The Pleistocene Pied-billed Grebes (Aves: Podicipedidae)

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ABSTRACT

Pleistocene specimens of pied-billed grebes (*Podilymbus*) were compared with a series of skeletons of the modern North American form, *Podilymbus podiceps podiceps*. Most of the fossils agreed closely with this form and are allocated to it. The co-types of *Podilymbus magnus* Shufeldt also fall within the range of variation of this form, hence *P. magnus* becomes a synonym of *P. podiceps*. A new species, *Podilymbus wetmorei,* characterized by a wide tarsometatarsus and a heavy femur, is described from the Pleistocene of Florida.

Introduction

The Pied-billed Grebe (*Podilymbus podiceps*) is widely distributed in the New World from Canada to southern South America. The only other living species of the genus, the Atitlán or Giant Pied-billed Grebe (*P. gigas*), is confined to Lake Atitlán, Guatemala. The genus is represented in upper Pliocene deposits of Idaho by a large species, *P. majusculus* (Murray, 1967), and in numerous Pleistocene deposits. Most of the Pleistocene specimens have been assigned to the living species, *P. podiceps,* but a few have been referred to an allegedly larger extinct species, *P. magnus*. The latter was first described by Shufeldt (1913:136–137) on the basis of two tarsometatarsi and a coracoid from Fossil Lake, Oregon. Later, Wetmore (1937:198–199) synonymized *P. magnus* with *P. podiceps,* pointing out that there is considerable sexual dimorphism in the genus and that Shufeldt had only one skeleton (a female) of the living species with which to compare his fossil material. Wetmore found that the larger of the tarsometatarsi described by Shufeldt was only slightly larger than those of two males of the living North American subspecies (*P. p. podiceps*) and was matched by an example of the slightly larger South American race (*P. p. antarcticus*). More recently, Brodkorb (1959: 273–274) revived the name *P. magnus* for twelve bones from Arredondo, Florida, using eight skeletons of the living North American form for comparison. He (1963a:113) also referred material from the Santa Fe River, Florida, to *P. magnus*. McCoy (1963:337) in his report on the fossil avifauna of the Itchtucknee River, a tributary of the Santa Fe, referred two tarsometatarsi to *P. magnus* and 47 other bones (including two other tarsometatarsi) to *P. podiceps*. Subsequently, Brodkorb (1963b:230) wrote that "specimens from Fossil Lake and some of the Floridian localities average large and are perhaps recognizable as a temporal subspecies, *Podilymbus podiceps magnus* Shufeldt."

The availability of a series of 39 skeletons of the modern North American form (*Podilymbus p. podiceps*) from Michigan and Wisconsin has permitted a better estimate of variation within a living population of this species than was heretofore possible, as well as providing a comparison of skeletal elements of this population with a large number of fossil elements from late Pleistocene deposits. The following fossil material has been examined:California: McKittrick, 1 tarsometatarsus; Rancho La Brea, 1 femur; Florida: Reddick, 3 coracoids, 1 humerus, 1 tibiotarsus, 2 tarsometatarsi; Haile, 1 coracoid, 1 ulna, 1 tibiotarsus; Arredondo, 2 coracoids, 3 humeri, 1 ulna, 3 carpometacarpi, 1 femur,

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TABLE 1.—Measurements (mm) of modern and late Pleistocene Pied-billed Grebe bones

