

NUMBER 452  
9 JUNE 1995

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# CONTRIBUTIONS IN SCIENCE

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KENNETH E. CAMPBELL, JR.



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NATURAL HISTORY MUSEUM  
OF LOS ANGELES COUNTY  
900 EXPOSITION BOULEVARD  
LOS ANGELES, CALIFORNIA 90007

Printed at Allen Press, Inc., Lawrence, Kansas  
ISSN 0459-8113

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# A REVIEW OF THE CRANES (AVES: GRUIDAE) OF RANCHO LA BREA, WITH THE DESCRIPTION OF A NEW SPECIES

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KENNETH E. CAMPBELL, JR.<sup>1</sup>

**ABSTRACT.** A review of all known specimens of cranes (Aves: Gruidae) from the asphalt deposits at Rancho La Brea, California, revealed that three species of *Grus* were present in the Los Angeles Basin in the late Pleistocene. These included the living species *G. americana* and *G. canadensis* and a new, smaller species described herein. The new species is distinguished most readily by cranial proportions, which indicate a longer, more slender skull with a relatively enlarged basicranial region. Numerous postcranial elements are also referable to this species. The 502 crane specimens from Rancho La Brea represent a minimum of 77 individuals.

## INTRODUCTION

The fossil bird collection from the upper Pleistocene asphalt deposits at Rancho La Brea, California, housed in the George C. Page Museum of La Brea Discoveries, is the largest collection of fossil birds in existence. The estimated size of the collection is approximately 350,000–400,000 specimens, and it includes both cranial and postcranial material. To date, 139 species of birds, representing 32 families of 14 orders, have been identified from the Rancho La Brea (RLB) collections. Of these, 24 species are extinct. The most thorough study to date of the Rancho La Brea paleoavifauna was that of Howard (1962a), wherein she analyzed the avian assemblages from individual pits and presented the most complete taxonomic list available for the collection.

The entire Rancho La Brea vertebrate collection has been reorganized since the opening of the George C. Page Museum in 1977, resulting in large numbers of fossil birds coming to light that had not previously been integrated into the avian collection. In addition, major new collections of RLB fossil birds from the ongoing excavation at Pit 91 and various salvage operations at adjacent construction sites have added to the original avian collection studied by Dr. Howard. Several new species have now been recognized in these collections, including the new crane described herein, a giant eagle, a lapwing, and a giant passerine of as yet unknown affinities. The last three species are being described elsewhere. Numerous additional new species are expected to be identified as work on the entire collection proceeds.

The cranes of Rancho La Brea comprise a small, but nonetheless significant, portion of the overall paleoavifauna. The first announcement of fossil cranes from the site was the report of three specimens by L. Miller (1910). Two of these specimens were referred to *Grus canadensis*, but a third specimen was described as a new species, *G. minor* L. Miller 1910. The species name *minor* was to indicate the supposed much smaller size of the new paleospecies compared to that of *G. canadensis*. In a later paper, however, L. Miller (1925) announced that *G. minor* was an invalid species. He explained that his earlier description of the species was based on a comparison with a single modern specimen that later proved to be misidentified to species. In addition, rather than being smaller than *G. canadensis*, *G. minor* proved to be larger than specimens of the former species available to L. Miller (1925:77) for comparison.

Subsequently, there have been no additional papers in which the cranes of RLB played a significant role. As with so many avian species from RLB with modern representatives, the occurrence of cranes was noted only in general summaries of the complete avifauna, and then only briefly (e.g., Howard, 1930, 1962a, 1962b). The most notable information recorded over the years was that the least number of cranes from RLB increased from 29 individuals of *Grus canadensis* and 1 of *G. americana* cited in Howard's (1930) first census to 41 individuals of *G. canadensis* and 2 of *G. americana* in her last (Howard, 1962a). However, part of this increase was undoubtedly attributable to a new method of determining least numbers of individuals (Howard, 1962a:7), wherein the least number of individuals was determined for each pit and the results totalled. This was in contrast to the original method that treated all of the pits as one collection. The current study raises the least number of individuals reported from RLB to 52 for *G. canadensis*,

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8 for *G. americana*, and 17 for the new species described herein. The new total of 77 individuals for all species of *Grus* is 80 percent greater than that last reported by Howard (1962a).

A number of the crane specimens in the RLB collection were noted by Howard (notes with specimens) to be particularly small cranes; presumably these were some of those referred to as representing the Little Brown race of *Grus canadensis* (Howard, 1962b). When I first began identifying the specimens of cranes newly added to the collections, I noted that there were subtle, but constant, combinations of osteological characters that distinguished the smallest of the crane specimens from counterpart elements of *G. canadensis*, including the smallest of modern comparative specimens. The discovery of a crane cranium with proportions notably different from those of *G. canadensis* confirmed that a third species of crane was present at Rancho La Brea.

## MATERIALS AND METHODS

Prior to this study, there were 440 catalogued specimens assigned to two species of *Grus*, or just to the genus, from Rancho La Brea. Of these, all but seven were found in the collection. The missing specimens include one proximal and one distal ulna, one carpal phalanx, one distal tibiotarsus, one distal tarsometatarsus, and two pedal phalanges. In addition, 15 of the specimens referred to *Grus* were found to be incorrectly identified to genus, leaving a total of 418 specimens previously identified as crane present and accounted for in the collection. Each collection of unidentified bird fossils from Rancho La Brea was searched for specimens of cranes, including those made both early in this century and in the past few years. This resulted in the identification of 86 new specimens of *Grus* spp., or an increase of 21 percent over those listed in the pre-existing catalogue.

Fourteen complete and two partial skeletons of Recent *Grus canadensis* were used for comparative purposes. An effort was made to use small individuals of *G. canadensis* for comparison because the new species overlapped the smaller size range of the former species. Measurements of these and the fossil material were made using dial calipers accurate to 0.1 mm. Anatomical terminology is from Howard (1980) and Baumel (1993). Least numbers of individuals represent the sum of the least numbers for each pit (Howard, 1962a:6).

