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THE PLEISTOCENE WESTERN GREBE *AECHMOPHORUS* (AVES, PODICIPEDIDAE) FROM FOSSIL LAKE, OREGON: A COMPARISON WITH RECENT MATERIAL

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Abstract.—Skeletons of Recent Western Grebes *(Aechmophorus occidentalis)* from Canada were compared with bones of the species from Fossil Lake, Oregon. The few significant differences between the two samples can be accounted for by geographic variation, postmortem abrasion of the fossils, or preparation techniques. Therefore, the form "*lucasi*" should not be recognized in combination with *Aechmophorus*.

INTRODUCTION

The Pleistocene Western Grebes *(Aechmophorus)* from Fossil Lake, Oregon, have had a checkered taxonomic history since they were first reported by Cope (1889). Three years later, Shufeldt (1892, p. 396) compared "many fossil bones" of this species with a single Recent specimen and found that the majority of fossil specimens were "typical" but that no humerus was quite as large as the Recent specimen. He also mentioned a slight but apparently constant difference in the distal margin of the ulnar crest of that element. Subsequently, L. H. Miller (1911, p. 83) described the Fossil Lake material as a new species, *Aechmophorus lucasi*, apparently comparing his fossil material with a single Recent specimen, as had Shufeldt. Two years later, Shufeldt (1913, pp. 128-136) assembled a large number of grebe bones from Fossil Lake. He did not recognize *lucasi* as valid and had much to say about the size and variation of the fossil sample, although he did not present means or even extremes to describe it. Howard (1946, pp. 148-151) reported on over 800 bones of *Aechmophorus* from Fossil Lake and made detailed comparisons with seven or eight Recent skeletons from Monterey Bay and southern California. She concluded that the fossils were slightly, but significantly, larger than her Recent sample and considered them to belong to part of a chronocline or temporal subspecies, *Aechmophorus occidentalis lucasi*. Unfortunately, none of these workers realized the degree of either sexual dimorphism or geographic variation now known to exist in *Aechmophorus*.

Dickerman (1963, 1973) was apparently the first to describe the geographic variation, pointing out that birds nesting on the Mexican Plateau are distinctly smaller than those from the United States and Canada. He also presented data on sexual dimorphism. Storer and Nuechterlein (1985) described further geographic variation in *Aechmophorus*, showing that birds from the southern part of the United States are smaller than those from the northern part of the United States and Canada. This made it appear likely that the differences between the Fossil Lake birds and those of Howard's sample might have resulted from geographic variation

rather than a temporal difference. This point has some theoretical significance because the reported difference between fossil and Recent Western Grebes has been cited as an evolutionary trend (Howard, 1947, p. 13). The aim of this paper is to determine if the Fossil Lake material falls within the size range of Recent material.

MATERIALS AND METHODS

Through the kindness of Robert W. Nero, the University of Michigan Museum of Zoology received skeletons of 119 Western Grebes that froze in Lake Newell, Alberta, Canada, in November, 1959 (Nero, 1960). This sample is the primary source of Recent skeletons used herein for comparison with Fossil Lake material. Possibly as a result of differential migration schedules, it is strongly biased in favor of males and immature birds. (The young birds, most of which were presumably hatched in June and therefore ca. five months in age, were separated from the adults on the basis of incomplete ossification of the tarsometatarsus.) Samples of 10 or 15 of each age and sex group were measured and compared in order to determine whether the young birds differed significantly from the adults. Differences between pairs of these samples were evaluated, using the Student's t-test. All measurements of the Recent skeletons were significantly larger (at the 0.01 level) in males than in females. In the Recent samples, most measurements of young birds averaged smaller than those of adults, although in approximately one-third of the measurements the differences were not significant at least at the 0.05 level. Because of these differences and because I found no incompletely fused tarsometatarsi among the fossil specimens, I combined two samples of ten adult birds of each sex from Canada to compare with the fossils. This assumed a 50:50 sex ratio for the fossil sample, which is probably not far from that found in Recent populations. (G. L. Nuechterlein found a small preponderance of males in nesting colonies that he studied, pers. comm.) This was further checked by graphing measurements of fossil femora, and checking the number of bones in each portion of the bimodal distribution.

Bones from Fossil Lake were measured at the University of California Museum of Paleontology at Berkeley, and the large sample from Fossil Lake in the American Museum of Natural History was borrowed. In all, 43 whole or partial femora, 33 tibiotarsi, 59 tarsometatarsi, 25 humeri, 1 ulna, 2 carpometacarpi, and 47 coracoids were measured. Seven of the Recent skeletons used by Howard for her analysis were borrowed from the Los Angeles County Museum and the University of California at Los Angeles (I was unable to locate an eighth). Both fossil and Recent bones were measured in the same way to the nearest 0.1 mm with dial calipers. Measurements included: the overall length, width of proximal and distal ends, and least width of the shaft of the femur, tibiotarsus, and tarsometatarsus; the length, proximal width, and least width and depth of the shaft of the humerus; the length of the ulna and carpometacarpus; and the proximal width and the length of the coracoid taken perpendicular to a line joining the two proximal-most points on the bone. Means and standard deviations for the various samples were calculated and comparisons made using Student's t-tests.