Character	Modern					Fossil				
	n	max.	min.	mean±σ_m	σ	*n*	max.	min.	mean±σ_m	σ
CORACOID				**MALES**						
Length	23	33.9	30.1	31.98±0.25	1.18	6	33.4	30.9	31.97	–
Width sternal end	32	12.0	10.4	11.28±0.01	0.47	5	12.2	10.7	11.26	–
Least width shaft	23	3.0	2.4	2.65±0.03	0.14	25	3.0	2.4	2.72±0.03	0.15
Width head	23	3.5	2.7	3.10±0.05	0.22	9	3.3	2.7	3.04	–
Depth head	23	5.5	4.6	5.17±0.05	0.24	10	5.5	5.0	5.18±0.05	0.16
HUMERUS										
Length	23	81.2	74.3	77.63±0.48	2.26	6	77.7	74.4	75.96	–
Width head	23	14.8	13.0	13.97±0.10	0.46	10	14.3	13.6	13.93±0.07	0.24
Least width shaft	23	3.3	2.9	3.09±0.03	0.12	27	3.3	3.0	3.10±0.01	0.10
Width distal end	23	7.5	6.6	7.20±0.05	0.25	26	7.6	6.7	7.12±0.04	0.25
ULNA										
Length	20	76.4	69.1	71.87±0.04	2.03	–	–	–	–	–
Least width	20	2.6	2.2	2.41±0.02	0.10	5	2.6	2.3	2.52	–
Width proximal end	20	6.0	5.3	5.69±0.04	0.18	1	–	–	5.8	–
Depth proximal end	20	5.8	4.6	4.98±0.06	0.26	1	–	–	5.1	–
Width distal end	20	4.6	3.9	4.31±0.05	0.20	5	4.5	4.0	4.24	–
Depth distal end	20	4.4	3.9	4.20±0.04	0.17	5	4.6	4.3	4.40	–
CARPOMETACARPUS										
Length	23	37.6	33.2	34.98±0.28	1.32	4	35.5	34.5	35.05	–
Width head	23	3.4	2.9	3.21±0.03	0.14	6	3.35	3.0	3.13	–
Length metacarpal I	23	5.5	4.6	4.98±0.05	0.26	6	5	4.9	4.92	–
Depth head	23	7.0	6.1	6.57±0.05	0.23	6	6.9	6.3	6.67	–
Depth distal end	23	4.2	3.4	3.95±0.04	0.19	4	4.1	3.8	4.0	–
FEMUR										
Length	23	42.7	38.9	40.42±0.28	1.29	8	42.4	39.0	41.05	–
Width head	23	10.0	8.8	9.47±0.08	0.36	9	10.0	9.5	9.74	–
Least width shaft	23	4.0	3.2	3.67±0.04	0.20	15	4.0	3.5	3.76±0.03	0.11
Width distal end	23	10.7	9.2	9.94±0.07	0.32	9	10.7	9.2	9.92	–
TIBIOTARSUS										
Length to articulation	22	75.7	69.8	72.68±0.37	1.70	2	72.0	71.1	71.55	–
Total length	22	88.7	80.9	84.48±0.43	1.99	1	–	–	84.1	–
Length crest*	22	12.8	11.1	11.80±0.13	0.59	2	12.1	11.8	11.95	–
Width head	23	7.9	6.8	7.30±0.07	0.31	5	7.9	6.9	7.48	–
Width distal end	23	8	6.9	7.56±0.05	0.23	7	7.8	7.4	7.61	–
Least width shaft	22	4.3	3.6	3.91±0.04	0.18	4	4.25	3.7	3.93	–
Least depth shaft	22	2.7	2.3	2.53±0.03	0.12	5	2.6	2.45	2.53	–
TARSOMETATARSUS										
Length	23	44.2	38.8	41.59±0.30	1.46	11	43.8	40.0	41.91±0.32	1.08
Least width shaft	23	3.6	2.95	3.30±0.03	0.17	19	3.6	3.2	3.48±0.03	0.13
CORACOID				**FEMALES**						
Length	15	30.0	27.4	28.47±0.23	0.85	3	28.7	26.8	28.0	–
Width sternal end	14	11.1	9.6	10.14±0.12	0.44	5	10.5	9.6	10.02	–
Least width shaft	16	2.6	2.2	2.36±0.03	0.11	11	2.5	2.3	2.40±0.02	0.08
Width head	16	3.2	2.6	2.87±0.04	0.15	4	2.9	2.5	2.75	–
Depth head	16	4.9	4.4	4.68±0.03	0.13	2	4.7	4.6	4.65	–