## SYSTEMATICS

Order Ralliformes  
(Reichenbach 1852)

Family Gruidae Vigors 1825

Genus *Grus* Pallas 1766

*Grus americana* Linnaeus 1758

## MATERIAL.

Clavicule: Right partial, K7349.  
Coracoids: Left complete, F1121; left fragment, B9517, K3379; right complete, F327.  
Scapulae: Left partial, H5651; right partial, H5652.

Carpometacarpi: Left complete, F350; right complete, F810.

Femur: Left distal, B8597.

Tibiotarsi: Left proximal, B5750; left shaft and distal, PMS 518; right proximal, R50795; right shaft and distal, PMS 519; right distal, F569.

Fibula: Left complete, PMS 522.

Synsacrum: Partial, B6073.

Tarsometatarsi: Left complete, PMS 523; left proximal, F652; left distal, F654; right complete, PMS 524; right proximal, G4893; right distal, F651.

Metatarsal I: Right fragment, PMS 527.

Pedal digit 2 phalanx 1: Left, J1959; right, J1960, PMS 531.

Pedal digit 2 phalanx 2: Left, PMS 533; right, J5305.

Pedal digit 2 phalanx 3: Left, PMS 538.

Pedal digit 3 phalanx 1: Left, J1932, PMS 530; right, F260, K2642.

Pedal digit 3 phalanx 2: Left, J5415, PMS 534.

Pedal digit 3 phalanx 3: Left, J5315, PMS 526.

Pedal digit 3 phalanx 4: Left, PMS 537.

Pedal digit 4 phalanx 1: Left, J3589, PMS 532; right, K7001.

Pedal digit 4 phalanx 2: Left, PMS 535.

Ungual phalanx: Left, PMS 537.

A total of 45 specimens from seven pits represents a minimum of eight individuals. However, 16 of the specimens were from the articulated distal hindlimbs of a single individual recovered from the Page Museum Salvage site.

## *Grus canadensis* Linnaeus 1758

### MATERIAL.

Crania: Partial, F387, F433, F471, F477, R38926.

Mandibles: Symphysis with partial dentary, F106, F920, F2950; dentary fragment, F102, F922; articular, K2359.

Quadrate: Right, F3377.

Claviculae: Left partial, J6532, K7188.

Sterna: Partial, F463, F475, F526, F536, F567.

Synsacra and pelves: Partial, C7263, E698, F697.

Scapulae: Left, F481, H5655, H6517, H6530, K5182, K5183; right, D5338, E212, F354, F784, F2051, H5654, K7351.

Coracoids: Left complete, F329, F345, F445, F528, F570, F607, F663, H3691; left proximal, B8891, H3693, K2733, K5187, K5190; left distal, B8996, F1067; left shaft, F145; right complete, B9291; D6510, F434, F483, F512, F573, F580, F1064, H3690, H3694, H4409, K5186, R40363; right proximal, F793, K5189.

Humeri: Left proximal, G2144, G2145, G2146, J9185, K5151, K5152; left distal, C4430, K5153; right proximal, C9991, R50827; right distal, C2502, D4593, D5166, D5471.

Ulnae: Left proximal, C2479, C2907, C7967, K5180; left distal, C4826, D5707, G6813, G6814, K5178; right complete, C967, C2986, F628; right proximal, C1903; right distal, C4970, D4845, F506, K2795, K2797.

Radial: Left proximal, K5185; left distal, H8338; right distal, H8360, H8384.

Carpometacarpi: Left complete, F182, F187, F455, F566, F977, F1065, F1103, H1675, H1678, K2809; right complete, E9559, F204, F205, F355, F458, F979, F1069, F1129; right proximal, K5176; right distal, C5557.

Carpal digit 2 phalanx 1: Left, C6009, D1415, D2711, D5563, F2024, J783, J786, K2828, K7337; right, C8053, C9341, D2709, J883.

Carpal digit 2 phalanx 2: Left, J1415; right, D2730.

Femora: Left complete, B9442, F348, F538, K5156; left proximal, E7759, K5160; left shaft, K5157; left distal, F4629, K5161; right complete, E6332, E6946, F549, F738, K5158; right distal, F4598, K5159.

Tibiotarsi: Left complete, K7330; left proximal, D5131, F67, F685, F961, F984, K5170; left distal, F149, F263, F442, F457, F460, F487, F507, F521, F534, F544, F568, F584, F598, F740, F787, F967, F980, F1009, F1070, F1134, F6735, F6736, F6738, F6765, F6772, K5173, K7334, R12073, R13199, R35165, R40182; left shaft, F597; right complete, K7329; right proximal, D5010, F1144, K7335; right distal, E8236, F32, F148, F332, F476, F480, F510, F517, F556, F559, F857, F919, F1148, F6737, F6762, F6763, F6764, F6766, K950, K1642, K2568, K2960, K5171, K5172, K7333, K7347, K7348, R42148.

Fibulae: Left proximal, H8521, K7331; right proximal, H8520, H8522.

Tarsometatarsi: Left complete, F577, F780, G4871, G4878, K3137, K7307; left proximal, E5980, E8444, F330, F421, F459, F462, F513, F551, F939, F963, F1061, F1127, G4889, G6224, K5162, K5164, K5166, K7346; left distal, E7922, E8282, F30, F461, F493, F509, F515, F537, F545, F564, F710, F834, F865, F933, F1131, G4880, G4895, G5970, G6116, G6171, K5163; right complete, G4875, G4881, K3138, K3139, K3140, K7306, R29018; right proximal, F514, F519, F525, F587, F684, F781, F791, F903, G5952, K746, K2013, K2014, K2524, K5168; right distal, E5574, E6791, E7212, E7676, E8269, E8488, E8574, F431, F522, F547, F571, F969, F1910, G4872, G4879, G4892, G4894, G6025, G6181, K2000, K5167, K5169, R10312, R15026, R18315; shaft fragments, E9962, F438, F516, F543, F1030, F1143.

Pedal digit 1 phalanx 1: Left, K1558.

Pedal digit 2 phalanx 1: Left, B8836, D916, D7785, D8204, D8272, F927, J1952, J1953, J1954, J1955, J1956, R39012; right, B5787, D2805, D5273, E7407, F162, F163, F924, J1957, J1958, K495, K1449, K1461, K7343, R52247.