The two widely sympatric color forms of *Aechmophorus*, formerly thought to be color morphs, are now considered different species (American Ornithologists' Union, 1985), but no valid differences between skeletal elements of the two species have been found yet. The Recent skeletons from Canada used in this analysis are all presumed to be of the dark form *Ae. occidentalis*, and that name is used throughout this paper, with the understanding that individuals of the light form, *Ae. clarkii*, may be represented in the fossil material and in Dr. Howard's sample.

RESULTS

Table 1 shows that the means for Howard's sample of California specimens are consistently lower than those from the Canadian sample. The former sample is made up of two first-year males, one adult male, two first-year females and two adult females. The smaller size of these birds can be accounted for by the known geographic variation based on study skins (Storer and Nuechterlein, 1985, p. 105) and, to a lesser degree, by the presence of first-year birds in the sample.

The largest Western Grebes are from Canadian populations. Therefore, a sample of Canadian birds made up of ten adult males and ten adult females was compared with the Fossil Lake birds. As can be seen from Table 1, in 12 of 19 measurements analyzed, there was no significant difference between the fossil and Recent birds at the 0.05 level. Five were significant at the 0.05 level and one each at the 0.01 and 0.001 levels. In five of the measurements in which significant differences were found, the fossils were smaller than the Recent Canadian sample. This might be expected, at least in samples of Recent birds from Oregon, because of the southward clinal decrease in size of Recent birds (Storer and Nuechterlein, loc. cit.).

In addition, three of these five measurements are of widths or depth of the ends of long bones, areas where postmortem abrasion or wear can be expected to be greatest, because these parts of the bones are subject to most abrasion with the substrate. The other two measurements, both of the coracoid, were taken from points that are also subject to postmortem wear. The two significant differences in which the measurements of the fossils were greater than those of the Recent birds are the widths of the shafts of the tibiotarsus and tarsometatarsus. The widths of the femur and humerus also averaged larger, although not significantly so, in the fossil sample.

I think two points may be significant here: the shafts of long bones are protected from postmortem wear by the larger ends of the bones, and the shaft widths are the smallest of the measurements taken; hence, any deposit on the surface would make the largest relative difference. The fossil specimens were preserved by soaking in resin, which could have left a film on the surface. The differences between the mean widths of the shafts of the fossil and Recent bones range from 0.07 to 0.26 mm (mean 0.16 mm); a film less than 0.1 mm thick could account for the differences in these shaft-width measurements, and a thickness of perhaps one-half this amount would reduce these differences to insignificance.

Of all measurements of long bones taken, the overall length is presumed to be the least subject to wear, because bones lying on a substrate would tend to lie flat, a position in which the wider and deeper portions near the ends of the bones would be subject to more abrasion than the shaft. Because of this, because of the large number of intact femora in the fossil sample, and because of the small difference (0.14 mm) between the means of the fossil and Recent samples, femur length was used to estimate the sex ratio in the fossil sample. Of the 43 femora measured, 23 fell into the range of Recent males and 20 into that of females. This agrees with the estimate of a small preponderance of males found by Nuechterlein in his field work.

Jefferson (1985) presented data on late Pleistocene *Aechmophorus* from Lake Manix, southern California, a significantly older deposit than that at Fossil Lake. The measurements Jefferson took that correspond with those I took of the Fossil Lake and Recent specimens fall within the range of the latter, with the exception of the width of the shaft of the tarsometatarsus, which, however, falls within that of the Fossil Lake birds and might not have been taken in the same way as mine. Among the Lake Manix material are a nearly complete associated postcranial skeleton and an associated partial skeleton with both femora, tibiotarsi, and tarsometatarsi. Differences between the Lake Manix and Recent material may, like that from Fossil Lake, be related to geographic variation, or, in part to differences in how the mea-

TABLE 1 - Comparison of measurements of Pleistocene Western Grebes (*Aechmophorus*) from Fossil Lake, Oregon, with those of 20 Recent specimens (10 of each sex) from Canada and 7 of the 8 specimens from California used by Howard (1946). Abbreviations: *n*, sample size; *OR* observed range; $\bar{x}$, sample mean; *s*, standard deviation; *V*, coefficient of variation; *t*, t-statistic. Measurements in mm. Statistical differences between the means of the fossil and Recent samples were tested using Student's t-test. Asterisks indicate levels of significance: * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$.