TABLE 1.—Continued

Character	Modern					Fossil				
	n	max.	min.	mean±σ_m	σ	*n*	max.	min.	mean±σ_m	σ
HUMERUS										
Length	15	74.3	65.6	69.17±0.63	2.34	8	70.9	66.5	69.62	–
Width head	15	13.0	11.8	12.28±0.09	0.35	7	12.6	11.9	12.44	–
Least width shaft	15	3.0	2.6	2.75±0.03	0.12	21	3.0	2.4	2.76±0.03	0.15
Width distal end	15	6.9	6.3	6.48±0.05	0.18	19	7.2	6.1	6.50±0.07	0.30
ULNA										
Length	16	67.2	61.6	64.61±0.04	1.72	1	–	–	62.7	–
Least width	16	2.3	1.9	2.20±0.03	0.10	4	2.4	2.1	2.26	–
Width proximal end	16	5.4	4.8	5.08±0.05	0.18	1	–	–	5.3	–
Depth proximal end	16	4.8	4.2	4.43±0.05	0.18	1	–	–	4.5	–
Width distal end	16	4.1	3.7	3.90±0.04	0.15	1	–	–	3.6	–
Depth distal end	16	4.1	3.5	3.80±0.04	0.17	3	4.0	3.6	3.82	–
CARPOMETACARPUS										
Length	16	32.8	29.2	31.13±0.27	1.05	1	–	–	33.2	–
Width head	16	3.0	2.7	2.87±0.03	0.10	1	–	–	2.9	–
Length metacarpal I	16	4.9	4.0	4.47±0.06	0.24	1	–	–	4.5	–
Depth head	16	6.1	5.7	5.99±0.04	0.15	1	–	–	6.2	–
Depth distal end	16	3.7	3.3	3.57±0.03	0.13	1	–	–	3.7	–
FEMUR										
Length	15	39.2	35.2	36.56±0.30	1.08	5	37.3	35.9	36.8	–
Width head	15	9.0	8.1	8.54±0.07	0.27	5	8.9	8.3	8.64	–
Least width shaft	15	3.4	3.0	3.25±0.04	0.15	6	3.5	3.1	3.33	–
Width distal end	15	9.1	8.3	8.68±0.06	0.23	5	9.0	8.5	8.82	–
TIBIOTARSUS										
Length to articulation	14	68.2	62.1	64.81±0.49	1.85	4	63.9	63.0	63.50	–
Total length	14	79	72.2	75.18±0.52	1.96	2	73.4	73.2	73.3	–
Length crest*	15	10.8	9.7	10.25±0.09	0.33	3	10.4	9.6	100.33	–
Width head	15	6.8	6.2	6.56±0.05	0.18	3	6.9	6.55	6.78	–
Width distal end	15	7.3	6.3	6.83±0.07	0.28	4	7.1	6.7	6.90	–
Least width shaft	14	3.8	3.3	3.49±0.04	0.16	5	3.6	3.3	3.44	–
Least depth shaft	14	2.3	2.1	2.19±0.02	0.08	5	2.25	2.1	2.19	–
TARSOMETATARSUS										
Length	15	39.0	35.8	37.43±0.27	1.05	5	37.5	36.0	36.98	–
Least width shaft	15	3.2	2.7	2.92±0.03	0.13	9	3.05	2.85	2.98	–

* Calculated by subtracting the length measured from the articulation from the total length.

3 tarsometatarsi; Catalina Lake, 1 coracoid; Hornsby Spring, 1 femur, 1 tibiotarsus; Itchtucknee River, 28 coracoids, 58 humeri, 7 ulnae, 7 carpometacarpi, 18 femora, 23 tibiotarsi, 20 tarsometatarsi; Jenny Spring, 1 humerus; Lake Monroe, 2 humeri, 1 femur, 1 tibiotarsus; Rock Spring, 2 coracoids, 5 humeri, 1 ulna, 6 tibiotarsi; St. John's Lock, 3 humeri, 1 ulna, 1 tibiotarsus, 1 tarsometatarsus; Vero Beach, 1 humerus. Nevada: Smith Creek Cave, 1 coracoid. Oregon: Fossil Lake, 4 tarsometatarsi (including the types of *P. magnus*). Total: 220 bones.

Using dial calipers reading to one tenth of a millimeter, 33 measurements were taken from the fossil and modern bones (Table 1). Each fossil specimen was "sexed" by comparing it with the largest and smallest element for each sex in the modern sample. There is very little or no overlap

between the sexes in the total lengths of the elements measured, males being larger. In instances in which a fossil was within a zone of overlap in length, it was almost always outside a zone of overlap in another measurement. Therefore, I believe that few, if any, of the fossils were assigned to the wrong sex and only a few fragmentary specimens could not be "sexed" in the above manner. Variability within the sexes of the modern material and the fossils "sexed" in this way proved similar, a further indication that most, if not all of the fossils were assigned to the correct sex.

The means and, where practical, the standard errors of the means and standard deviations of the measurements for these bones were calculated and compared with those of the modern material (Table 1).