Pedal digit 2 phalanx 2: Left, D6363, F996, J5263, J5736; right, B8843, J5264, J5265, J5437, K1778.

Pedal digit 3 phalanx 1: Left, B5988, E8034, F505, J3278, J3713, J3714, J3715, J3727, J3728, J3732, J3734, K2644, K7338, K7339; right, B9840, D4369, D7527, F360, F447, F911, F1105, J1933, J3711, J3712, J3729, J3730, K2643, R12194.

Pedal digit 3 phalanx 2: Left, C8235, J5222, J5227, J5382, K1462; right, C5620, J5225, J5385, J5386, J9957, K1269, K1463.

Pedal digit 3 phalanx 3: Left, D9062, J5490, K1288; right, K2137.

Pedal digit 4 phalanx 1: Left, D3213, D3305, J3588, J4560, K1488, K1489; right, J4417, J4559, J4561, J4562, K7340.

A total of 417 specimens from 19 pits represents a minimum of 52 individuals.

### *Grus pagei*, new species

#### Figure 1

**HOLOTYPE.** Partial cranium, F735.

**DIAGNOSIS.** The holotype cranium represents a species of *Grus* that differs from that of *G. americana* by being of much smaller size and from that of *G. canadensis* by having (1) width across ossa frontales at orbits narrower, whereas widths across the ala parasphenoidalis (= ala tympanica) and the

lamina parasphenoidalis (= basitemporal plate) are greater; (2) distance from prominencia cerebellaris to end of ossa frontales at nasofrontal hinge greater, with ossa frontales sloping more gently toward hinge area; and (3) condylus occipitalis larger, although overall cranium smaller.

**TYPE LOCALITY.** Pit A, Rancho La Brea, Hancock Park, Los Angeles, California, USA.

**TYPE HORIZON AND AGE.** Asphalt-intruded upper Pleistocene (Rancholabrean Land Mammal Age) alluvial deposits of the Los Angeles Basin, previously designated Submember C of Member C of the Palos Verdes Sand (Woodard and Marcus, 1973).

**MEASUREMENTS.** See Tables 1 and 2.

#### REFERRED MATERIAL.

Scapulae: Right partial, E4928, H5653, K5184.

Coracoids: Left partial, F966, K5188; right partial, F486.

Humeri: Left proximal, G2141; left distal, K5155; right distal, D7861.

Ulna: Right distal, K5179.

Carpometacarp: Left complete, F183, H1679; right complete, F76, H1680; right distal, K7344.

Carpal digit 2 phalanx 1: Right, D7171.

Femur: Right distal, F4636.

Tibiotarsi: Left distal, F563, K5174; right complete, K3133; right proximal, F1017; right distal, F494, F557, K5177, K7336, K7345.

Tarsometatarsi: Left proximal, E8298, E8352, G4877, K4100, K5165; left distal, E8073; right complete, F452, G4874; right distal, E8486, G4873, K4097.

Pedal digit 2 phalanx 1: Right, K7342.

Pedal digit 3 phalanx 1: Left, J3703; right, E8101.

Pedal digit 4 phalanx 1: Left, K7341.

A total of 42 specimens, including the holotype, from 11 pits represents a minimum of 17 individuals.

**ETYMOLOGY.** Named for George C. Page, in recognition of his gift of the George C. Page Museum of La Brea Discoveries to the people of Los Angeles and the world. His generosity brought the study of the complete avifauna of Rancho La Brea into the realm of possibilities.

**DESCRIPTION.** All elements of *Grus pagei*, new species, average smaller in size than the respective elements of *G. canadensis*, whereas the only other North American species, *G. americana*, and all other Recent species of *Grus* average much larger than *G. canadensis* (Johnsgard, 1983). Therefore, *G. pagei* will be compared only to *G. canadensis*. For measurements of all elements, see Table 1.

**Skull.** The outstanding feature of the cranium of *Grus pagei* is how it differs in its proportions from those of *G. canadensis*. This can be seen visually (Figs. 1–3) and through ratios (Table 2). Although the maximum width of the cranium of *G. pagei* overlaps the lower size range of *G. canadensis*, the ossa frontales are much narrower, whereas the width across the ala parasphenoidalis and lamina parasphenoidalis is greater. The cumulative effect of these differences is a proportionately larger basi-cranial region and a more slender, elongated frontal

**Table 1.** Measurements of bones of species of *Grus* from Rancho La Brea and Recent specimens. OR = observed range; M = mean; N = number of specimens.

Element	<i>Grus americana</i>		<i>Grus canadensis</i>		<i>Grus pagei</i>	
	Rancho La Brea	Recent	Rancho La Brea	Recent	Rancho La Brea	
<b>Cranium</b>						
Width across ossa frontales at orbits	OR		17.3–21.4	14.9–18.3		
	M		18.6	17.3	14.5	
	N		5	14	1	
Distance from prominentia cerebellaris to nasofrontal hinge	OR			60.5–72.0		
	M		72.9	66.3	71.8	
	N		1	14	1	
Width across alae parasphenoidalis	OR		30.7–33.8	26.8–31.7		
	M		31.8	28.9	31.9	
	N		3	14	1	
Width across lamina parasphenoidalis	OR		13.7–15.6	12.8–14.6		
	M		14.3	13.5	15.5	
	N		4	14	1	
Maximum width of cranium	OR		38.1–42.3	35.3–41.0		
	M		40.4	38.2	37.9	
	N		5	13	1	
Width across ossa frontales between ossa lacrimales	OR		11.7–14.5	9.5–12.0		
	M		13.3	11.3	13.1	
	N		3	14	1	
Distance from center of nasofrontal hinge to posterior edge of orbit	OR		37.2–44.5	39.5–47.9		
	M		42.0	43.2	48.7	
	N		4	13	1	
<b>Coracoid</b>						
Head to angulus medialis	OR		58.2–74.8	51.8–69.0	54.4–58.4	
	M	74.1	72.9	67.0	60.9	56.4
	N	1	1	14	14	2
Head to external end of facies articularis sternalis	OR		79.2–86.9	64.1–86.6		
	M	91.5	94.9	82.7	74.8	68.7
	N	1	1	5	14	1
Least width of shaft	OR	15.3–15.6		12.5–15.7	10.7–13.7	11.9–12.8
	M	15.4	15.3	14.1	11.7	12.4
	N	3	1	27	15	3
Head through facies articularis scapularis	OR		27.4–38.2	25.4–34.4	30.1–30.7	
	M	37.9	39.5	32.7	29.7	30.4
	N	1	1	23	16	2
<b>Scapula</b>						
Length of facies articularis humeralis	OR	16.4–16.6		12.0–16.2	11.0–15.6	10.1–11.1
	M	16.5		13.7	13.0	10.6
	N	2		11	15	3
Acromion length	OR	17.6–18.2		11.7–15.6	10.9–14.7	
	M	17.9		13.8	13.2	12.6
	N	2		10	15	1
Maximum depth through acromion and facies articularis humeralis	OR	25.7–26.9		20.0–24.8	18.1–24.0	
	M	26.3		22.9	21.0	19.5
	N	2		10	15	1
<b>Humerus</b>						
Total length	OR			177.9–225.2		
	M			200.2		
	N			10		

