partial left tibiotarsus (Howard, 1955).

DISCUSSION. LACM 2471, a very small, left distal tibiotarsus, was placed within the Phalaropodinae but could not be confidently assigned to the genus *Phalaropus* by Howard (1955). No additional comparable specimens have been recovered.

Family Laridae

Genus *Larus* Linnaeus, 1758

Larus cf. *L. oregonus* Shufeldt, 1892

REFERRED MATERIAL. LACM 123444, associated left humerus, radius, and carpometacarpus; LACM 123802, left first carpal phalanx, digit two.

DISCUSSION. The Lake Manix specimen, LACM 123444 (Fig. 2), represents a robust, medium-sized gull morphologically similar to *L. canus* (Mew Gull) and *L. delawarensis* (Ring-billed Gull). It is larger and more robust than the largest *L. canus* examined, and smaller than *L. delawarensis*. Dimensions of the limb elements differ from the wing of *L. delawarensis* in being shorter and having thicker or stouter mid-shafts. It is most similar to extinct *L. oregonus* from Fossil Lake, Oregon.

The humerus, although slightly smaller, is comparable in robustness to the type of *L. oregonus*. The maximum width of the proximal end of LACM 123444 (the bicipital crest margin shows slight damage) is 16.8 mm, compared to 17.7 mm in the type specimen, AMNH 3494 (measurements from cast). Minimum mid-shaft breadth is 5.8 mm, compared to 6.6 mm in the type, and the breadth of the shaft immediately distal to the base of the bicipital crest in LACM 123444 is 8.8 mm, versus 9.1 mm.

Howard (1946:186), in describing AMNH 3494, stated that "the depression below the head anconally . . . bounded by the sharp apex of the shaft on one side and the median crest on the other, tends to narrow almost to a point." This condition in LACM 123444 is similar to that in *L. canus*. The depression in *L. delawarensis* is more rounded, intermediate between *L. oregonus* and the wide depression in *L. californicus*. In this character, LACM 123444 is less pointed

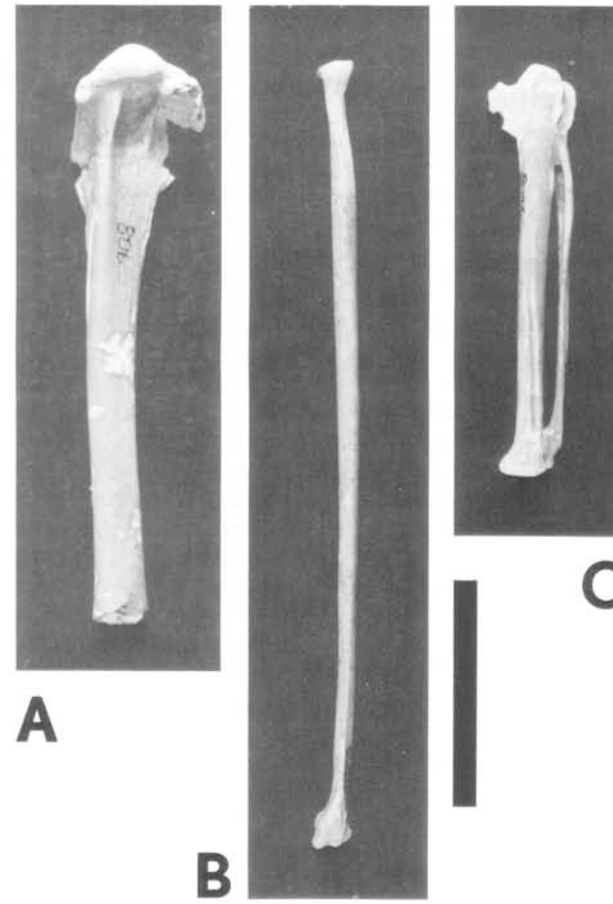

Figure 2. *Larus* cf. *L. oregonus* associated left wing elements, LACM 123444. A, anconal view of humerus. B, anconal view of radius. C, external view of carpometacarpus. Scale bar is 30 mm.

than AMNH 3494, not as wide or rounded as in *L. delawarensis*, and most similar to the largest specimens of *L. canus*, which exhibit the most rounded condition in this species.

Radii and carpometacarpi of *L. oregonus* are not known from Fossil Lake. The Lake Manix radius, although almost a centimeter shorter than the radii of *L. delawarensis*, measures 102.1 mm in length and is markedly stouter. Maximum thickness of the proximal portion of the shaft is 3.6 mm, much greater than in *L. canus* (LACM Ornithology 87200, 3.2 mm; 87201, 3.2 mm) or *L. delawarensis* (LACM Ornithology 87204, 3.1 mm; 87205, 3.2 mm; 87206, 2.9 mm; 87207, 3.1 mm). The bicipital tubercle is more pronounced and distally elongated in LACM 123444, and the groove bounded by the interosseous crest is longer and deeper in palmar view.

The carpometacarpus is morphologically similar to that of *L. canus* and *L. delawarensis*, but it is shorter and exhibits a considerably thickened main shaft. It measures 53.3 mm in length. LACM 123802, a first carpal phalanx, articulates

almost exactly with the carpometacarpus of LACM 123444, and measures 24.8 mm in length.

