A REDESCRIPTION OF TWO PLIOCENE CORMORANTS

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Two extinct species of cormorant have been described from the Pliocene of Idaho: *Phalacrocorax idahensis* (Marsh), based on the proximal 45 mm of a carpometacarpus from the Castle Creek local fauna (Middle Pliocene), and *Phalacrocorax macer* Brodkorb, based on a carpometacarpus lacking metacarpals I and III from the Hagerman local fauna (Upper Pliocene, see Hibbard et al. 1965). Wetmore (1933) referred the distal portion of an ulna from the Hagerman local fauna to *idahensis*, and Brodkorb (1955) referred the proximal portion of another ulna from the Bone Valley formation (Lower Pliocene) of Florida to *idahensis*, but later (1963) stated that these referred specimens probably represent other species. Brodkorb (1958) suggested that two small, unidentified coracoids from the Hagerman local fauna, reported by Wetmore (1933), represent *macer*. The Recent *Phalacrocorax auritus* (Lesson) has also been reported from the Hagerman local fauna (Wetmore 1933; Brodkorb 1958).

In the collections of avian fossils from the Upper Pliocene Hagerman and Sand Point local faunas (Hibbard 1959; Hibbard et al. 1965) obtained by Claude W. Hibbard and his field parties of The University of Michigan Museum of Paleontology and by Reid Macdonald of the Los Angeles County Museum of Natural History are the bones of two species of cormorant, a larger one and a smaller one. These are apparently *idahensis* and *macer*, respectively. Because these species are poorly known, a description of this new material is presented.

MATERIALS

Most of the new material is from the Hagerman local fauna in Twin Falls County, Idaho, in section 5 of Township 8 south, Range 13 east, and in sections 16, 17, 21, 28, 29, 32, and 33 of Township 7 south, Range 13 east (see Murray 1967). The remaining specimens (The University of Michigan Museum of Paleontology (UMMP) V45146, V45148, V49018, V49020, V52671) are from the Sand Point local fauna in Owyhee County, Idaho, in SW ¼ of section 1, Township 6 south, Range 8 east (Hibbard 1959).

In addition to the new material, I have examined the following fossil specimens: *idahensis*, Yale Peabody Museum (YPM) 527 (type), U.S. National Museum (USNM) 12240, and from the collection of Pierce Brodkorb, PB 311; *macer*, UMMP V33918 (type), and USNM 12827, 12828; *auritus*, USNM 12239, UMMP V33908, V33913. I have also examined specimens referable to *Phalacrocorax kennelli* Howard from the San Diego Pliocene: Los Angeles County Museum (LACM) 2528, 2529, 2566, 2645, 2817, 2833, and 2843.

For comparison I used six Recent skeletons of *auritus* from The University of Michigan Museum of Zoology collections (UMMZ 71920, 85465, 99527, 107479, 107485, and 153818) and five from the U.S. National Museum (USNM 18049, 18050, 19262, 347833, and 347834). Because of the small sample of Recent skeletons, I have used the term $\sqrt{\Sigma d^2/n-1}$ to determine the standard deviation of some of the measurements. The "statistical range" refers to six standard deviations centered on the mean. Those specimens of *idahensis* and *macer* that exceeded the measured ranges of *auritus* skeletons were tested statistically (*t*-test, Simpson et al. 1960:182–183) to determine if they could represent a population, the mean of which differed significantly from the mean of the sample *auritus* population.

Phalacrocorax idahensis (Marsh)

Of the new material, I refer the following specimens to *idahensis*: two associations of many bones, each representing a single individual (UMMP V52472 and LACM 210/17819), parts of four coracoids (UMMP V54148, V52440 (2), V53736), scapula (UMMP V48903), humerus (UMMP V52671), radius (UMMP V45146), ulna (UMMP V49637), carpometacarpus (UMMP V55564), tibiotarsus (UMMP V52418), a nearly complete tarsometatarsus (UMMP V49571), and a cervical vertebra (UMMP V49018).

