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# A PLEISTOCENE AVIFAUNA FROM JALISCO, MEXICO

By

Rafael Alvarez

## INTRODUCTION

Mexican fossil avifaunas are only poorly known, our knowledge being based on a limited number of reports. Avian fossils recovered from San Josecito Cavern (Nuevo Leon) were reported on by L. H. Miller (1942, 1943). Howard described a Pliocene fauna from Chihuahua (1966) and summarized Pleistocene avian records for three localities in Central Mexico (1969). Bird remains from a Recent cave deposit in Yucatan have been described by Fisher (1953). These studies provide the only sources of information to date for any substantial assemblages of Mexican fossil birds. A late Pleistocene avifauna from Puebla, Mexico, is presently under study by the author (Alvarez, in prep.). As far as I am aware, the few remaining reports which deal with Mexican avifossils simply record the occurrence of single or but a few species (see Brodkorb and Phillips, 1973; Howard, 1965; Miller, 1944; Storer, 1954; and Wetmore, 1949). The paucity of reports is rather unfortunate, as the Mexican avifauna of today is quite varied (with over 1,000 species) and any insight gained into the past would be most rewarding in helping to understand the diversity which exists in the present.

Among the vertebrate fossils collected by Dr. Robert R. Miller and party, of the University of Michigan, during a series of visits to the western edge of Lago de Chapala (Jalisco, Mexico) was a rather small faunal assemblage of mostly fragmentary bird bones. The avian fossils collected by Dr. Miller comprise the subject of this report, and are of interest as they provide an additional glimpse of the Pleistocene ornithology of Mexico. A total of fifty-nine bones were identified at the species level, four were assigned only to genera, and two additional bones could safely be identified only at the family level. Fragments of vertebrae, the shafts of some long bones, several fragmentary coracoids, a left acetabulum, and a single unidentifiable bone were not assigned to taxa. The following taxa are represented in the Chapala fauna:

### PODICIPEDIDAE

*Podiceps caspicus* (Hablizl)

*Aechmophorus occidentalis* (Lawrence)

*Podilymbus podiceps* (Linnaeus)

### PHALACROCORACIDAE

\**Phalacrocorax goletensis* Howard

\**Phalacrocorax chapalensis*, new species

*Phalacrocorax* sp.

### ANHINGIDAE

*Anhinga anhinga* (Linnaeus)

### ARDEIDAE

*Tigrisoma* (?) sp.

### ANATIDAE

*Aythya americana* (Eyton)

*Aythya marila* (Linnaeus)

*Aythya* sp. [probably *A. americana*]

\**Oxyura zapatanima*, new species

SCOLOPACIDAE

*Calidris fusicollis* (Vieillot)

ICTERIDAE

*Sturnella* (?) sp. [closest to *S. magna*]

\* – Extinct

Distributional data for the living species were taken largely from Friedmann *et al.* (1950). Data on the fossil occurrences of neo- and paleospecies were taken from Brodkorb (1963, 1964, 1967) and elsewhere as cited. Osteological terminology follows Howard (1929) except where noted, in which case a definition of the term in use is given. Comparative Recent and fossil material used in identifications of the specimens came from the Los Angeles County Museum and the University of Michigan Museums of Paleontology (UMMP) and Zoology (UMMZ). The fossils described in this paper are presently housed in the collections of the University of Michigan Museum of Paleontology.

#### DESCRIPTION OF THE FOSSIL LOCALITY

Lago de Chapala is located at an elevation of approximately 2,800 meters in the state of Jalisco, and is one of a number of lakes found in the Mesa Central of the Mexican Plateau; it is also the largest lake in Mexico. The lakes of the Mesa Central were apparently formed during Mid-Pleistocene upliftings (Clements, 1963). Terraces north of the town of Chapala are thought to have been formed by wave action during pluvial periods of the Pleistocene when Lago de Chapala was considerably larger than it is today (Clements, 1963) or by changes in the drainage pattern of the lake (Barbour, 1973).

The avian fossils were recovered from a gravel pit about 5 km west of the town of Jocotopec, Jalisco, on Highway 15. The abundant fish fossils taken from the same quarry have been described by Smith *et al.* (1975), and these authors suggested (page 1) that "the habitat of the fauna was the shallow water of a lake margin or a flowing stream, according to geological and ecological inferences." The paleoichthyofauna exhibited only slight differences in morphology when compared to their Recent counterparts (a total of seven species were represented, *Micropterus relictus* Cavender and Smith being the only extinct form), and from this it is suggested that the climate of Lago de Chapala and the Mesa Central has not changed appreciably since the late Pliocene or early Pleistocene, the time during which the fossils were deposited. There is some equivocation as to the exact age of the vertebrate fossils, but the presence of several neospecies of birds in the fauna may indicate a Pleistocene rather than Pliocene age. In addition to the fish and bird fossils, herps and mammals were also exposed. Downs (1958) noted the occurrence of numerous vertebrate remains in the fossiliferous deposits at the floor of Lago de Chapala; the specimens were free-lying and non-imbedded, and are characteristic of the late Pleistocene (with the exception of two horses, *Nannippus* and a large species of *Equus*, of Pliocene age). The fact that these equine fossils were not found imbedded in place suggests that erosional effects of the circulating water in the lake might have been responsible for freeing the bones from a previously intact state in older sediments of the lake floor. The total faunal assemblage of the type Chapala indicates a Plio-Pleistocene age (Clements, 1963). The diatom stratigraphy of Lake Texcoco (a neighboring lake of the Mesa Central) as determined by Bradbury (1971) indicates that climatic fluctuations in central Mexico were not particularly great during the Pleistocene history of the area, a conclusion corroborated by the evidence from the fossil fishes of Lago de Chapala (Smith *et al.*, 1975).

## SYSTEMATIC PALEONTOLOGY

## Order PODICIPEDIFORMES

## Family PODICIPEDIDAE

*Podiceps caspicus* (Hablizl)

*Referred Material.*— Distal portion of right humerus, UMMP 63252.

*Description.*— Agrees with *Podiceps* but differs from *Podilymbus* in having a narrower and not so deeply excavated brachial depression and in having the ectepicondylar process almost flush with the shaft. External tricipital groove more clearly defined in *Podilymbus* than in *Podiceps* (fossil agrees with *Podiceps* in this respect). The fossil humerus is about the size of a small ♀ *Podiceps caspicus*.