ACKNOWLEDGMENTS.—I am indebted to Pierce Brodkorb of the University of Florida (PB) and to the curators of the American Museum of Natural History (AMNH), the Natural History Museum of Los Angeles County (LACM), the Museum of Comparative Zoology (MCZ), the University of Florida (UF), and the University of Michigan Museum of Paleontology for permission to use material under their care. The figure was prepared by Mark Orsen. Part of this work was subsidized by the National Science Foundation through Grant GB-8269.

Discussion

The late Pleistocene material is discussed below by skeletal element. Unless otherwise indicated, all specimens in the following sections are from the Itchtucknee River.

CORACOID.—In both sexes, the means of all measurements of the modern and Pleistocene coracoids are very close. One specimen (PB1209 "♀") falls outside the expected range (i.e., mean ± 2σ) of the modern sample in the width of the head (2.5 mm as opposed to 2.6 mm in the smallest modern specimen).

HUMERUS.—With five exceptions, the fossil humeri agree with the modern series in size. A distal portion (UF 15309) measures 3.0 mm in shaft width and 6.5 mm in distal width, the former measurement being near the mean for males and the latter near the mean for females in the modern series. (This bone was not included in the calculations of the fossil sample because it could not be assigned with confidence to either sex.) Humerus PB 8005 has a shaft width of 3.4 mm, which is approximately 2.5 standard deviations above the mean for males, whereas its other measurements are well within the range of modern males. (It was not included in the calculations of the fossil sample because its identification was not certain; it might belong to the new species described herein.) UF 15297 has a shaft width of 2.4 mm, three standard deviations below the mean for modern females, and a distal width of 6.3 mm, which is within the range of modern females. UF 15280 and UF 15307 have distal widths of 7.2 and 7.0 mm, respectively, which are somewhat outside the expected range of the modern sample.

ULNA.—One partial ulna (PB 7687 from Rock Spring) has a distal width of 4.6 mm or 2.35 standard deviations above the mean for modern males. In other measurements, it is within the expected range of modern specimens, as are the other fossil ulnae examined.

CARPOMETACARPUS.—The fossil carpometacarpi are all within the expected range of variation of the modern sample.

FEMUR.—With two exceptions (UF 15214 and UF 15220), all the fossil femora fall within the expected range of modern specimens. The two exceptions are referred to the new species and are not included in the calculations of the fossil sample.

TIBIOTARSUS.—Four fossils are outside the range of the modern sample. UF 15251 "♂" is more than 2 standard deviations above the means for males in distal width (8.2 mm) and least width of shaft (4.4 mm). Two modern specimens are 8.0 mm in distal width and one is 4.3 mm in shaft width.) UF 15254 is 68.7 mm in length, measured from the articulation, which is between the ranges of the two sexes but slightly nearer the mean of females, 3.7 mm in width of shaft, within the range of either sex, and 2.4 mm in depth of shaft, within the range of modern males. MCZ 2606 "♂" and PB 1851 "♀" have cnemial crests well below the range expected for their assigned sexes. In other measurements, they are within the range of modern specimens or differ by only a tenth of a millimeter. These four fossils were not included in the calculations of means for the fossil samples.

TARSOMETATARSUS.—All but three fossils of this element fall within the expected range of the mod-

ern sample. Two of these (UF 15223 and PB 1762 from Reddick) are very broad and are referred to the new species. The third (PB 1854) measures 44.8 mm in length and 3.5 in least width of shaft. The former measurement is 2.2 and the latter 1.2 standard deviations above the mean for the modern series. These three fossils are not included in the calculations of the fossil sample.

Thus, most of the Pleistocene fossils agree well with the sample of modern specimens. These fossils include the type tarsometatarsi of *P. magnus,* which measure 43.6 and 42.9 mm in length and 3.5 and 3.2 mm in least width. I have not examined the coracoid Shufeldt (1913, pl. 38:fig. 449) tentatively assigned to *P. magnus,* but his photograph of it agrees better with the modern form than two other coracoids (his figures 461, 462) he did assign to *P. podiceps.* Wetmore (1937:199) referred this specimen to the modern form. The 12 fossils from Arredondo referred to *P. magnus* by Brodkorb (1959:273–274) fall within the expected range of variation of the modern form. I have not seen the fossil (or fossils) from the Santa Fe River referred without comment to *P. magnus* by Brodkorb (1963a:115). The tarsometatarsi from the Itchtucknee River referred to *P. magnus* by McCoy (1963:337) also fall within the expected range of the modern form, although one (PB 1854) is 0.6 mm longer than the longest modern specimen measured. Both measure 3.5 mm in least width and are equaled or surpassed by both fossil and modern specimens in this dimension. Thus, I can find no evidence that the late Pleistocene birds were significantly larger than the modern ones. Because the types of *P. magnus* are indistinguishable from the modern form, *Podilymbus magnus* Shufeldt must be considered a synonym of *Podilymbus podiceps* (Linnaeus).