Table 1. Continued.

Element		<i>Grus americana</i>		<i>Grus canadensis</i>		<i>Grus pagei</i>
		Rancho La Brea	Recent	Rancho La Brea	Recent	Rancho La Brea
Proximal width	OR		42.0–45.7	33.1–43.1		
	M		44.0	38.0	40.6	
	N		3	14	1	
Depth of head	OR		13.5–14.5	10.6–14.0		
	M		13.8	12.2	13.0	
	N		5	14	1	
Distal width	OR		33.1–34.7	26.8–32.8		
	M		34.0	29.7	27.7	
	N		6	13	1	
Condylus dorsalis depth	OR		18.0–19.4	14.5–18.9	15.3–15.6	
	M		18.5	16.5	15.5	
	N		6	13	2	
<b>Ulna</b>						
Total length	OR			241.5–243.1	200.8–247.4	
	M			242.3	225.4	
	N			2	14	
Proximal width	OR			22.7–24.9	19.5–22.6	
	M			23.5	21.1	
	N			6	14	
Proximal depth	OR			16.5–18.6	14.4–17.9	
	M			17.5	16.0	
	N			6	14	
Distal depth	OR			14.5–16.3	12.9–16.5	
	M			15.6	14.7	14.2
	N			13	14	1
Distal width	OR			15.6–18.8	14.5–17.6	
	M			17.2	16.1	15.4
	N			13	14	1
<b>Carpometacarpus</b>						
Total length	OR	137.0–137.2		104.6–125.2	89.9–111.1	94.8–97.1
	M	137.1	117.9	115.4	99.8	96.4
	N	2	1	17	13	4
Proximal width	OR	26.8–27.6		20.2–25.3	18.8–21.9	17.6–19.9
	M	27.2	23.7	23.2	20.6	18.8
	N	2	1	16	14	4
Os metacarpalis alulare length	OR	16.2–17.1		12.0–15.9	11.7–14.4	11.9–12.9
	M	16.7	15.0	14.6	13.2	12.4
	N	2	1	18	14	4
Distal depth	OR	17.3–18.9		13.9–17.6	13.1–15.0	11.2–13.9
	M	18.1	15.5	16.2	14.3	12.9
	N	2	1	13	13	5
Os metacarpale majus width	OR			9.0–11.5	8.3–9.9	7.9–8.4
	M	11.5	9.8	10.2	9.2	8.2
	N	1	1	13	13	2
<b>Carpal digit 2 phalanx 1</b>						
Total length	OR			42.7–49.0	39.7–45.1	
	M			46.8	42.3	35.0
	N			12	11	1
Maximum width	OR			12.1–14.3	10.8–12.7	
	M			13.0	11.8	11.5
	N			12	11	1

Table 1. Continued.

Element	<i>Grus americana</i>		<i>Grus canadensis</i>		<i>Grus pagci</i>
	Rancho La Brea	Recent	Rancho La Brea	Recent	Rancho La Brea
<b>Femur</b>					
Total length	OR		100.5–119.2	100.8–129.0	
	M		111.7	114.4	
	N		9	16	
Proximal width	OR		22.1–26.1	21.1–25.9	
	M		24.7	23.5	
	N		11	16	
Proximal depth	OR		19.5–21.9	17.1–22.0	
	M		20.7	19.4	
	N		9	16	
Midshaft width	OR		9.8–12.2	8.9–11.1	
	M	13.5	11.1	10.4	8.8
	N	1	14	16	1
Midshaft depth	OR		9.5–11.9	8.8–11.8	
	M	13.7	10.7	9.9	8.3
	N	1	14	16	1
Distal width	OR		22.4–27.7	21.4–26.3	
	M	31.6	25.7	23.5	20.0
	N	1	11	16	
Distal depth	OR		21.5–25.4	20.1–25.9	
	M	30.0	23.4	22.8	18.6
	N	1	9	16	1
<b>Tibiotarsus</b>					
Total length	OR		251.5–253.1	199.3–293.0	
	M		252.3	247.1	226.5
	N		2	14	1
Proximal width	OR		18.6–22.7	13.7–20.9	16.3–16.5
	M	24.1	22.3	20.5	16.4
	N	1	1	7	15
Proximal depth	OR		24.0–30.9	21.2–28.1	21.2–22.5
	M	33.5	28.5	27.1	24.7
	N	1	1	7	15
Distal width	OR	26.4–27.2		17.9–23.9	16.7–20.6
	M	26.9	22.7	20.7	18.8
	N	3	1	51	15
Condylus lateralis depth	OR	23.9–24.7		15.7–22.4	15.3–19.5
	M	24.4	20.4	19.0	17.2
	N	3	1	46	15
Condylus medialis depth	OR	25.0–25.8		16.0–22.9	15.3–19.9
	M	25.5	20.6	19.5	18.1
	N	3	1	50	15
<b>Tarsometatarsus</b>					
Total length	OR		217.2–255.0	175.1–254.1	188.3–194.8
	M	235.7	282.0	229.7	219.6
	N	1	1	11	14
Proximal width	OR	28.4–30.1		20.9–25.9	19.0–23.5
	M	29.1	25.6	23.3	21.3
	N	3	1	33	14
Hypotarsus length	OR	23.1–29.5		14.9–22.1	14.5–19.7
	M	26.3		18.6	17.2
	N	2		35	14



Table 1. Continued.