*Distribution.*— The Eared Grebe is widely distributed in Central and Eastern Europe, Asia Minor, Africa, and North America south to Guatemala. Scattered breeding records in Mexico include the states of Baja California, Chihuahua, Nayarit, Puebla, and Jalisco (Dickerman, 1969), but North American birds are widespread winter visitors throughout most of Mexico. This is the first fossil record of *Podiceps caspicus* in Mexico.

*Aechmophorus occidentalis* (Lawrence)

*Referred Material.*— 3 humeri, UMMP 61752; 1 carpometacarpus, UMMP 61752; 9 femora, UMMP 61100, 61752, 61754; 4 tibiotarsi, UMMP 61076, 61752, 63255; 6 tarsometatarsi, UMMP 61100, 61752, 61754; pedal phalanx, UMMP 61752; 10 cervical vertebrae, UMMP 61076.

*Remarks.*— This distinctive grebe is the most abundantly represented bird in the Chapala fauna. Thirty-four bones representing at least five individuals were identified. All of the long bones with the exception of two of the femora are preserved as fragmented pieces only; the femora measure 40.9 mm and 42.0 mm in overall length.

Qualitatively, the fossil material differs conspicuously from Recent *Aechmophorus occidentalis* in but a single character. The shafts at the distal ends of 3 of the 4 fossil tibiotarsi (only the distal ends of these 3 bones were preserved; the fourth is a proximal end) are much stouter than in the Recent counterpart, and give the appearance of having been rather heavy-bodied bones. Relying on but this single character, one could easily be misled into thinking that the difference warrants specific distinction, it seems so great (especially in UMMP 63255). Howard (1946) observed a similar tendency towards stoutness in the large assemblage of *Aechmophorus occidentalis* tarsometatarsi from Fossil Lake, Oregon (Upper Pleistocene). The leg bones were, in general, longer than Recent *A. occidentalis*, but, aside from the tarsometatarsi, did not appear to diverge significantly in stoutness. The tarsi were also narrow proximally, and this must have certainly contributed to their stout appearance. Unfortunately, because of the fragmented nature of the leg bones of the Chapala *Aechmophorus*, their long diameters cannot be measured. But Howard's data suggest that the leg bones of *A. occidentalis* have become progressively shorter with decreasing geological age, and a chronocline relationship between Pleistocene and Recent forms of this species can be recognized. The tarsometatarsi have also become slimmer. If the Chapala specimens are now taken into account, a marked change in the stoutness of the tibiotarsus is also evident. Morphological and morphometric changes in the wing elements, by comparison, have been relatively conservative. As *Aechmophorus occidentalis* is a foot-propelled diving bird, changes of this sort should be expected in this important locomotor apparatus during the course of its adaptive development.

*Distribution.*— This is the second occurrence of the Western Grebe as a fossil in Mexico. Previous records are from the Pleistocene of western North America and from the Valley of Mexico. Its present distribution includes much of western North America south into Central Mexico.

*Podilymbus podiceps* (Linnaeus)

*Referred Material.*— Proximal portion of right tarsometatarsus, hypotarsus worn, UMMP 61100.

*Description.*— The presence in the hypotarsus of *Podilymbus* of an accessory canal for the insertional tendon of *M. flexor perforatus digiti II* provides a ready means for distinguishing it from both *Aechmophorus* and *Podiceps*, in which the extra canal is absent (Storer, 1963). The worn nature of the hypotarsus of the grebe reported here, however, precluded any such distinction. Characters used by Murray (1967) in distinguishing the tarsometatarsi of *Podilymbus* from *Podiceps* were useful, notably, the internal rotation of the shaft at its proximal end about the long axis, and the appearance of the shaft in cross-section, being nearly square. A further distinction can be made. In proximal view, the intercotylar prominence appears rotated externally about the long axis of the shaft in *Podilymbus*, while no such rotation is evident in *Podiceps*. These differences (internal rotation of proximal end of shaft and the external deflection of the intercotylar prominence in *Podilymbus*) are of probable functional significance, and may reflect differences in the rotational movements of the tarsometatarsus made during the recovery stroke while the bird is progressing in water. The size of the fossil tarsometatarsus matches that of Recent ♀ *Podilymbus podiceps*.

*Distribution.*— Widely distributed in North America, south through Middle and South America to Chile and Argentina, the Pied-billed Grebe is also abundantly represented in the fossil record. It has previously been recorded in the Pleistocene of Mexico (Wetmore, 1949).

## Order PELECANIFORMES

## Family PHALACROCORACIDAE

*Phalacrocorax goletensis* Howard

*Referred Material.*— Distal portion of right humerus, UMMP 61987.

*Description and Remarks.*— *Phalacrocorax goletensis* was described on the basis of a nearly complete right coracoid (Howard, 1965). The referred distal portion of a left humerus agreed with the type coracoid in being significantly smaller than comparable elements of living *Phalacrocorax olivaceus*. Measurements taken on the Chapala specimen reported here are only slightly greater than those taken by Howard on the original specimen from Michoacan (see Table 1). Through the courtesy of Dr. Howard, the referred humerus of *P. goletensis* (Los Angeles County Museum collection number 3166) was loaned to me for direct comparison with the cormorant humerus from Chapala. The Chapala specimen is somewhat stouter of shaft directly beneath the ectepicondylar prominence in a line through the palmar surface perpendicular to the long axis of the shaft: 10.1 mm (Chapala) vs. 9.1 mm (Michoacan). The same measurements taken on two specimens of *P. olivaceus* available for comparison are as follows: 11.2 mm (♂) and 10.6 mm (♀). The two fossil specimens are virtually indistinguishable qualitatively, and share a common feature which, along with their smaller size, serves to distinguish them from *olivaceus*. The entepicondylar prominence of *goletensis* is relatively, and actually, stronger than in *olivaceus*, and projects internally to a greater extent. This difference is most conspicuous when the humeri are compared in anconal view. Given the often marked sexual dimorphism reflected in the skeletal measurements of cormorant neospecies, I consider the slight difference in size shown between the two humeral elements of *goletensis* now known to be within a reasonable range of variation expected for the species. Since the original humerus of *goletensis* was distinguished from Recent *olivaceus* chiefly on the basis of its generally smaller size (Howard, 1965), it should be noted that the slightly larger *goletensis* humerus from Chapala is still significantly smaller than the smallest *olivaceus* humerus used for comparison in Dr. Howard's description.