The type of *idahensis* (YPM 527) is the well-preserved, proximal 45 mm of a carpometacarpus. Marsh (1870) described the specimen in detail but distinguished it, as *Graculus*, from *Phalacrocorax* by the presence of the anterior carpal fossa, which is not even a good specific character. I have found only two distinguishing features. The first is the shape of metacarpal I, a feature noted by Howard (1946) when she compared *idahensis* with *Phalacrocorax macropus* (Cope). The curve between the extensor attachment and the pollical facet has a smaller radius, giving the process of metacarpal I a squarish appearance and causing it to project forward at a greater angle to the axis of the shaft of metacarpal II than in

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TABLE 1. Measurements (in mm) of carpometacarpi of some cormorants (*Phalacrocorax*).

	Overall length			Width metacarpal II			Trochlea depth			Width through metacarpal I		
	$\bar{x}$	Range	SD	$\bar{x}$	Range	SD	$\bar{x}$	Range	SD	$\bar{x}$	Range	SD
auritus												
males ($n = 6$)	74.2	70.7–77.2	2.11	4.9	4.7–5.1	0.16	6.6	6.2–6.8	0.21	13.9	13.4–14.5	0.41
females ($n = 4$)	70.2	68.1–72.5	1.93	4.7	4.4–5.2	0.36	6.3	5.7–6.6	0.40	13.6	12.3–14.4	0.89
idahensis												
(type), YPM 527	—			5.3**			7.1**			16.0**		
UMMP V52472	—			—			7.0*			15.0**		
UMMP V55564	78.6*			5.4**			7.2**			15.5**		
LACM 210/17819	72.3			5.2			6.6			14.5		
macer												
(type), UMMP V33918	67.5*			4.6			5.5*			—		
UMMP V52282	—			—			5.5*			12.7		
kennelli												
LACM 2843	—			—			5.8			12.1*		

** Significantly different from *P. auritus* at 0.05 level.
* Not significant. All other values not tested.

auritus; the process of metacarpal I in *auritus* is trapezoidal in shape. Second, the internal rim of the carpal trochlea is less round and forms a less sharp angle with metacarpal III than in *auritus*. Carpometacarpus V55564 is an almost perfect copy of the type (except for being more complete and of a different color) in size and features. The carpometacarpi of the two associations (UMMP V52472 and LACM 210/17819) are smaller but in qualitative features are like *idahensis* rather than like *auritus*. Most measurements of carpometacarpi referable to *idahensis* are within the statistical range of *auritus* but are statistically different from *auritus* means (table 1). On the basis of the carpometacarpi, then, the two associations of bones are referred to *idahensis*. Single bones are referred to *idahensis* if they resemble the bones of the associated skeletons.

The humeri (V52472, V52671, and 210/17819) do not differ in size from those of *auritus* (table 2). However, *idahensis* differs from *auritus* on the basis of the scar of the *infraspinatus* attachment, which interrupts the curve from the distal edge of the bicipital crest to the internal tuberosity in *idahensis* but not in *auritus* (seen from ventral view) and the slight dip between the head and the area ventral to the capital groove, which is present in *auritus* but absent in *idahensis* (seen on palmar view).

One complete ulna of *idahensis* (V52472) is barely outside the statistical range of *auritus* ulnae in length but does not differ in other measurements (table 3). Despite the greater overall length of the ulna, the scar of *brachialis anticus* is not longer than the average for *auritus* (27.5 mm against a mean of 28.2 for six *auritus*). In this specimen and in LACM 210/17819 the flange of the proximal radial depression extends outward at a greater angle to the shaft and does not extend so far distally as in *auritus*. The ratio, ulna length/coracoid length, of specimen V52472 is 2.60, whereas in *auritus* it ranges in six males from 2.34 to 2.46 (mean, 2.41), and in four females from 2.35 to 2.47 (mean, 2.41). *P. idahensis* may have been slightly longer-winged than *auritus*.

The first phalanx of the second digit of the wing (V52472) differs from that of *auritus* in having a ridge extending only about one-third the distance from the metacarpal facet to the digital facet, whereas this ridge extends nearly to the digital facet in *auritus*.

The nearly complete femur (V52472) is slightly but not significantly longer than that of *auritus* (table 4). In both V52472 and LACM 210/17819 the internal and external condyles are separated by a deeper groove (seen from either anterior or posterior view), a result of the internal condyle being longer than in *auritus*.