Element	<i>Grus americana</i>			<i>Grus canadensis</i>		<i>Grus pagei</i>
		Rancho La Brea	Recent	Rancho La Brea	Recent	Rancho La Brea
Distal width	OR	26.0–26.5		18.9–25.1	17.6–21.8	17.6–19.3
	M	26.3	24.9	22.1	20.0	18.5
	N	3	1	53	14	5
Trochlea metatarsi tertii depth	OR	13.4–13.7		9.5–13.0	8.6–13.8	8.5–9.7
	M	13.6	12.8	11.0	10.5	9.2
	N	2	1	50	14	5
Trochlea metatarsi tertii width	OR	11.0–11.5		7.7–10.1	6.9–8.8	6.9–8.1
	M	11.3	9.9	8.9	7.9	7.5
	N	2	1	48	14	5
<b>Pedal digit 1 phalanx 1</b>						
Length	OR				10.3–11.2	
	M			19.4	10.8	
	N			1	2	
Proximal width	OR				3.3–3.8	
	M			5.0	3.6	
	N			1	2	
Distal width	OR				2.7–3.0	
	M			3.9	2.9	
	N			1	2	
<b>Pedal digit 2 phalanx 1</b>						
Total length	OR	40.4–43.1		25.8–32.0	21.8–30.5	
	M	41.3		28.9	27.3	21.8
	N	3		26	14	1
Proximal width	OR	9.3–10.6		7.4–9.4	6.2–8.5	
	M	10.0		8.4	7.6	6.2
	N	3		26	14	1
Distal width	OR	6.9–7.6		5.1–6.7	4.8–6.6	
	M	7.2		6.0	5.5	4.4
	N	3		26	14	1
<b>Pedal digit 2 phalanx 2</b>						
Total length	OR	36.1–37.7		25.4–30.2	19.9–22.8	
	M	36.9		27.4	21.4	
	N	2		7	2	
Proximal width	OR	7.6–7.7		6.1–7.5	4.8–5.4	
	M	7.7		6.5	5.1	
	N	2		8	2	
Distal width	OR	6.5–6.8		5.1–6.3	4.1–4.6	
	M	6.7		5.5	4.4	
	N	2		8	2	
<b>Pedal digit 3 phalanx 1</b>						
Total length	OR	44.3–48.9		31.2–36.9	26.7–35.8	25.4–27.5
	M	46.6		34.0	32.2	26.5
	N	4		28	14	2
Proximal width	OR	10.5–12.5		8.9–11.8	7.8–9.7	7.2–7.8
	M	11.5		9.9	8.8	7.5
	N	4		26	14	2
Distal width	OR	7.8–9.6		6.3–8.1	5.3–6.6	5.2–5.9
	M	8.5		7.1	6.2	5.6
	N	4		28	14	2

Table 1. Continued.

Element		<i>Grus americana</i>		<i>Grus canadensis</i>		<i>Grus pagei</i>
		Rancho La Brea	Recent	Rancho La Brea	Recent	Rancho La Brea
<b>Pedal digit 4 phalanx 1</b>						
Total length	OR	31.1–36.0		24.2–27.2	19.1–27.9	
	M	34.0		25.8	24.4	20.0
	N	3		11	14	1
Proximal width	OR	10.0–11.7		8.2–9.9	7.2–9.2	
	M	11.0		8.9	8.3	7.4
	N	3		10	14	1
Distal width	OR	6.5–7.8		5.4–6.4	4.6–5.7	
	M	7.2		5.8	5.3	5.1
	N	3		10	14	1

region. No maxillaries or premaxillaries of *G. pagei* have been found; therefore, it is not possible to determine whether or not the elongation of the bill continued to its tip.

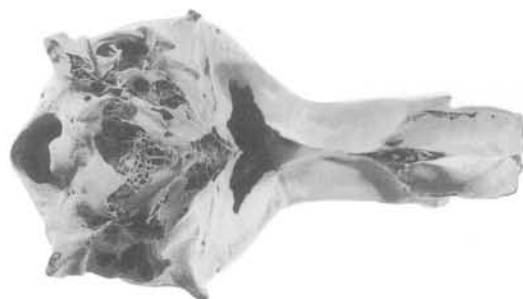
**Coracoid.** The coracoid of *Grus pagei* differs from that of *G. canadensis* by having (1) head broader, relatively more massive, and less pointed cranial adjacent to tip of impressio lig. acrocoracoideum, as seen in dorsal and internal view; (2) cotyla scapularis fairly well-defined pit (large, shallow to deep depression, but not a pit, in *G. canadensis*); (3) facies articularis scapularis prominently developed posterodorsal to cotyla scapularis, extending only

short distance externad, but extending internad to processus procoracoideus (not as prominent in *G. canadensis*); (4) processus procoracoideus shorter, curving ventrad less rapidly, providing for more open canalis triossealus; (5) distal end of facies articularis clavicularis a more prominent projection that impinges more upon canalis triossealus; (6) facies articularis humeralis proportionately wider; and (7) facies articularis sternalis narrower, especially near angulus medialis.

**Scapula.** The scapula of *Grus pagei* differs from that of *G. canadensis* by having (1) facies articularis clavicularis only slightly elevated above margo dor-

Table 2. Ratios of cranial measurements of species of *Grus*. Top row of each pair consists of actual measurements (mm), whereas the bottom row presents the ratios of five cranial measurements against the width across the ossa frontales at the orbits.