TABLE 1  
 HUMERAL MEASUREMENTS (IN MM)  
 OF *PHALACROCORAX GOLETENSIS* AND *PHALACROCORAX OLIVACEUS*

	<i>P. goletensis</i>		<i>P. olivaceus</i>	
	Michoacan <sup>a</sup>	Chapala	(4 specimens) <sup>a</sup>	(2 specimens) <sup>b</sup>
Greatest breadth				♀ ♂
distal end	10.6	10.7	11.0-12.0	12.1 13.0
Distal breadth				
across condyles	8.9	8.9	9.4-10.8	9.9 10.9
External depth				
distal end	7.4	7.5	8.1- 8.8	8.4 9.6
Internal depth				
distal end	8.8	8.9	9.2-10.0	9.9 10.9

a -- Data taken from Howard, 1965

b -- Data taken from specimens in UMMZ

*Distribution.*— Previously known only from the type locality (near La Goleta, Michoacan, Mexico; Middle or late Pliocene), the Lago de Chapala specimen (from roughly 120 miles west-northwest of the type locality) provides a second record for *Phalacrocorax goletensis* and extends the geological range of the species into Lower Pleistocene times (if a Pleistocene age for the Chapala fauna is accepted).

*Phalacrocorax chapalensis*, new species

*Holotype.*— Proximal portion of left tarsometatarsus and part of shaft, UMMP 61753. Figure 1.

*Measurements of Holotype.*— [Measurements taken on 5 specimens of living *Phalacrocorax auritus* (2 ♀♀, 2 ♂♂, and one unsexed) are indicated in parentheses for comparative purposes, giving the range and mean]. Greatest width through cotylae posterior to intercotylar prominence: 15.6 mm (12.1-14.0; 12.8); greatest depth through internal cotyla: 11.2 (8.5-9.6; 9.1); proximal depth of hypotarsus from intercotylar prominence through innermost calcaneal ridge: 19.6 (15.7-18.9; 17.2); depth of external cotyla through outermost tendinal canal: 7.7 (6.4-7.2; 6.7); shaft width at antero-proximal edge of inner extensor groove: 8.0 (6.0-7.0; 6.2); greatest shaft depth at same point: 9.0 (6.9-8.4; 7.6).

*Paratypes.*— a) upper end of left coracoid, lacking head and part of coracohumeral surface; b) left scapula, lacking distal portion of blade; c) proximal portions of two left humeri, imperfectly preserved, d) shaft of left humerus; e) proximal portion of left ulna; f) distal portion of left ulna and part of shaft, g) proximal portion of left tibiotarsus, articular surfaces broken off; h) shaft of left tarsometatarsus, including external and part of middle trochleae; i) middle trochlea of left tarsometatarsus; j) part of shaft of left tarsometatarsus; k) left quadrate; l) right and left articular portions of lower jaw. All specimens in this series have the collection number UMMP 61100.

*Measurements of Paratypes.*— a) greatest width of glenoid facet: 7.6 mm (5.4-7.0; 5.7), greatest length of glenoid facet: 14.8 (11.3-13.2; 12.2), width of neck directly above scapular facet: 12.6 (9.7-11.3; 10.4); b) proximodistal length of flattened portion of glenoid facet: 9.8 (7.5-8.1; 7.7),

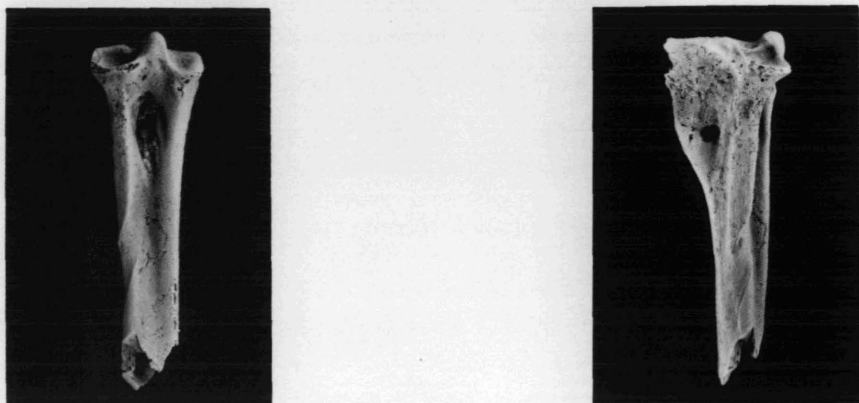


FIG. 1 — *Phalacrocorax chapalensis*, new species. Holotype tarsometatarsus (UMMP 61753). Anterior (left) and medial (right) views. X 1.

length from distalmost point of glenoid facet to tip of acromion: 20.6 (14.9-17.9; 16.4), neck width directly behind glenoid facet: 7.7 (6.2-6.5; 6.3); c) length of head from external tuberosity to upper edge of capital groove: 19.1 (15.0-17.6; 16.1), greatest width through head: 9.0 (7.0-7.7; 7.3), shaft width at distal termination of deltoid crest: 11.6 (8.9-10.1; 9.6); e) width through cotylae: 12.8 (10.8-12.5; 11.6), depth through internal cotyla: 11.4 (10.1-11.6; 10.8), shaft width at proximal edge of brachial impression: 10.1 (8.3-9.4; 8.8); f) depth through external condyle: 9.8 (7.9-8.5; 8.2), width from tendinal pit to tip of carpal tuberosity: 10.4 (8.5-9.3; 9.0), shaft width directly beneath external condyle: 7.4 (5.4-6.2; 5.8); g) shaft width at proximal termination of fibular crest: 9.1 (7.1-8.1; 7.4), shaft depth at same point, measured over external side: 8.3 (5.4-7.1; 6.2); h) greatest breadth through outer trochlea: 5.0 (3.9-4.6; 4.3), length from distalmost edge of distal foramen to inner tip of outer trochlea: 9.4 (8.0-9.1; 8.6); i) greatest breadth: 6.4 (4.4-5.3; 4.8), length from distalmost edge of distal foramen to outer tip of trochlea: 10.1 (8.7-9.6; 9.0); k) greatest width through mandibular articulations: 14.3 (11.0-12.4; 11.7), greatest external length from quadratojugal socket to squamosal articulation: 21.0 (15.6-18.3; 17.0); l) height of right mandibular ramus directly in front of quadrate articulation: 10.7 (7.4-8.5; 8.1).