Tibiotarsus V52472 is slightly but significantly longer than that of *auritus* (table 5). In both V52472 and LACM 210/17819 the most anterior portion of the internal articular surface flares upward less sharply than in *auritus*, and the internal edge of the proximal end is not interrupted by a ligamental attachment as it is in *auritus*. The external ligamental prominence at the distal end does not bulge as markedly as in *auritus*.

Tarsometatarsus V49571 is significantly longer than those of *auritus* (table 6). Other-

TABLE 2. Measurements (in mm) of humeri of some cormorants (*Phalacrocorax*).

	Overall length		Breadth distal end		Breadth shaft		Depth shaft	
	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
auritus								
males ($n = 7$)	152.2	146.5–158.6	16.6	16.2–17.2	8.2	7.9–8.7	7.2	6.9–7.8
females ($n = 3$)	145.0[a]	139.0–148.0	16.1[a]	14.8–17.2	8.2[a]	7.0–8.9	7.2[a]	6.0–7.8
idahensis								
UMMP V52472	—		17.1		8.6		7.6	
LACM 210/17819	150.0		16.1		8.6		8.6	
UMMP V52671	—		—		—		—	
kennelli								
LACM 2833	—		14.7		7.3		6.1	
LACM 2817	—		—		—		—	

	Proximal width		Head depth		Length of ligamental furrow	
	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
auritus						
males ($n = 7$)	24.2	23.5–25.1	7.9	7.6–8.2	13.3	12.5–14.5
females ($n = 3$)	23.2[b]	21.6–24.7	7.3[b]	6.5–7.9	12.8[b]	12.0–13.5
idahensis						
UMMP V52472	—		—		—	
LACM 210/17819	23.9		7.2		12.0	
UMMP V52671	—		8.2		—	
kennelli						
LACM 2833	—		—		—	
LACM 2817	20.7		6.0		11.0	

[a] Actual measurement of third specimen.
[b] $n = 4$.

wise it appears indistinguishable from *auritus* tarsometatarsi.

The remaining portions of the coracoids (table 7), sternum, furculum, scapulae, radii, synsacrum, and tarsometatarsus of V52472 and the scapulae, furculum, coracoids, and tarsometatarsus of LACM 210/17819 are indistinguishable from these elements of *auritus*. Unless specimens are significantly larger than *auritus*, as is tarsometatarsus V49571, single fossil bones of these elements can be either *idahensis* or *auritus*. The only evidence of the presence of *auritus* in the Pliocene is a tarsometatarsus (USNM 12239; Wetmore 1933), the distal portion of a carpometacarpus (UMMP V33908; Brodkorb 1958), and the proximal portion of a scapula (UMMP V33913; Brodkorb 1958), all from the Hagerman local fauna. These specimens cannot be distinguished from either *idahensis* or Recent *auritus*, and thus probably represent *idahensis*. I recommend that *Phalacrocorax auritus* be removed from the list of Recent species that occur in the Pliocene until unambiguous evidence becomes available.

The ulna (USNM 12240) referred to *idahensis* by Wetmore (1933) but questioned by Brodkorb (1963) is somewhat larger than ulna V52472. It is the undiagnostic distal end. I refer it to *idahensis* because it is not so large as to be outside the possible range of *idahensis*. The Bone Valley ulna (PB 311; Brodkorb 1955) is considerably larger than V52472 (maximum shaft diameter at distal end of scar of *brachialis anticus*, 9.0 mm) but there are no diagnostic features remaining on the fragment. I agree with Brodkorb (1963) that this specimen probably represents an unknown species.

The distal end of an ulna (UMMP V57469) from locality 3 of the Rexroad local fauna in Kansas (Woodburne 1961), previously unreported, is too fragmentary to permit positive identification, but its size suggests it is probably *idahensis*. That *idahensis* should occur in the Rexroad local fauna is not surprising as species of fossil grebes (Murray 1967), rails (Feduccia 1968), and an owl (Ford and Murray 1967) are common to both the Rexroad and Hagerman local faunas.

TABLE 3. Measurements (in mm) of ulnae of some cormorants (*Phalacrocorax*).