Measurement	Sample	OR	*n*	$\bar{x}$	*s*	*V*	*t*
FEMUR							
Length	Fossil	41.9 - 50.1	43	46.16	1.97	4.28	0.24
	Recent	43.0 - 50.0	20	46.30	2.29	4.95	
	Howard	41.7 - 47.3	7	44.46			
Prox. W.	Fossil	12.7 - 15.5	42	14.01	0.76	5.41	2.26*
	Recent	13.1 - 16.0	20	14.53	0.99	6.80	
	Howard	12.4 - 14.4	7	13.39			
W. Shaft	Fossil	5.0 - 6.3	43	5.63	0.31	5.48	1.35
	Recent	5.0 - 6.3	20	5.51	0.39	7.08	
	Howard	4.7 - 5.7	7	5.23			
Dist. W.	Fossil	13.3 - 16.0	37	14.73	0.81	5.48	2.62*
	Recent	14.0 - 17.1	20	15.34	0.90	5.89	
	Howard	13.3 - 15.4	7	14.34			
TIBIOTARSUS							
Length	Fossil	119.2 - 128.9	5	123.80	4.03	3.25	0.93
	Recent	113.2 - 132.0	20	121.21	5.84	4.82	
	Howard	110.9 - 124.2	7	117.71			
Prox. W.	Fossil	10.3 - 12.5	7	11.19	0.81	7.27	0.36
	Recent	10.1 - 12.0	20	11.08	0.60	5.45	
	Howard	9.3 - 11.3	7	10.37			
W.Shaft	Fossil	5.7 - 6.6	20	6.20	0.29	4.67	2.23*
	Recent	5.4 - 6.6	20	5.94	0.41	6.89	
	Howard	5.1 - 6.3	7	5.76			
Dist. W.	Fossil	10.0 - 12.7	28	11.23	0.64	5.73	1.66
	Recent	9.9 - 12.1	20	10.90	0.71	6.49	
	Howard	9.5 - 11.5	7	10.30			
TARSOMETATARSUS							
Length	Fossil	69.2 - 85.9	25	77.98	3.96	5.08	1.22
	Recent	71.0 - 84.7	20	76.52	4.09	5.35	
	Howard	69.7 - 79.4	7	74.27			
Prox. W.	Fossil	11.5 - 14.6	36	12.96	0.80	6.15	0.58
	Recent	12.2 - 14.3	20	13.09	0.71	5.41	
	Howard	11.9 - 14.0	7	12.60			
W. Shaft	Fossil	3.3 - 4.4	46	3.74	0.27	7.14	2.81**
	Recent	3.1 - 4.0	20	3.54	0.29	8.22	
	Howard	3.0 - 3.6	7	3.30			
Dist. W.	Fossil	7.3 - 9.5	38	8.61	0.53	6.18	0.56
	Recent	8.0 - 9.5	20	8.69	0.47	5.42	
	Howard	7.5 - 9.5	7	8.37			
HUMERUS							
Length	Fossil	110.3 - 124.6	5	118.74	5.75	4.84	0.63
	Recent	110.5 - 129.9	20	120.53	5.68	4.71	
	Howard	108.9 - 124.3	7	114.06			

TABLE 1 - Continued.

Measurement	Sample	OR	*n*	$\bar{x}$	*s*	*V*	*t*
HUMERUS (cont.)							
Prox. W.	Fossil	10.0 - 12.0	30	11.10	0.66	5.96	0.96
	Recent	10.0 - 12.0	20	11.30	0.80	7.09	
	Howard	10.1 - 12.1	7	10.86			
W. Shaft	Fossil	4.5 - 5.7	24	5.20	0.32	6.12	0.67
	Recent	4.6 - 5.7	20	5.13	0.34	6.67	
	Howard	4.2 - 5.1	7	4.66			
Depth Shaft	Fossil	3.6 - 4.7	34	4.20	0.26	6.24	5.48***
	Recent	4.2 - 5.2	20	4.63	0.29	6.31	
	Howard	3.5 - 4.6	7	3.99			
ULNA							
Length	Fossil		1	101.4			
	Recent	101.7 - 118.7	20	108.41	4.75	4.39	
	Howard	96.5 - 111.1	7	101.74			
CARPOMETACARPUS							
Length	Fossil	51.3 - 54.3	5	52.74	1.26	2.39	0.19
	Recent	49.2 - 58.5	20	52.97	2.55	4.82	
	Howard	46.9 - 55.3	7	49.74			
CORACOID							
Length	Fossil	41.6 - 50.7	50	45.83	2.36	5.16	2.19*
	Recent	43.7 - 51.3	20	47.21	2.35	4.98	
	Howard	40.7 - 48.9	7	44.49			
Prox. W.	Fossil	13.0 - 15.8	33	14.50	0.74	5.09	2.51*
	Recent	13.0 - 17.4	20	15.16	1.18	7.76	
	Howard	12.8 - 16.0	7	13.96			

surements were taken. It would be worthwhile to check the proportions of the associated skeletons with those of Recent ones from the northern as well as the southern part of the range of *Aechmophorus*, but all measurements should be made by the same person.

In conclusion, the few significant differences between the Pleistocene specimens of Western Grebe from Fossil Lake, Oregon, and those of Recent specimens can perhaps best be accounted for by geographic variation, postmortem wear in the fossils, or preparation techniques. Therefore, I believe that, even if real, the differences between the Fossil Lake and Recent populations are too slight to warrant recognition of "*lucasi*" as a distinct form of *Aechmophorus*.

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