*Locality and Age.*— Holotype: Jocotopec Sand and Gravel Quarry. West edge of Lago de Chapala. 2.9 miles west of Jocotopec, Jalisco, Mexico, on road to Guadalajara. Late Pliocene or early Pleistocene. Collected by C. D. Barbour and R. J. Douglass, 17 June 1969. Data for paratypes: UM-Mex-1-72 (R. R. Miller Loc.). Bed A of highest west wall of Lower Quarry (equals floor level of Upper Quarry). West edge of Lago de Chapala, Jalisco, Mexico. Late Pliocene or early Pleistocene. Collected by R. R. Miller, F. H. Miller, and N. A. Neff, 30 November 1972.

*Etymology.*— Named after the type locality.

*Diagnosis.*— The type tarsometatarsus of *Phalacrocorax chapalensis* is larger than that of all living cormorants, being approached in size only by *P. carbo*. Differs from *carbo* in having the width of the shaft (in anterior view) greater in relation to cotylar width. External depth of innermost calcaneal ridge in relation to cotylar width greater in *chapalensis* than in *carbo*. In internal view, intercotylar prominence rises more abruptly from articular surfaces in *chapalensis* and is more pointed terminally as well, its posterior face forming a steep, almost vertical angle. The corresponding angle in *carbo* is not so steep, the transition from intercotylar area to prominence being a more gradual one. The steep



posterior face and pointed tip of the intercotylar prominence of *chapalensis* are features which consistently distinguish it from the living species of cormorants examined (*auritus*, *olivaceus*, *carbo*, *pelagicus*, and *penicillatus*). The intercotylar depression is deeper in *chapalensis* than in *carbo*, and separated from the internal calcaneal ridge by a distinct barrier in the former but continuous in the latter. Lateral margin of external cotyla low and slightly rounded in *chapalensis*, rather steeply inclined in *carbo*. The postero-medial margin of the internal cotyla forms a conspicuous inner protuberance in *carbo*, the corresponding area in *chapalensis* being smoothly rounded. In posterior view, the inner and outer proximal foramina exit the shaft at the same level in *carbo*; in *chapalensis*, the outer foramen is produced anterior to the inner foramen, and is partially concealed by a narrow ledge of bone.

*Descriptions.*— *Phalacrocorax chapalensis* most closely resembles living *P. auritus* in qualitative characters, but can be distinguished from that species solely on the differences in size. The paratype material of *chapalensis* is compared below chiefly to *auritus*.

**HUMERUS.** Immediately distal to the external tuberosity, the preserved portion of the deltoid crest swings sharply upward from the bicipital furrow, so that, in proximal view, the crest extends somewhat beyond the palmar surface of the head, more so than in any of the neospecies examined. The fossil humerus bears an additional feature not found in any of the living cormorants seen. If the long axes of the shaft of *auritus*, for example, and *chapalensis* are aligned in parallel fashion and the humeri are then viewed proximally, the head of *auritus* lies at an oblique angle to that of *chapalensis*.

**CORACOID.** Rather similar to *auritus*, but much larger, and having the shaft margins directly beneath the procoracoid sharply angular instead of smooth and rounded. The shaft width is proportionately greater beneath the scapular facet than the neck width directly above in *chapalensis* than in *carbo*.

**SCAPULA.** The scapula of *chapalensis* does not differ significantly in any qualitative characters from *auritus*, but is again much greater in size.

**ULNA.** Measurements taken on the preserved proximal end are not substantially greater than comparable elements of *auritus*. The shaft width directly beneath the cotylae is proportionately greater in the fossil, however, and the assignment of this fragment to *chapalensis* is made on that basis. The distal two-thirds or so of a left ulna may have been part of the same bone from which the proximal fragment came. The shaft is much stouter in *chapalensis* in relation to its greater size.

**TIBIOTARSUS.** The external surface of the outer cnemial crest is broadly excavated in *chapalensis*, the same surface of *auritus* being relatively flat. This excavation in *chapalensis* is separated above from the articular surfaces by a swollen ledge of bone.

**TARSOMETATARSUS.** The lateral wing of the outer trochlea shows greater external deflection in *chapalensis*, and is also flatter distally.

**MANDIBULAR FRAGMENTS.** These may or may not have come from the same individual; the right half is preserved well, the left half shows much abrasion. These elements closely resemble *auritus* in qualitative features, but are proportionately larger in all respects.

**QUADRATE.** The orbital process is broken off, and the external lip of the quadratojugal socket is slightly abraded, but otherwise this element is in a good state of preservation. The excavation found between the quadratojugal socket and the pterygoid articulation is relatively deeper in *chapalensis* than in *auritus*.

*Phalacrocorax mediterraneus* Shufeldt [Lower or Middle Oligocene, Colorado], *P. marinavis* Shufeldt [Lower Miocene, Oregon], *P. idahensis* (Marsh) [Middle Pliocene, Idaho], *P. rogersi* Howard [Lower Pleistocene, California], and *P. macropus* (Cope) [Middle Pleistocene, Oregon] are all extinct cormorants of a size roughly comparable to *P. chapalensis*. The coracoid of *chapalensis* differs from that of *rogersi* (Howard, 1935) in having the region directly beneath and posterior to the procoracoid depressed and slightly excavated, rather than smoothly rounded. Available for direct comparison in