Of the few fossils falling outside the range of the modern series, several are heavier than the corresponding elements of *P. p. podiceps* and are established here as a new species.

Podilymbus wetmorei, new species

FIGURE 1*b,d*

HOLOTYPE.—Nearly complete left tarsometatarsus in the collection of Pierce Brodkorb (PB 1762) from the Dixie Lime Products quarry, locality IA, 1.6 km south of Reddick, Marion County, Florida. Collected by Pierce Brodkorb, 2 March 1957.

TABLE 2.—Measurements (mm) of *Podilymbus wetmorei*

Character	"Male"	"Female"
TARSOMETATARSUS	UF 15223	PB 1762 (type)
Length	42.0	36.8
Least width shaft	3.75	3.5
FEMUR	UF 15214	UF 15220
Length	42.4	36.8
Width head	10.2	8.4
Least width shaft	42.0	3.7
Width distal end	10.8	9.0

AGE.—Late Pleistocene (Rancholabrean) fide Webb (1974:13).

RANGE.—Known so far only from two localities in peninsular Florida.

DIAGNOSIS.—Similar in length and general configuration to the tarsometatarsus of *Podilymbus podiceps,* the shaft much heavier (Figure 1; Table 2). Differs from *Podilymbus majusculus* Murray (1967), from the upper Pliocene of Idaho, in being shorter, comparatively wider in the shaft, and in having the ridge along the external side of the anterior surface of the bone much reduced for its distal third. Shorter and relatively heavier than the tarsometatarsus of *P. gigas.*

REFERRED MATERIAL.—One tarsometatarsus (UF 15223) and two femora (UF 15214 and UF 15220) all from the Itchtucknee River, Columbia County, Florida. Like the type, the second tarsometatarsus has a notably heavy shaft; the femora have thick shafts and wider heads and distal ends than *P. podiceps* (Table 2). Two exceptional humeri mentioned above (UF 15309 and PB 8005 from the Itchtucknee River) have wide shafts and may likewise represent *P. wetmorei.* Two tibiotarsi (MCZ 2606 and PB 1851 from the Itchtucknee River) have short cnemial crests. The former is wide at both articulations and has a thick (deep) shaft, suggesting that it may also belong to the new form. However, the second bone is small in all these dimensions and probably is an aberrant or worn example of *P. podiceps.* The placement of the other fossils that fall outside the range of the modern form is uncertain, and will probably remain so until more material becomes available.