	Width across ossa frontales at orbits	Distance from prominentia cerebellaris to naso-frontal hinge	Width across alae parasphenoidalis	Width across lamina parasphenoidalis	Width across ossa frontales between ossa lacrimales	Distance from center of nasofrontal hinge to posterior edge of orbit
<i>Grus pagei</i> , new species						
Holotype	14.5	71.8	31.9	15.5	13.1	48.7
	1	4.95	2.20	1.07	0.90	3.36
<i>Grus canadensis</i> : Rancho La Brea						
Mean of all specimens	18.6	72.9	31.8	14.3	13.3	42.0
	1	3.92	1.71	0.77	0.72	2.26
Most complete specimen	18.2	72.9	33.8	15.6	14.5	44.5
	1	4.01	1.86	0.86	0.80	2.45
<i>Grus canadensis</i> : Recent specimens						
Mean of all specimens	17.3	66.3	28.9	13.5	11.3	43.2
	1	3.83	1.67	0.78	0.65	2.50
Smallest skull	14.9	60.5	26.8	13.8	10.6	39.7
	1	4.06	1.80	0.93	0.71	2.66
Largest skull	18.8	68.1	28.8	13.9	9.5	43.1
	1	3.62	1.53	0.73	0.50	2.29



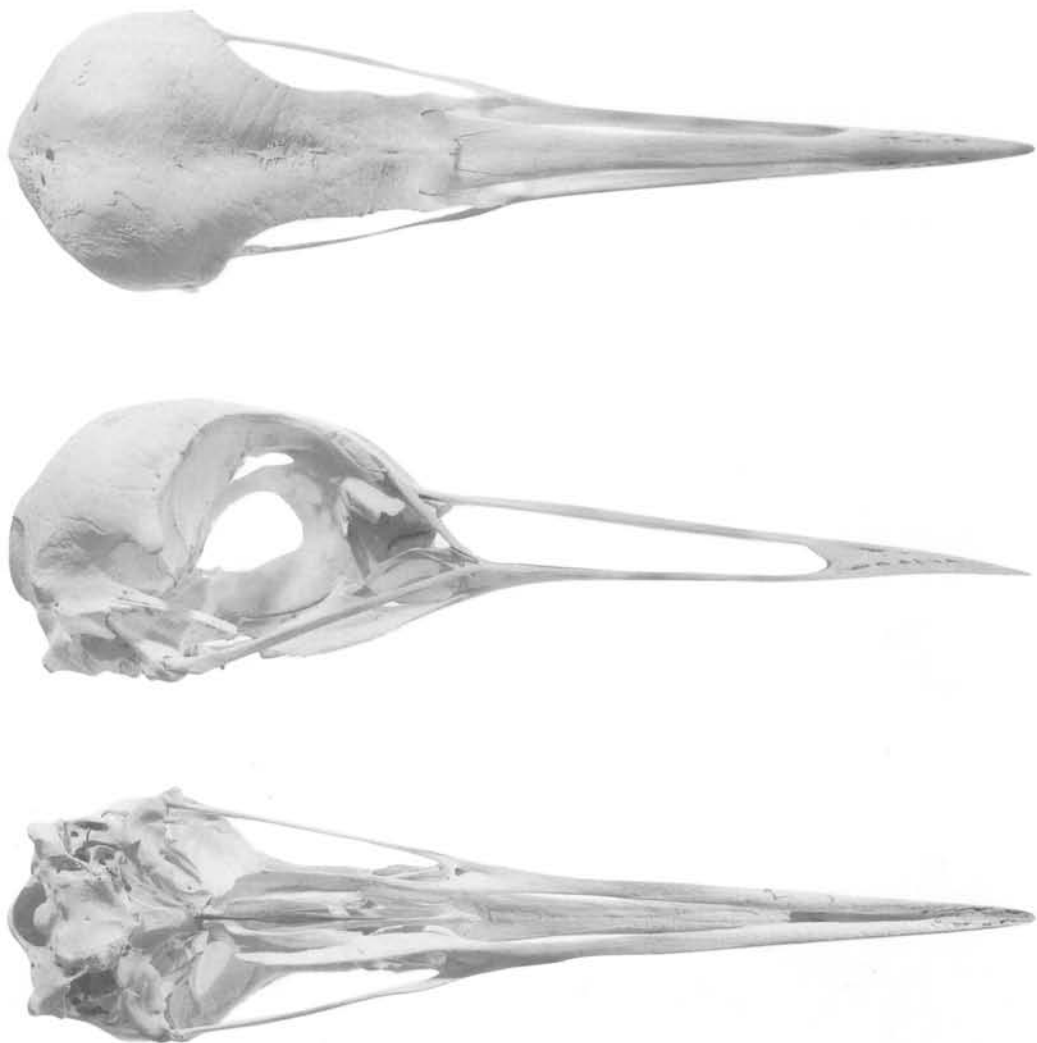
**Figure 1.** Holotype cranium of *Grus pagei*, new species, George C. Page Museum, Hancock Collection F735, in dorsal, lateral, and ventral views. Note the narrowness of the ossa frontales, the greater width across the alae parashenoidalis, and the greater distance from the prominentia cerebellaris to the nasofrontal hinge, in comparison to the corresponding dimensions of *G. canadensis* (Figs. 2, 3).  $\times 1$ .

**Figure 2.** The most complete cranium of *Grus canadensis* from Rancho La Brea, George C. Page Museum, Hancock Collection F477, in dorsal, lateral, and ventral views. This specimen has the same proportions as the crania of modern *G. canadensis*.  $\times 1$ .

salis, with latter sloping gradually to former (considerably elevated above margo dorsalis, which turns abruptly dorsad to meet it, in *G. canadensis*); (2) facies articularis humeralis with anteroventral projection small, sharply pointed, with facies articularis coracoideus on facies costalis short and v-shaped, almost notched (anteroventral projection large, rounded, with facies articularis coracoideus on facies costalis long, broadly convex, and wide in *G.*

*canadensis*); and (3) tubercle on facies costalis dorsal to pneumatic foramina small, but prominent, neither completely rounded nor pointed (prominent and fairly sharply pointed in *G. canadensis*).