the UMMP are a series of bones (right femur, proximal and distal ends of right tibiotarsi, right tarso-metatarsus, distal end of left tarsometatarsus and part of shaft, and a pedal phalanx; UMMP V63156) referable to *P. macropus*. These are from the Upper Pliocene of Idaho (Glenns Ferry Formation; Fossil Creek locality), and are being reported on by R. W. Storer and the author elsewhere (Storer and Alvarez, in prep.). As noted above, the proximal end of the tibiotarsus of *chapelensis* is marked by a well-defined excavation on the external surface of the outer cnemial crest; the corresponding area of *macropus* is flat. Also, the posterior edge of the outer cnemial crest is bluntly rounded in *macropus*, but a sharp ridge in *chapelensis*. The usefulness of this last character as a diagnostic feature may be subject to question, however, as evidenced by the variation observed for it within living species of cormorants. The inner and outer cnemial crests are spaced farther apart on the anterior face of the tibiotarsus in *chapelensis*, and extend distally along a greater length of the shaft as well. The tarsometatarsi of the two fossil species show conspicuous differences. The area directly beneath the outermost calcaneal canal is deeply excavated in *macropus*, nearly flat in *chapelensis*; the tendinal canal of the middle trochlea is relatively broader in *macropus*; and, the distal surface of the outer trochlea is, in anterior view, more rounded medial to the tendinal canal in *chapelensis*. The inner and outer proximal foramina exit the shaft posteriorly at the same level in *macropus* (outer produced above inner in *chapelensis* as previously noted). The tarsometatarsi agree in lacking the spine-like projection on the flattened portion of the innermost calcaneal ridge. Compared to the specimens of *macropus* illustrated by Shufeldt (1913, plates XX-XXIII), the corresponding elements of *chapelensis* are all considerably smaller. Some qualitative differences can also be noted. The external articular process of the mandible appears to slope away from the articular more steeply in *macropus*. Comparing the tarsometatarsi still further, the narrowness of the intercotylar prominence of *chapelensis* is again distinctive, and the trochleae appear more elongate in that species.

Unfortunately, in describing *P. mediterraneus* and *P. marinavis*, Shufeldt (1915) did not relate much information concerning the diagnostic features of the fossils. The type specimens are not comparable to the elements of *chapelensis* reported here, as in each case only proximal fragments of carpometacarpi are preserved. The Oligocene form *mediterraneus* was said by Shufeldt to be of a large size equal to its congener *perspicillatus*. *Phalacrocorax perspicillatus* was a very large-bodied cormorant with greatly reduced wings which rendered the bird nearly flightless. Heavy predation by man led to its extinction during the mid-1800's (Greenway, 1967). For diagnostic purposes, a comparison of the carpometacarpus of *mediterraneus* to that of *perspicillatus*, followed by an extrapolation of the possible size of the fossil species based on that comparison, would obviously be undesirable. *P. marinavis* was of a size somewhat smaller than living *P. carbo*, a species which *chapelensis* generally exceeds in size. The much greater age of *mediterraneus* and *marinavis* should be sufficient reason for believing that neither of the two are represented in the fossil elements presently described as *chapelensis*.

Also in the UMMP are numerous bones of the Pliocene cormorant *P. idahensis*. These have been described in detail by Murray (1970) and were found to be significantly larger than living *P. auritus*. In several of the skeletal elements preserved, qualitative differences were noted, but in most respects the two appeared nearly indistinguishable but for the larger size of the fossil species. Comparing *chapelensis* to *idahensis*, the difference in size is quite striking, *chapelensis* being the larger of the two. In many aspects of its morphology, *chapelensis* differs from *idahensis* in the same way that it differs from *auritus*, and also by having: the area beneath the scapular facet of the coracoid more deeply excavated; and, the shaft of the tarsometatarsus flatter medial to the inner calcaneal ridge. The intercotylar prominence of the tarsometatarsus is again much higher in *chapelensis* than in *idahensis*. The difference in size between *chapelensis* and *idahensis* is of an order of magnitude greater than that between *idahensis* and *auritus*.

*Phalacrocorax* sp.

The shaft of a cormorant tarsometatarsus (UMMP 61100) is not as robust as any of the comparable elements of *P. chapalensis* described above, but more closely resembles *P. auritus* in its slenderer nature. Its length, however, would tend to ally it with *chapalensis* rather than *auritus*. Also of note is that the distal foramen as preserved in the fossil is longer than in any of the five skeletons of *auritus* examined, but matches the condition seen in *chapalensis*. The trochleae and hypotarsus are lacking in the fossil tarsus, and in the absence of these diagnostic features, specific identification is considered unwise.

The distal end of a right ulna (UMMP 6132) is about the size of a small ♀ *P. auritus*, but its abraded nature would make specific assignment uncertain.

## Family ANHINGIDAE

*Anhinga anhinga* (Linnaeus)

*Referred Material.*— Proximal portion of right humerus, UMMP 61100; 2 right tarsometatarsi, UMMP 61751.

*Description and Remarks.*— The Pleistocene elements referred to this species came from birds that were slightly larger than Recent forms of *Anhinga anhinga*. The greatest distal width in a series of 8 humeri of *A. anhinga* examined by Martin and Mengel (1975) was 16.0 mm (15.2-16.0, range). Two ♀ *A. anhinga* humeri I measured had distal widths of 15.4 mm; the greatest proximal width of both (measured from external tuberosity through head to internal tuberosity over anconal surface) was 17.0. The fossil humerus reported here has a proximal width of 18.4 mm. Assuming constancy of proportions between Recent and fossil forms, the predicted greatest distal width for this fossil humerus would be 16.6 mm (0.6 mm greater than the largest humerus measured by Martin and Mengel). Aside from its slightly larger size, the fossil humerus differs from the two skeletons of *A. anhinga* I have examined in the following characters: external slope of head less steep; pneumatic fossa deeper; median crest appears more strongly produced and altogether thicker; and, bicipital crest is undercut by bicipital furrow proximally, producing a slight overhang in this area.

*Anhinga grandis* Martin and Mengel (1975) from the Upper Pliocene of Nebraska was described on the basis of the distal half of a left humerus. Its greatest distal width is 19.7 mm, and was therefore a much larger bird than the Chapala anhinga.

The tarsometatarsi are too abraded and worn to allow accurate characterization, and because parts of the trochleae are lacking, their overall lengths can only be approximated. Length from intercotylar prominence to distalmost edge of tendinal canal of middle trochlea: 41.3 mm; 42.0 mm. Width of shaft at level of metatarsal facet: 8.3 mm; 8.4 mm. The first measurements fall within the range (39.4-42.8) observed by Owre (1967) for six specimens of *A. anhinga*, the second slightly beyond (7.6-8.2).