REMARKS.—Having both a thick tarsometatarsus

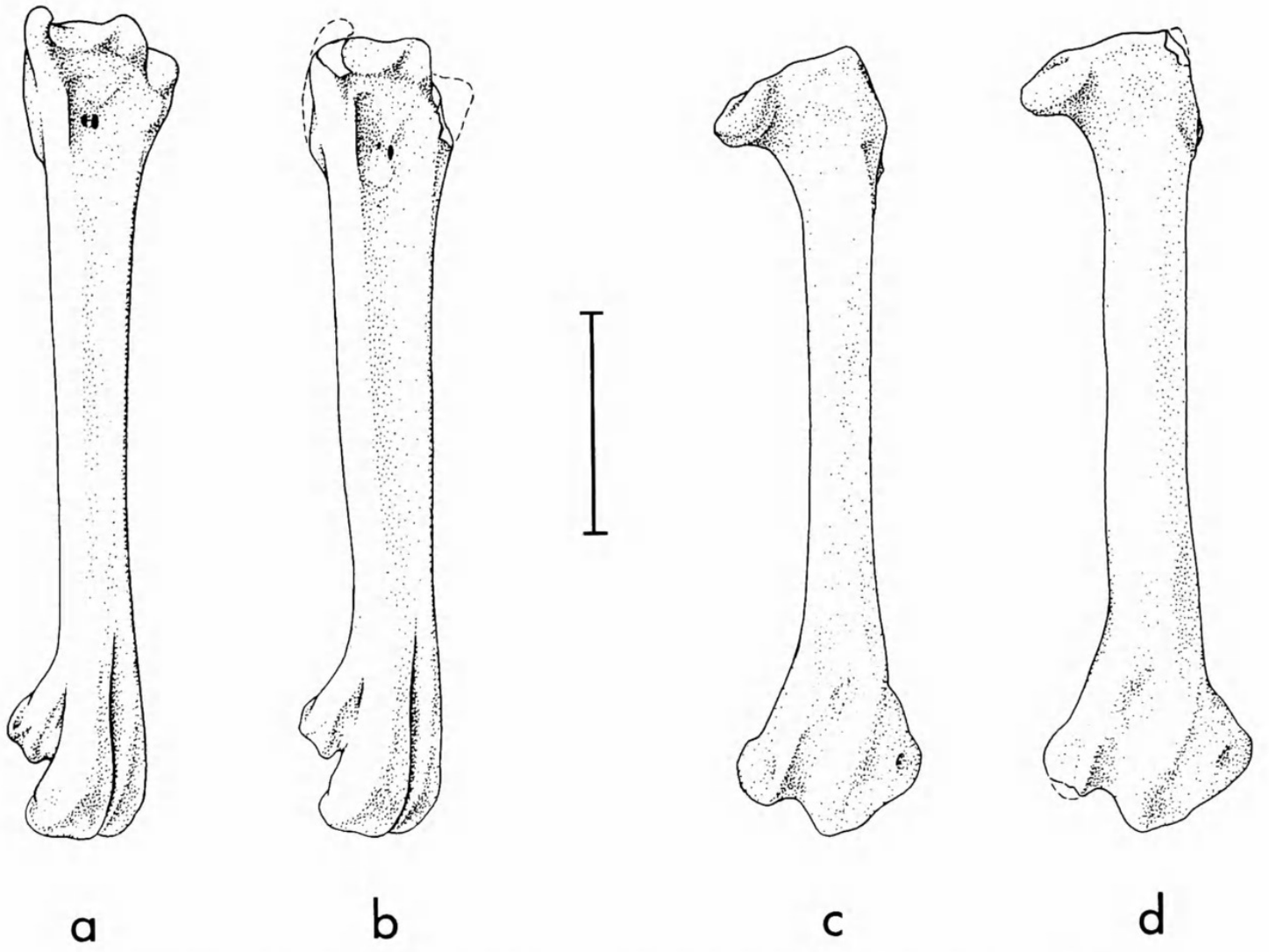

FIGURE 1.—Left tarsometatarsi and left femora of species of *Podilymbus: a, c, P. podiceps* (UMMZ 151328); *b, P. wetmorei,* new species (holotype, PB 1762); *d, P. wetmorei* (UF 15220). (Scale = 10 mm.)

and a heavy femur is paradoxical in a foot-propelled diving bird, because the complex of structural modifications which appear adaptive for rapid locomotion under water includes a short, heavy femur, a long cnemial crest, and a narrow tarsometatarsus. In the case of *P. wetmorei,* a thickened but not shortened femur might have provided a greater area for the attachment of muscles used in swimming (notably the gastrocnemius), which could compensate for the area lost through the shorter cnemial crest. Modern pied-billed grebes inhabit bodies of water with considerable emergent vegetation and have wider tarsometatarsi than grebes inhabiting more open water. Presumably this is an adaptation for diving almost directly downward, breast first, rather than springing forward like most other grebes. The even wider tarsometatarsi of *P. wetmorei* probably represent a further extension of this adaptive trend already evident in modern species of *Podilymbus.*

The presence of two species of *Podilymbus* in the same Rancholabrean deposits in Florida suggests that one (*P. wetmorei*) may have been a resident form that differentiated from the widespread *P. podiceps,* which latter may only have wintered there. The situation between the fossil form known as *Gallinula brodkorbi,* also from the Itchtucknee, and *G. chloropus* (Olson, 1974:174) suggests an interesting parallel and might be accounted for similarly.

ETYMOLOGY.—I take great pleasure in naming this species in honor of Alexander Wetmore.

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