	Overall length			Greatest measurement: Across internal and external cotylae			Across internal cotyla and olecranon		Maximum diameter of shaft at distal end of scar of brachialis anticus	
	$\bar{x}$	Range	SD	$\bar{x}$	Range	SD	$\bar{x}$	Range	$\bar{x}$	Range
auritus										
males ($n = 6$)	161	155–168	4.4	12.8	12.3–13.2	0.37	11.8	10.8–12.2	7.4	6.8–7.8
females ($n = 4$)	154	149–157	3.4	12.3	11.4–13.2	0.75	10.8	10.0–11.5	7.1	6.6–7.6
idahensis										
UMMP V52472	175**			12.8			11.6		7.7	
LACM 210/17819	—			12.3			11.2		7.2	
macer										
UMMP V48901	—			10.8*			10.0		6.8	
kennelli										
LACM 2529	141**			10.5			10.1		6.6	

** Significantly different from *P. auritus* at 0.05 level.
* Not significant. All other values not tested.

Phalacrocorax macer Brodkorb

The following specimens are referred to *macer*: proximal portion of an ulna (UMMP V48901), proximal end of a carpometacarpus (UMMP V52282), a tibiotarsus lacking the condyles (UMMP V48889), and the distal portion of a femur (UMMP V52269).

Brodkorb (1958) distinguished the type carpometacarpus (UMMP V33918) by its being slightly smaller than in *auritus* and *wetmorei* and by its having a deep but much shorter cuneiform fossa that extends proximad only to the level of the external ligamental attachment, and a shorter distal fornix. In comparing the type with my series of *auritus* I have been unable to observe these differences, except that it is slightly smaller than the smallest measured *auritus* specimen (table 1). This difference is not statistically significant. Nevertheless, I think the specimen does represent a species of cormorant that is, on the average, smaller than *auritus*. The only qualitative difference I have found is that the internal rim of the carpal trochlea of the type and referred (V52282) carpometacarpi resembles the carpometacarpi of *idahensis* and differs from those of *auritus* and *kennelli* (LACM 2843) in being less round and forming a less sharp angle with metacarpal III. The process of metacarpal I (in V52282, lacking in V33918) resembles *auritus* rather than *idahensis* in being trapezoidal in shape and directed more proximad than forward.

The ulna (V48901) is at the short end of the range of *auritus* (table 3). It is like *idahensis* and unlike *auritus* in the shape of the radial depression.

The femur (V52269) is smaller than measured *wetmorei* (Brodkorb 1955) and *auritus* and *kennelli* (table 4) but resembles *idahensis*

TABLE 4. Measurements (in mm) of femora of some cormorants (*Phalacrocorax*).

	Overall length			Breadth across condyles		
	$\bar{x}$	Range	SD	$\bar{x}$	Range	SD
auritus						
males ($n = 7$)	59.8	56.3–62.7	2.24	17.0	16.0–18.3	0.77
females ($n = 4$)	56.1	53.7–58.3	1.88	16.3	15.5–17.2	0.70
idahensis						
UMMP V52472	63.7*			17.4		
LACM 210/17819	—			16.0		
macer						
UMMP V52269	—			13.6**		
kennelli						
LACM 2528	55.4			15.6		

** Significantly different from *P. auritus* at 0.05 level.
* Not significant. All other values not tested.

TABLE 5. Measurements (in mm) of tibiotarsi of some cormorants (*Phalacrocorax*).

	Overall length			Breadth across condyles		Narrowest measurement: Shaft breadth			Shaft depth		
	$\bar{x}$	Range	SD	$\bar{x}$	Range	$\bar{x}$	Range	SD	$\bar{x}$	Range	SD
auritus											
males ($n = 7$)	110.4	104.0–116.5	4.1	12.7	11.5–13.3	7.0	6.8–7.2	0.16	5.2	5.0–5.5	0.30
females ($n = 4$)	105.2	102.0–107.0	2.2	12.2	11.7–12.9	6.8	6.6–7.0	0.18	5.0	4.8–5.3	0.26
idahensis											
UMMP V52472	120.5**			13.2		7.8**			5.3		
UMMP V52418	—			12.2		—			—		
LACM 210/17819	—			12.3		7.3*			5.3		
macer											
UMMP V48889	—			—		5.4**			3.9**		
kennelli											
LACM 2566	105.5			11.8		7.3			4.9		
LACM 2645	—			12.4		7.3			4.9		

** Significantly different from *P. auritus* at 0.05 level.
* Not significant. All other values not tested.

and not *auritus* or *kennelli* in having a deep groove between the internal and external condyles.