As only two skeletons of Recent *A. anhinga* could be checked against the fossil material for qualitative characters, it remains to be seen (pending an examination of a greater number of specimens) if the differences noted above, particularly those involving the humerus, are of any significance insofar as altering the specific identification that has been made. I prefer to assign the fossil material to *A. anhinga* for the moment and assume that it falls within the range of variation of the species rather than to suggest the existence of a new species.

*Distribution.*— *Anhinga anhinga* enjoys a distribution which includes all or parts of the southeastern United States, Cuba, Mexico, Central America, and South America south to Argentina. Previous records of its occurrence as a fossil have been confined to Pleistocene and prehistoric sites of Florida.

## Order CICONIIFORMES

## Family ARDEIDAE

*Tigrisoma* (?) sp.

A basal pedal phalanx of the third digit matches that of the members of this genus, but is somewhat smaller than either of the two species examined. I hesitate to make a definitive statement on this element.

## Order ANSERIFORMES

## Family ANATIDAE

*Aythya americana* (Eyton)

*Referred Material.*— Proximal portion of left ulna, UMMP 61100.

*Description.*— The ulnae of *Aythya americana* and *A. marila* bear a close resemblance to one another, but differ consistently in several important features. In palmar view, the distalmost edge of the external cotyla is a straight line perpendicular to the long axis of the shaft in *americana*, the same edge in *marila* being more rounded and inclined with respect to the axis of the shaft. The external cotyla also appears relatively larger in *americana*. The fossil ulna matches *americana* in these two characteristics, and is the size of a ♂ of that species. The olecranon is sharply pointed terminally in *americana* but bluntly flattened in *marila*; it is not possible to evaluate the condition of the fossil's olecranon because it shows too much abrasion.

*Distribution.*— A breeder in Western Canada and the United States, the Redhead's wintering range includes most of the United States and Mexico south to the Valley of Mexico. Known from several Pleistocene records in the United States, this is its second occurrence as a fossil in the Pleistocene of Mexico.

*Aythya marila* (Linnaeus)

*Referred Material.*— Upper end of right coracoid, UMMP 61100.

*Description.*— The size of Recent *Aythya americana* and *A. marila*, the fossil coracoid agrees with the latter but differs from the former in having: 1) the triosseal canal flatter, 2) the brachial tuberosity less pronounced and producing only a moderate overhang above the triosseal canal, 3) the glenoid facet flatter, with its outer margin less inflected, and 4) the width through the coracohumeral surface directly above the glenoid facet relatively greater.

*Distribution.*— The Greater Scaup is widely distributed throughout Asia, Northern Europe, and North America. It winters chiefly at sea, and is a fairly rare bird in Mexico, known only from a few records in Baja California and Sinaloa. Though recorded from the Pleistocene of both Old and New Worlds, this is the first Mexican fossil record of *Aythya marila*.

*Aythya* sp.

The worn proximal end of a left ulna (UMMP 61075) and the slightly better preserved proximal end of a right ulna (UMMP 61100) are referred to the diving duck genus *Aythya*. In size and general appearance, both seem closest to *A. americana*. But in view of their abraded nature, I refrain from making this particular identification.

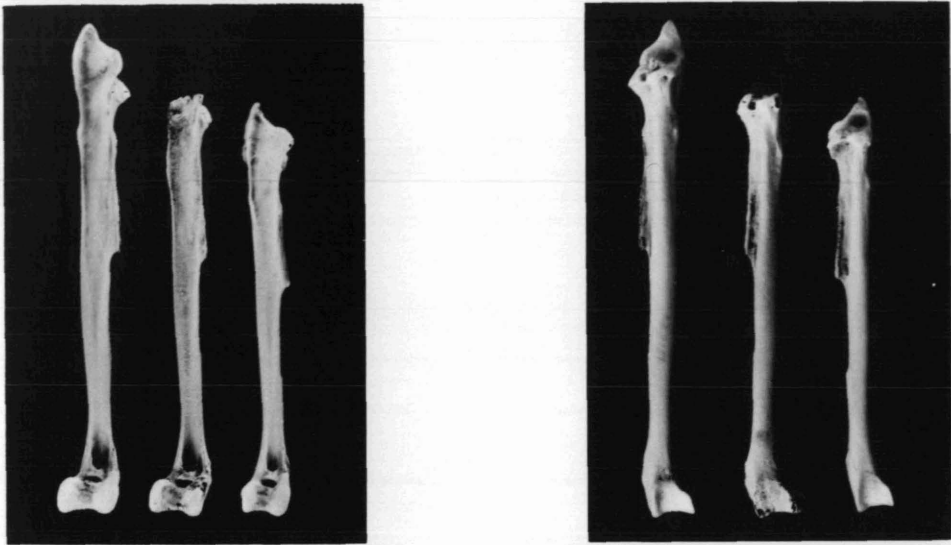


FIG. 2 — *Oxyura zapatanima*, new species. Holotype tibiotarsus (UMMP 63255) compared to ♀ *Oxyura jamaicensis* (UMMZ 151841, left) and ♂ *Oxyura dominica* (UMMZ 158621, right). Anterior (left) and posterior (right) views. X 1.

*Oxyura zapatanima*, new species

*Holotype*.— Left tibiotarsus, lacking inner and part of outer cnemial crests, UMMP 63255. Figure 2.

*Measurements of Holotype*.— See Table 2.

*Paratype*.— The badly worn distal end of a left humerus, UMMP 61232, is tentatively referred to this species.

*Locality and Age*.— UM-Mex-1-72 (R. R. Miller loc.). Bed A of highest west wall of Lower Quarry (equals floor level of Upper Quarry). West edge of Lago de Chapala, Jalisco, Mexico. Collected by R. R. Miller, F. H. Miller, and N. A. Neff, 30 November 1972. Late Pliocene or early Pleistocene. Data for paratype same as that of holotype.

*Etymology*.— Honoring the spirit (L., *animus* = m. spirit; *anima* = f. soul) of Emiliano Zapata, the Mexican revolutionary hero.