Larus sp.
Gull

REFERRED MATERIAL. LACM 123803, left proximal radius, coracoid, distal ulna, and proximal and distal carpometacarpus; SBCM A 500-1508, proximal portion of left carpometacarpus; SBCM A 500–1505, distal left carpometacarpus.

DISCUSSION. The specimens represent a large gull of the size of *L. argentatus* (Herring Gull) or *L. occidentalis* (Western Gull), but larger than *L. californicus* (California Gull). Larger specimens of *L. occidentalis* and *L. californicus* exhibit considerable overlap in size with smaller specimens of *L. argentatus*. LACM 123803 and SBCM A 500-1508 fall within this range. However, SBCM A 500-1505 is slightly larger than the largest *L. argentatus* examined. The fossil specimens cannot be distinguished from larger species of the genus *Larus*.

Remains of gulls are extremely rare in Quaternary marine deposits of western North America (Miller, 1924; Brodkorb, 1967). Although abundant and varied at Fossil Lake, Oregon (Howard, 1946), fossil specimens representing the Laridae previously were not known from Pleistocene asphalt or other terrestrial deposits in California (Miller and DeMay, 1942; Howard, pers. comm., 1983). The record from late Pleistocene marine deposits includes a single specimen of *Larus glaucescens* from the upper San Pedro Sand, California (Miller, 1930) and a second specimen from New Port Bay Mesa, California (Howard, 1949). The distribution of *Larus* at Rancho La Brea (Howard, 1936) and in Alaska (Brodkorb, 1967) is restricted to the Holocene. The only known Tertiary specimen is from the Pliocene San Diego Formation of southern California (R. Ceruti, pers. comm., 1983). Although samples are small, taphonomic or preservational biases do not seem to fully account for the very poor representation of gulls at Rancho La Brea or in late Pleistocene coastal marine deposits that yield numerous remains of other, similar-sized avian taxa (Howard, 1949). The inland late Pleistocene record of gulls appears to contrast with their appearance in Holocene coastal communities. These records suggest that a shift in the distribution or population density of gulls may have occurred in response to the disappearance of most inland lacustrine habitats at the end of the Pleistocene.

Order Strigiformes

Family Strigidae

Genus *Bubo* Dumeril, 1806

Bubo virginianus (Gmelin, 1788)
Great Horned Owl

REFERRED MATERIAL. UCR 10514, distal left tibiotarsus.

DISCUSSION. The width of the distal condyles on tibiotarsus UCR 10514 is 13.1 mm, identical to the mean of fifty Rancho La Brea specimens which range from 12.2 to 13.4 mm. A sample of twelve Recent specimens range between 11.9 and 13.4 mm (Howard, pers. comm., 1967). The large extinct owl, *Bubo sinclairi* (Miller, 1911c), overlaps the size of the largest Rancho La Brea specimens, exceeding UCR 10514.

BIOGEOGRAPHY AND PALEOENVIRONMENT

All of the extant species represented in the Lake Manix avifauna are at least seasonally present in southern California. Most taxa are found along the California coast during the winter or are winter visitors on inland lakes, such as the Salton Sea, or along the Colorado River. *Pelecanus* is a summer visitor most common at the Salton Sea. Only *Oxyura* and *Fulica* are wide ranging throughout the year. *Cygnus* is rare in southern California and found in winter on inland lakes or reservoirs to the north (Cogswell and Christman, 1977; Garrett and Dunn, 1981).

All extant, migratory species leave southern California in the spring. They travel northward along the coast or follow inland portions of the north–south Pacific Coast flyway. During Pleistocene pluvial periods, this inland route would have been over the lakes of the Mojave Desert, the lakes east of the Sierra Nevada Mountains including China Lake, the western part of Lake Lahontan, and the lakes of southeastern Oregon, including Fossil Lake (Snyder et al., 1964).

Two-thirds of the extant taxa (9 of 17), represented by 80 percent of the fossil specimens (Table 3), presently prefer, or feed exclusively on, small fish (Cogswell and Christman, 1977): *Gavia arctica, Podiceps nigricollis, Aechmophorus occidentalis, Pelecanus erythrorhynchos, Phalacrocorax auritus, Mergus merganser, Aquila chrysaetos, Haliaeetus leucocephalus,* and *Larus* spp. Abundant fossil remains of the small Tui (Mojave) Chub, *Gila bicolor mojavensis,* are present in the lacustrine deposits (Jefferson, 1968). No other fishes have been reported.

Most of the remaining taxa feed on a variety of water plants and freshwater invertebrates (Cogswell and Christman, 1977): *Cygnus columbianus, Anas crecca, A. platyrhynchos, Oxyura jamaicensis, Fulica americana, Actitis* sp., and *Branta canadensis. Aquila* is mainly a scavenger, and *Bubo virginianus* primarily feeds on small mammals.

The Lake Manix assemblage samples a complex of freshwater lake and lake margin habitats. Judging from food preferences, procurement methods, and nesting habits (Cogswell and Christman, 1977) of the extant forms represented, open water, sandy beach flats, and extensive reedy marshlands must have been persistent lacustrine features. An extensive lacustrine environment is confirmed by lithostratigraphy and reconstructions of the depositional environments (Jefferson, 1968).

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