

# A LATE PLEISTOCENE AVIFAUNA FROM SAN MIGUEL ISLAND, CALIFORNIA

Daniel A. Guthrie

**ABSTRACT.** Upper Pleistocene deposits on San Miguel Island (12,000 B.P. and 25,000–39,000 B.P.) contain an avifauna comprising 41 species of birds, including 3 extinct species and 2 extinct subspecies. The paleoavifauna includes both pelagic and terrestrial species, the latter primarily raptorial birds, and it provides us with much new information on life on and around the northern Channel Islands of southern California in the late Pleistocene.

Key words: Pleistocene, avifauna, Channel Islands, evolution, biogeography.

## INTRODUCTION

San Miguel Island, one of the northern Channel Islands located 50 km from the coast of southern California (Fig. 1) is well known for its archeological sites (Rozaire, 1976), and bird remains from these sites from 10,700 B.P. to Recent were described by Guthrie (1980). Pleistocene material from the island known prior to 1984 consisted of only a few isolated finds of mammoth, but reports by Johnson (1972) and by archeologists involved in survey work on the island indicated that bones were present in sediments below the earliest archeological sites. These reports led to a survey of San Miguel by the author during the summers of 1984 and 1985. The result was the discovery of several previously undescribed fossiliferous localities that contain abundant remains of birds. The geology of these deposits and their paleoavifauna is described here.

## GEOLOGY

The basement rocks on San Miguel Island are Eocene and Miocene marine sediments and volcanics (Bremner, 1933). Prior to the late Pleistocene, a deep wave-cut bench was formed in these rocks, especially along the northwest-facing shores, the side most affected by prevailing winds. During the late Pleistocene, at times of slightly lowered sea level, this bench was covered by wind-blown sand from the nearby beaches on the northwest coast and by alluvium washed down from the island's interior.

Today, much of San Miguel is covered by a layer of wind-blown sand. However, on the northwest-facing slopes of the island, there are several pockets where wind erosion is uncovering upper Pleistocene deposits that are highly fossiliferous. Major collecting localities in these fossiliferous areas are shown in Fig. 1. More detailed information on fossil localities is on

file at Channel Islands National Park headquarters in Ventura, California.

Radiocarbon ( $^{14}\text{C}$ ) dates based on collagen from bones from several sites (Table 1) indicate two ages for the island's fossil material. Two fossil localities that are slightly inland and above the wave-cut bench (V-4, V-12) date about 12,000 B.P. All other localities are within the wave-cut bench and date between 25,000 and 39,000 B.P. These two periods of deposition correspond with times when sea level was at or near its current level (Curry, 1965; Vedder and Howell, 1980). A further indication that the upper Pleistocene deposits were formed near sea level is a layer of tar sand within the deposits at Cuyler Harbor (locality V-10). This layer was formed as a result of oil from a natural seep off the northwest shore of San Miguel Island washing up on the beach. This asphaltic layer, which dates to about 30,000 B.P., is

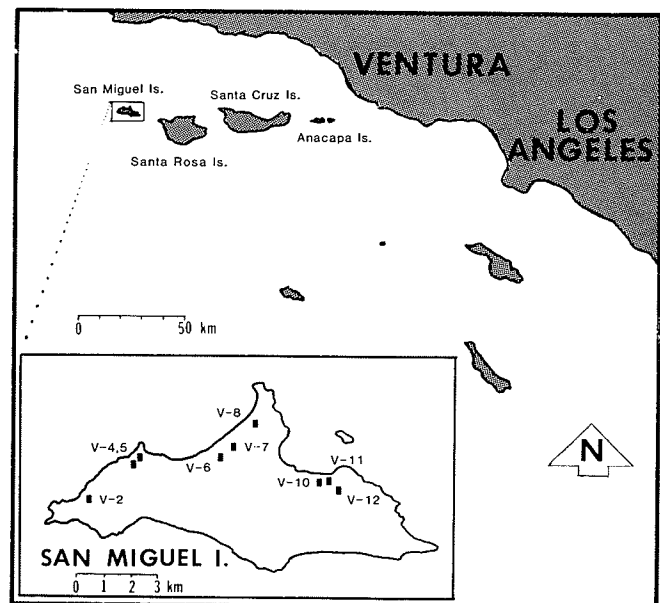


Figure 1. Map of the northern Channel Islands, with detail of San Miguel Island, showing fossil localities.