**Humerus.** The humerus of *Grus pagei* differs from that of *G. canadensis* by having (1) sulcus lig. transversus noticeably more constrained by proximal extension of the ventral portion of the intumescentia humeri (= bicipital surface); (2) attach-



**Figure 3.** This small skull of *Grus canadensis* is approximately of the same maximum cranial width as the holotype of *G. pagei*, new species; shown in dorsal, lateral, and ventral views. Note the smaller distance between the alae parasphenoidalis in this specimen compared to that in the holotype of *G. pagei* (Fig. 1).

ment of *M. proscapulohumeralis brevis* a more elevated bump; (3) tuberculum ventrale (= internal tuberosity) relatively more massive; (4) condylus ventralis less bulbous in anterior view, without as marked a central extension, being more elongated dorsoventrally; (5) epicondylus ventralis with a more pronounced posteroventral corner, but overall it does not extend as far distad and is more compressed dorsoventrally than that of *G. canadensis*, especially with the ventral limit of epicondylus ventralis in posterior view closer to the condylus ventralis; and (6) attachments of *M. extensor metacarpi radialis*, pars anconalis and palmaris, positioned slightly more distad and forming shorter, more pronounced shelf.

**Ulna.** The ulna of *Grus pagei* differs from that

of *G. canadensis* by having (1) sulcus tendineus larger, with proximal end positioned closer to tuberculum carpale; (2) tuberculum carpale more pointed and more slender, but with larger ridge of bone leading to it from the shaft; and (3) condylus ventralis ulnae more compressed cranially.

**Carpometacarpus.** The carpometacarpus of *Grus pagei* differs from that of *G. canadensis* by having (1) facies articularis ulnocarpalis narrower distally; (2) external rim of facies articularis ulnaris more rounded in dorsal (= external) view, without a "peak" just proximal to the attachment of *M. flexor carpi ulnaris brevis*; (3) os metacarpale alulare smaller, with processus extensorius less projecting, less twisted ventrad (= internad), and lacking prominent, undercut ridge along dorsal edge distally, i.e.,

with slight, centrally located depression only; and (4) facies articularis digiti minoris smaller, not projecting distad beyond facies articularis digiti majoris (does project distad beyond facies articularis digiti majoris in *G. canadensis*).

**Femur.** The femur of *Grus pagei* differs from that of *G. canadensis* by having (1) condylus lateralis shorter anteroposteriorly and more undercut at its proximal posterior extension, more distinct from posterior surface of shaft, and oriented at slightly greater angle to shaft; and (2) shaft more flattened, with less of a ridge leading to posterior end of condylus lateralis, and broadening more gradually to meet condylus lateralis. Only distal end available.

**Tibiotarsus.** The tibiotarsus of *Grus pagei* differs from that of *G. canadensis* by having (1) crista cnemialis lateralis closer to exterior articular surface, i.e., flaring less anteriorly; (2) facies articularis medialis smaller; (3) shaft distal to facies articularis medialis flattened, not rounded; (4) condylus medialis narrower, not as rounded, with distal flange less flaring medially; (5) both condylae proportionately shorter anteroposteriorly; and (6) trochlea cartilaginea tibialis sloping internad from condylus lateralis at a greater angle in distal view, being deeper adjacent to condylus medialis.

**Tarsometatarsus.** The tarsometatarsus of *Grus pagei* differs from that of *G. canadensis* by having (1) eminentia intercondylaris more rounded in anterior view and less bulbous in lateral view; (2) cotyla medialis deeper and slightly narrower, giving a more constricted form; (3) area between the cotylae and hypotarsus a deeper, more enclosed basin, with posterior edge of cotylae more elevated (opens internally in *G. canadensis*); (4) hypotarsus more compressed anteroposteriorly, with internal ridge over enclosed sulcus hypotarsi more elevated and more separate, curving externad distally; and (5) trochlea metatarsi tertii slightly more compressed anteroposteriorly, with distal end rotated slightly anteriorly.

## DISCUSSION

The cranes of Rancho La Brea were not specifically discussed by Howard (1962a) in her analysis of pit assemblages, but she did list *Grus canadensis* as a typical member of the Rancho La Brea Pleistocene avifauna. *Grus canadensis* and *G. pagei* occur together in 11 of the 19 pits in which the former species occurs (Table 3), including both older (e.g., Pit 4) and younger (e.g., Pit 10) pits. Clearly, these two species were sympatric at Rancho La Brea in the late Pleistocene. *Grus americana* was more limited in its occurrence, appearing in only 6 of the 19 pits in which *G. canadensis* occurred and in one pit where the latter has not yet been found.

As already noted, *Grus minor* was named by L. Miller (1910) based on a comparison with a larger crane misidentified as *G. canadensis* (L. Miller, 1925). In his first paper, Miller referred only the

holotype to *G. minor*, and at that time he referred two other specimens from Rancho La Brea to *G. canadensis*. However, in his second paper he referred all cranes from RLB (four specimens) to the former species. The holotype of *G. minor*, UCMP 12533, could not be examined for this study because all collections of the Museum of Paleontology, University of California, Berkeley, were being transferred to new facilities. However, from the illustration of the holotype tibiotarsus (L. Miller, 1910, fig. 8), it can be noted that it differs from that of the more gracile *G. pagei* by having larger condyles and a more massive shaft. L. Miller (1925:77) also stated that "osteological distinctions, noted in the original description [of *G. minor*], fall to the ground on comparing the fossil bird with true *G. canadensis*. . . ."

The holotype distal tibiotarsus of *G. minor* measured 18.8 mm in distal width and 17.9 mm in depth through the condylus medialis, measurements equal to and slightly less, respectively, than the mean of those for Recent *G. canadensis* and smaller than the mean of those of contemporary *G. canadensis* from Rancho La Brea (Table 1), but well within the range of the latter. These measurements of *G. minor* are outside the range of those of specimens assigned to *G. pagei* in this study (Table 1). Thus, I have no hesitation in agreeing with L. Miller (1925:77) that the holotype of *G. minor* is in fact a specimen of *G. canadensis* and that the former species is invalid.