The tibiotarsus (V48889) is smaller than the statistical range of tibiotarsi of *auritus* (table 5) and *wetmorei* (Brodkorb 1955). The ligamental attachment interrupts the inner edge of the proximal end, and the anterior portion of the internal articular surface flares upward sharply, resembling *auritus* and *kennelli* rather than *idahensis*.

The two coracoids (USNM 12827 and 12828) reported by Wetmore (1933) and referred to *macer* by Brodkorb (1958) are more lightly built than *auritus* and probably do represent *macer*.

UNIDENTIFIED MATERIAL

One carpometacarpus (UMMP V49576) is the size of *macer* but its metacarpal I is more like that of *idahensis*. Either *idahensis* and *macer* overlap in size, or the shape of metacarpal I is variable in *macer*. I think the former is probably the case, judging from the small amount of variation in the shape of metacarpal I in Recent skeletons. There are a few other specimens I have not identified: the sternal portions of two coracoids (UMMP V52385 and V56014), two ulnae (UMMP V49637 and LACM 210/22217), a tarsometatarsus (UMMP V49020), and a complete quadrate (UMMP V53702).

DISCUSSION

There were at least two species of cormorants living in the Late Pliocene of Idaho. *Phalacrocorax idahensis* was slightly larger than *auritus*, and *macer* was smaller than *auritus*, but specimens of each broadly overlap *auritus* and may even overlap each other. *P. kennelli* (Howard 1949; Miller and Bowman 1958) and *wetmorei* (Brodkorb 1955) overlap *macer* and probably overlap *idahensis*. These cormorants point up the difficulties of studying single bones of fossil species in comparison with a small series of Recent skeletons. By assuming that large specimens of cormorants were *idahensis* and smaller specimens in the same deposit were *auritus*, *idahensis* has been considered larger than it really is (Wetmore 1933;

TABLE 6. Measurements (in mm) of tarsometatarsi of some cormorants (*Phalacrocorax*).

	Overall length			Trochleae breadth			Proximal breadth		
	$\bar{x}$	Range	SD	$\bar{x}$	Range	SD	$\bar{x}$	Range	SD
auritus									
males ($n = 7$)	64.6	61.8–67.8	1.89	15.1	14.0–15.6	0.57	13.6	12.9–14.3	0.51
females ($n = 4$)	62.7	60.7–63.8	1.73	14.6	13.8–15.5	0.72	13.1	12.5–14.0	0.63
idahensis									
UMMP V49571	69.2**			16.2*			14.4*		

** Significantly different from *P. auritus* at 0.05 level.
* Not significant. All other values not tested.

TABLE 7. Measurements (in mm) of coracoids of some cormorants (*Phalacrocorax*).

	Head to internal tip sternal facet		Head to sternal edge of scapular facet		Dorso-ventral head depth	
	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
auritus						
males ($n = 7$)	66.1	62.6–68.9	24.1	23.4–25.0	12.4	11.8–13.0
females ($n = 4$)	63.8	60.4–66.7	23.3	21.9–24.5	11.7	11.1–12.4
idahensis						
UMMP V52472	67.2		24.6		12.5	

Howard 1946; Brodkorb 1958). In one individual of *idahensis* (UMMP V52472) the coracoid is near the mean size of male *auritus* coracoids (table 7), whereas its ulna exceeds the mean of male *auritus* ulnae by more than three standard deviations (table 3). Without having an associated skeleton, the difference in proportions could not have been known, and so the fossil record of *auritus* was extended erroneously back into the Pliocene.

Another aspect of interest is that a species may have characteristics in common with two or more species. For instance, in the characteristics I found, the femur of *macer* is like that of *idahensis* and different from *auritus* and *kennelli*, whereas the tibiotarsus of *macer* is more like those of *auritus* and *kennelli* than like that of *idahensis*. Characterization and identification of species on the basis of a single bone, or even a few bones, should be tentative, especially when the variation within related Recent species is not well known.

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