now about 15.5 m above current sea level. During the interval between the depositional dates (14,000–25,000 B.P.), sea level was much lower than today, and the shore of San Miguel Island, the source of depositional sand, would have been about 3 km away from the present northwest shore (Vedder and Howell, 1980). During this period, extensive soil layers that are generally unfossiliferous formed over much of San Miguel Island (Johnson, 1972, 1980).

Although the upper Pleistocene deposits on San Miguel Island are over 31 m thick and represent a considerable time period, the fauna within these deposits is rather uniform, and so far no changes in morphology or species composition have been detected. For this reason, the deposit is treated here as a single unit. Although over 95 percent of the vertebrate material from these deposits is avian, non-avian forms are also represented. The non-avian fauna, which is being described elsewhere (Guthrie, in press), consists of a rattlesnake, a lizard, two small rodents, a shrew, and dwarf forms of fox and mammoth. The only abundant invertebrate in the deposits is the terrestrial snail *Helminthoglypta ayresiana* (Newcomb 1861).

#### SYSTEMATICS

The classification system for Aves follows the 6th edition of the *Check-list of North American Birds* (American Ornithologists' Union, 1983). The collections are housed at the Santa Barbara Museum of Natural History (SBMNH) in Santa Barbara, California.

#### Class Aves

#### Order Gaviiformes

#### Family Gaviidae

#### *Gavia arctica* (Linnaeus 1758)

**MATERIAL.** Distal end of left tibiotarsus, SBMNH 26; right radius and 3 cervical vertebrae, SBMNH 44; thoracic vertebra, SBMNH 89.

**REMARKS.** *Gavia arctica* is known from Pleistocene deposits at San Pedro and Newport Bay, California (Howard, 1949:22).

#### Order Podicipediformes

#### Family Podicipedidae

#### *Podiceps nigricollis* Brehm 1831

**MATERIAL.** Distal end of right humerus, SBMNH 23; proximal ends of left and right tarsometatarsi, SBMNH 13, 22.

**REMARKS.** These bones, although within the size range of *Podiceps nigricollis*, are small, a characteristic noted by Howard (1949:23) for bones referred to this species from the upper Pleistocene of San Pedro.

#### *Aechmophorus* sp. cf.

#### *A. occidentalis* (Lawrence 1858)

#### or *A. clarkii* (Lawrence 1858)

**MATERIAL.** Left carpometacarpus, SBMNH 20.

**REMARKS.** This bone measures 56.6 mm, about 5 percent larger than Recent material of these two species. Although the

Table 1. Radiocarbon ( $^{14}\text{C}$ ) dates from San Miguel Island. All dates corrected for  $^{18}\text{O}/^{13}\text{O}$  ratios. Abbreviations: Beta, Beta Analytic, Coral Gables, Florida; AA, University of Arizona, Laboratory of Isotopic Geochemistry.

Identification No.	Locality	Level	Age (B.P.)	Material dated
Beta 14659	V-12	—	12,020 ± 270	<i>Chendytes lawi</i>
AA 1319	V-10	C	32,143 ± 787	<i>Chendytes lawi</i>
AA 1320	V-4	A	11,890 ± 95	<i>Fratercula</i> sp.
AA 1818	V-7	A	25,160	<i>Fratercula</i> sp.
AA 1819	V-7	C	>38,000	<i>Fratercula</i> sp.

carpometacarpus is not identifiable to species, it is within the size range of the Pleistocene subspecies *Aechmophorus o. lucasi* L. Miller 1911 (Howard, 1949:22).