The average *Grus pagei* was about the same size as the smallest individuals of Recent *G. canadensis* (Table 1). *Grus pagei* averaged much smaller than contemporary *G. canadensis* from RLB, the largest of the former just barely achieving the size of the smallest of the latter. The proportions of the cranium of *G. pagei* suggest that its head was larger and more slender than that of *G. canadensis* (Table 2), even though the former was of approximately the same width as smaller examples of the latter. This may have provided a means of partitioning the habitat and reducing competition between these two cranes. Both of these species, of course, are much smaller than *G. americana*, which probably limited direct competition between the larger and the two smaller species. Both *G. americana* and *G. canadensis* are migratory species, although some subspecies of *G. canadensis*, e.g., *G. canadensis pratensis*, appear to be sedentary (Johnsgard, 1983).

Cranes take a variety of foods, both plant and animal, and occur in a variety of habitats. Although generally associated with marsh lands, they commonly feed in upland terrestrial areas; in both types of habitat, however, they prefer more open, grassy environs (Johnsgard, 1983). It can only be assumed that *Grus pagei* shared the typical habitat preferences of species of *Grus*. Thus, by themselves, cranes do not provide much detailed information about what the habitat might have been like at Rancho La Brea in the late Pleistocene.

Intraspecific size variation in species of *Grus* is

**Table 3. Distribution of species of *Grus* among the various pits at Rancho La Brea.**

Pit number	<i>Grus americana</i>		<i>Grus canadensis</i>		<i>Grus pagei</i> , new species	
	Number of specimens	Least number of individuals	Number of specimens	Least number of individuals	Number of specimens	Least number of individuals
Pit 2			2	2		
Pit 3			26	2	3	1
Pit 4	1	1	86	7	6	1
Pit 6			1	1		
Pit 10			5	1	7	5
Pit 13	2	1	48	5	2	2
Pit 16	22	2	122	8	6	1
Pit 36	1	1	15	4	1	1
Pit 37			10	2		
Pit 60			5	1		
Pit 61–67			15	3	4	2
Pit 77			9	3		
Pit 81			2	1		
Pit 91	1	1	19	4		
Pond dump <sup>1</sup>			1	1	1	1
Bliss 29 <sup>2</sup>			2	1	3	1
Pit A			7	2	1	1
Academy <sup>3</sup>	2	1	34	2	8	1
PMS <sup>4</sup>	16 <sup>5</sup>	1				
No data			8	2		
Total	45	8	417	52	42	17

<sup>1</sup> Mixed talings from Pits 3, 4, and 61–67.

<sup>2</sup> Bliss 29 includes four separate pits: Pits A–D. For many specimens, the pit of origin was not noted, and these are lumped together under the name “Bliss 29.” Specimens are separated to pit when this is known.

<sup>3</sup> Excavation by Southern California Academy of Science prior to 1913; materials now part of LACM collections. Pit reopened by LACM in 1913 and designated Pit 17.

<sup>4</sup> PMS (Page Museum Salvage) refers to specimens collected during salvage operations during the construction of the George C. Page Museum from a site under the new museum building.

<sup>5</sup> All specimens were from the articulated distal hindlimbs of a single individual.

considerable (Table 1; Johnsgard, 1983), as is intraspecific size variation. When this variation is combined with the seasonal mixing of migratory races that may occur, it is easy to see that the potential for size variation within a species may be considerable. Indeed, were only a single postcranial specimen of *G. pagei* available it would be very difficult to convincingly demonstrate that it represented a species different from *G. canadensis*. However, the combination of a fairly large number of specimens, including a cranium, from Rancho La Brea does make description of the species possible.

Both *Grus americana* and *G. canadensis* are well represented from numerous Pleistocene and Holocene sites in North America, but *G. pagei* is the only known Pleistocene paleospecies of the genus (Brodkorb, 1967; Cracraft, 1973; Olson, 1985). There are two described species of *Grus* from the Pliocene of North America, *G. conferta* A.H. Miller and Sibley 1942 and *G. nannodes* Wetmore and Martin 1930. Olson (1985) stated that the generic

placement of *G. conferta* was suspect, and the shape of the facies articularis of trochlea metatarsi II of that species differs quite noticeably from that of *G. pagei*. *Grus nannodes* is based on a fairly undiagnostic distal end and shaft of a carpometacarpus that is smaller than the smallest carpometacarpus referred to *G. pagei*, new species. In addition, it differs by having a fairly pronounced curvature of the os metacarpale majus opposite the point of its fusion with the os metacarpale minor, a curvature that is lacking in *G. pagei*.

#### SUMMARY

A review of all collections of fossil birds from Rancho La Brea housed at the George C. Page Museum has shown that 502 specimens representing at least 77 individuals are properly assignable to three species of *Grus*: *G. americana*, *G. canadensis*, and *G. pagei*, new species. This represents an increase of 21 percent in the number of specimens and 80 percent in the number of individuals over what had

been reported previously. The holotype of the paleospecies *G. minor* from Rancho La Brea is recognized as being a specimen of *G. canadensis*, as previously determined by L. Miller (1925); thus, the former species is invalid. Compared to *G. canadensis*, *G. pagei* is characterized by a longer, more slender cranium, which nonetheless has a proportionately larger basicranium. The differences in proportions between the skulls of *G. canadensis* and *G. pagei* are suggestive of habitat partitioning through the use of different food resources. *Grus pagei* is widespread both temporally and spatially among the pits at Rancho La Brea, but it was not found in collections from other late Pleistocene asphalt deposits of California. *Grus pagei* is the only paleospecies of *Grus* reported from the Pleistocene of North America, and it is the first paleospecies to be described from Rancho La Brea since 1948.

#### ACKNOWLEDGMENTS

I thank F. Hertel (UCLA) and R.B. Payne and R.W. Storer (University of Michigan Museum of Zoology) for making available modern comparative specimens. F. Hertel and L. Martin kindly provided critical comments on drafts of this paper. I am grateful to the staff and volunteers of the George C. Page Museum, who have been invaluable in gathering together and preparing the multitude of avian specimens at Rancho La Brea. A special effort on the photographs by R. Meier, LACM photographer, is much appreciated.

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Received 24 June 1994; accepted 14 December 1994.