*Diagnosis*.— In overall length, *zapatanima* is intermediate to living *Oxyura jamaicensis* and *O. dominica*. The fossil resembles *jamaicensis* in general appearance, but is significantly smaller (8-14% smaller than a series of 11 ♀♀). *Zapatanima* differs from *dominica* but agrees with *jamaicensis* in having the outer cnemial crest produced in a more posteriorly directed manner, and positioned at approximately a 60° angle to the antero-posterior plane of the shaft. In *dominica*, the outer cnemial crest extends farther distally along the length of the shaft and, near its distal termination in external view, forms a conspicuous ledge above the fibular crest not found in either *jamaicensis* or *zapatanima*. The fossil differs from both *jamaicensis* and *dominica* in having: 1) the anterior articular surface more rounded in posterior view, sloping more steeply externally, 2) the cotylar width proportionately narrower in relation to the shaft diameter at the midpoint of the overall length of the tibiotarsus, 3) the peroneal groove (the area adjoining the fibular crest and shaft on the posterior side) more

TABLE 2  
MEASUREMENTS (IN MM) OF STIFF-TAIL DUCK (*OXYURA*) TIBIOTARSI

	<i>O. zapatanima</i>	<i>O. jamaicensis</i>	<i>O. dominica</i>	<i>O. vittata</i>		<i>O. ferruginea</i>	
				♀	♂	♀	♂
Length from anterior articular surface to intercondylar ledge	55.7	61.6 (60.1-63.5) <sup>a</sup>	49.4 (48.3-51.2) <sup>b</sup>	63.7	64.3	65.5	68.8
Width of shaft at midpoint of length	3.5	3.7, 3.7 3.8 <sup>c</sup>	3.1 <sup>d</sup>	3.7		3.6	3.6
Maximum width through condyles	7.1	8.0, 7.6 8.3 <sup>c</sup>	6.3 <sup>d</sup>	8.1		8.6	9.0
Width of shaft at proximal margin of supratendinal bridge	5.3	4.9, 5.6 5.7 <sup>c</sup>	4.5 <sup>d</sup>	5.2		6.2	6.6

a - Based on 11 ♀♀; 3 from UMMZ and 8 from U.S. Natl. Mus.

b - Based on 3 ♂♂; 1 from UMMZ and 2 from U.S. Natl. Mus.

c - Based on 3 ♀♀ from UMMZ

d - Based on 1 ♂ from UMMZ

deeply excavated, 4) the distal edge of the supratendinal bridge straight rather than curved or notched, and 5) the internal ligamental prominence more strongly produced and clearly visible in anterior view (somewhat obscured by internal condyle in neospecies). When the tibiotarsus of *zapatanimia* is held at a slightly inclined angle and viewed from the proximal end, the posterior intercondylar sulcus appears rather flat as compared to *jamaicensis* and *dominica*, and the inner margin of the internal condyle is less inflected as well.

*Descriptions.*— In comparison to other living oxyurine ducks, the resemblance of the fossil tibiotarsus to the larger *O. vittata* is quite striking, particularly the nature of the distal end of the bone. Aside from its much smaller size, *zapatanimia* differs from *vittata* in having the internal ligamental prominence sharply and strongly developed, a character which consistently distinguishes the fossil from the neospecies examined. Directly anterior to the internal ligamental prominence of both *zapatanimia* and *vittata* is a deep, spherical pit; the prominence of these two species does not appear to be as clearly circumscribed distally from the edge of the condyle as in *jamaicensis* and *dominica* (in these last two forms, there is evidence of a pit anterior to the prominence, but in none of the specimens examined was it as deep or well defined as in *zapatanimia* or *vittata*). In distal view, the anterior margins of the internal and external condyles are produced subequally in *zapatanimia*, *dominica* (1 specimen examined), *vittata* (1), and *ferruginea* (2), but are produced equally in *jamaicensis* (9 specimens examined). This difference is due to the degree of inflection of the internal condyle, being greater in *jamaicensis* than in the other species.

Middle Pleistocene deposits from the Palm Spring formation of Vallecito Creek, San Diego County, California, contained oxyurine elements upon which Howard (1963) based her description of *Oxyura bessomi*, an extinct species of a size somewhat comparable to living *O. jamaicensis* but alto-

gether stouter in appearance, and distinguished from it by a number of qualitative features as well. As only wing and pectoral girdle elements are known for *bessomi*, no direct comparisons can be made between it and *zapatanima*. But one might expect a discrepancy in the linear dimensions between the tibiotarsi of *bessomi* (should they become known) and the tibiotarsus of *zapatanima*, if the robustness and size of the known elements of *bessomi* are any indication.

The distal end of a left humerus which I have referred to *O. zapatanima* is done so only with some reservation. The degree of abrasion and wear is so extensive that, if the humerus had not been found in association with the type tibiotarsus, it would have been rather difficult to identify even to the family level. Nevertheless, I am assigning it to the genus *Oxyura* and to *zapatanima* specifically on the basis of its *general* resemblance to the humeri of living species of stiff-tailed ducks. The humerus is only slightly larger than the single ♂ *O. dominica* available for comparison.

### Order CHARADRIIFORMES

#### Family SCOLOPACIDAE

#### *Calidris fuscicollis* (Vieillot)

*Referred Material.*— Complete left ulna, UMMP 61086.

*Description and Remarks.*— The charadriid (plover) ulna is characterized by a marked palmar curvature of the proximal third of the bone; scolopacid (sandpipers) ulnae are, by comparison, straighter along the greater portion of their lengths. The impression of the brachialis anticus is relatively deeper and wider in charadriids, nearly flat in scolopacids. The fossil ulna resembles the scolopacid pattern as so described, agreeing in size (length 30.5 mm; cotylar width 3.4 mm; greatest distal width 3.0 mm) with Recent *Calidris fuscicollis* and *C. bairdii*. Agrees with *fuscicollis* but differs from *bairdii* in having the distalmost slope of the carpal tuberosity sinuous rather than straight, and in having the bicipital attachment produced as a narrow ledge of bone that extends up to the edge of the internal cotyla. The fossil ulna is in an excellent state of preservation, allowing these fine distinctions to be made. The ulna of *Calidris fuscicollis* bears a strong resemblance to that of the phalarope *Lobipes lobatus*, but in palmar view of the distal end, the condyles are produced farther distally beyond the carpal tuberosity in *Calidris*, and is also more pointed at its tip rather than bluntly rounded as in *Lobipes* (these distinctions hold true at least insofar as *C. fuscicollis* is concerned; other calidrid sandpipers were not compared to *Lobipes*).

*Distribution.*— The White-rumped Sandpiper breeds in arctic regions of North America, and is a widespread winter resident in South America. Its status as a migrant in Mexico is uncertain, with only a few records from Yucatan and Cozumel Island. It has heretofore been unrecorded as a fossil, and as such its presence in the Pleistocene of Mexico represents a new addition to the list of Recent birds known as fossils.

### Order PASSERIFORMES

#### Family ICTERIDAE

#### *Sturnella* (?) sp.

The well-preserved distal end of a left ulna (UMMP 61086) represents the only passeriform element present in the Chapala fauna. The fossil ulna appears very close to Recent *Sturnella magna magna* (a North American race), but is proportionately smaller in all respects. The ulnae of two ♀ *S.*

*m. magna* were measured as follows: greatest distal width — 3.8 mm, 4.0 mm; greatest depth through external condyle — 2.7 mm, 2.9 mm. Comparable measurements on the fossil are 3.5 mm and 2.5 mm. It should be noted that the Mexican subspecies of *Sturnella magna* are considerably smaller than their northern counterparts. No skeletons of the smaller Mexican races were available for comparison, however. The difference in size is the only distinguishing feature between the fossil and living *S. m. magna*, but specific determination is withheld until more diagnostic elements are discovered.

## DISCUSSION

The Chapala fossil avifauna as described in this paper is clearly one which is dominated by water-inhabiting forms. Given the nature of the site, however, this bias would seem altogether natural and quite expected. Of particular interest is the relative abundance (90% of those identified to species) of foot-propelled diving birds. *Anhinga anhinga* usually stalks its prey in the tangled vegetation found within the stagnant waters of swamps, and requires the presence of emergent vegetation, upon which it climbs laboriously when leaving the water. The prey species of Recent *Anhinga anhinga* are predominantly comprised of laterally-compressed fish, which they impale with their spear-like bills (Owre, 1967). Cormorants (*Phalacrocorax*) pursue their prey in relatively open waters, and need uninterrupted expanses of water upon which to run and patter prior to taking flight. In contrast to anhingas, their bills are hooked terminally rather than being straight and rapier-like, and used to grab rather than to impale fish (Owre, 1967). They are therefore capable of taking fairly stout-bodied fish which anhingas would be unable to impale. The two species of diving ducks, *Aythya americana* and *A. marila*, feed primarily in deep waters, and a substantial portion of their food consists of aquatic plants (more so in *americana* than in *marila*), but mollusks and aquatic insects are occasionally taken. Stiff-tailed ducks (*Oxyura*) are remarkably adept divers, and their diet is again preponderantly vegetable in nature. The grebes, of course, are highly adapted for diving. *Aechmophorus occidentalis* feeds largely on fish and other aquatic animals; aquatic invertebrates (particularly insects and their larvae) form the major part of the diet of *Podiceps caspicus*, but tadpoles, small frogs, and plants are also eaten; small fish, mollusks, and crustaceans are the main food of *Podilymbus podiceps* (Bent, 1963; Kortright, 1942).

All of the species of diving birds present in the fossil avifauna, with the exception of *Anhinga anhinga*, form a fairly homogeneous group insofar as their preferred aquatic environments are concerned, tending to frequent areas of relatively open water.

The presence of a *Sturnella*-like icterid in the fossil avifauna might suggest a proximity in the surrounding environs of the Pleistocene lake of marshy or grassy areas. Such an expectation would be consistent with the habitat preferences of Recent species of *Sturnella* (meadowlarks). Recent *Calidris fuscicollis* are typically mudflat inhabiting birds; but during migration they, of course, travel over a variety of habitats. If its present habits are any indication, the occurrence of *Calidris fuscicollis* suggests that the habitat of the lake might have included frequently exposed mudflats or other similar areas.

It is difficult just on the basis of the avian material to evaluate the probability of pre-depositional transport for the total paleovertebrate assemblage of Chapala, and there is in fact no reason to assume that the circumstances under which deposition occurred were similar in all cases. Any indication of transport prior to deposition might, however, be considered fairly strong evidence in favor of Barbour's (1973) interpretation of the terraces found north of present-day Lago de Chapala; namely, that changes in the drainage patterns of the lake during Pleistocene times, and not pronounced pluvial periods as had been suggested by Clements (1963), were responsible for the terraces. Perhaps a more critical examination of other associated vertebrates in the Chapala fauna will help clarify the issue



of stream transport. But it should be noted that although some of the avian bones are in fairly good condition, and even fewer are preserved in their entirety, the great majority are fragmented and abraded. Paleocological inferences from the fossil birds of Lago de Chapala nevertheless suggest that the habitat of the fauna was a lake margin rather than a flowing stream (see page 2 of this paper).

*Podiceps caspicus*, *Phalacrocorax chapalensis* (sp. n.), *Anhinga anhinga*, *Aythya marila*, *Oxyura zapatanima* (sp. n.), and *Calidris fuscicollis* represent new additions to the Pleistocene avifauna of Mexico. The total number of bird species known from Pleistocene deposits of Mexico now stands at 69. This figure includes all forms identified only to species. *Pliolymbus baryosteus* (extinct grebe), *Phalacrocorax olivaceus* (Mexican Cormorant), and *Phoenicopterus ruber* (American Flamingo) have been recorded from the Pleistocene of Chapala (Howard, 1969). Specifically assigned birds from Chapala fossil sites number 13, of which three are extinct. This gives an extinction ratio of approximately 23%, compared to 29% for the birds from San Josecito Cavern (Nuevo Leon) studied by Miller (1943), and to a figure of 27% for the total Pleistocene assemblage of Mexican birds. Only those forms which have been identified to the species level were included in calculating percentages of extinction indeterminate forms were not considered. The indeterminate forms could conceivably represent extinct species, and if included in the calculations would thereby increase the percentages.

The relatively lower Pleistocene extinction percentage of the Chapala region in comparison to the total Mexican avifossil assemblage (23% vs. 27%) might in some way reflect the stable climatic conditions of the Mesa Central during the Pleistocene suggested by Bradbury (1971) and Smith *et al.* (1975). But I am inclined to believe that any inferences to this effect based on the paleornis would be a bit premature considering the small sample size presently available for scrutiny.

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