#### Order Procellariiformes

#### Family Diomedeidae

#### *Diomedea albatrus* Pallas 1769

**MATERIAL.** Partial skull, SBMNH 56; left quadrate, SBMNH 21; distal end of left tibiotarsus, SBMNH 48; pelvic fragment, SBMNH 51; left carpometacarpus, SBMNH 61; right tarsometatarsus, SBMNH 65.

**REMARKS.** *Diomedea albatrus* was a common nearshore species prior to 1900, and it is well represented in Pleistocene marine deposits along the Pacific coast.

#### Family Procellariidae

#### *Fulmarus glacialis* (Linnaeus 1761)

**MATERIAL.** Two right humeri, SBMNH 33; distal end of a left humerus and 2 incomplete left ulnae, SBMNH 16; right humerus, SBMNH 161.

**REMARKS.** The humeri are 107.8 and 107.5 mm long, within the size range of Recent material of this species. The other bones are too fragmentary for measurement. This is another nearshore species common in Pacific coast marine Pleistocene deposits.

#### *Puffinus griseus* (Gmelin 1789)

**MATERIAL.** Right femur and distal end of left ulna, SBMNH 32; left tibiotarsus and tarsometatarsus, SBMNH 34; distal end of left humerus, right tarsometatarsus, and 2 left radii, SBMNH 40; right ulna, SBMNH 57; right humerus, coracoid, 2 right ulnae, and 2 right carpometacarpi, SBMNH 63.

**REMARKS.** This species is also known from upper Pleistocene deposits at Newport Bay (Howard, 1949:21).

#### *Puffinus opisthomelas* Coues 1864

**MATERIAL.** Right coracoid, SBMNH 3; left carpometacarpus, SBMNH 7; 2 left coracoids and 2 fragmentary left radii, SBMNH 78.

**REMARKS.** This species is known from several California Pleistocene deposits.

Family Hydrobatidae

*Oceanodroma homochroa*  
(Coues 1864)

**MATERIAL.** Left tarsometatarsus, SBMNH 163.

**REMARKS.** This species nests in small numbers on islands off the north shore of San Miguel Island (Sowls et al., 1980). It was previously unrecorded from Pleistocene deposits (Brodkorb, 1963:247).

Order Pelecaniformes

Family Pelecanidae

*Pelecanus occidentalis*  
Linnaeus 1766

**MATERIAL.** Thirteen cervical and thoracic vertebrae, SBMNH 56.

**REMARKS.** Bones of this species are unexpectedly rare in Pleistocene deposits (Brodkorb, 1963:267).

Family Phalacrocoracidae

*Phalacrocorax penicillatus*  
(Brandt 1837)

**MATERIAL.** Right carpometacarpus, SBMNH 18; distal end of left ulna, SBMNH 47; right coracoid, tibial shaft, and 2 cervical vertebrae, SBMNH 60.

**REMARKS.** Although *Phalacrocorax auritus* (Lesson 1831) is the commoner large cormorant in California coastal Pleistocene deposits (Howard, 1949:23), the San Miguel material is dominated by *P. penicillatus*.

*Phalacrocorax pelagicus*  
Pallas 1811

**MATERIAL.** Right quadrate, SBMNH 4; distal end of left coracoid, SBMNH 25; distal end of right tibiotarsus, SBMNH 162.

**REMARKS.** Although the specimens are fragmentary, all are at or just above the upper limit of size for Recent material of this species. The bones are of a different configuration and too small to be included in either *Phalacrocorax penicillatus* or *P. auritus*.

Order Ciconiiformes

Family Ardeidae

*Ardea herodias* Linnaeus 1758

**MATERIAL.** Fragmentary left humerus, right ulna, and right tibiotarsus, SBMNH 81.

**REMARKS.** The maximum width of the distal end of the humerus is 28.7 mm, which compares to measurements of 23.6–27.2 mm in Recent material. The proximal end of the ulna is missing, but this bone is shorter than Recent material, as indicated by the position of the attachments for the anterior articular ligament. Moreover, the anconal papillae are closer together than on Recent material. The position of the intermuscular line in Recent material crosses the ulna well proximal to the nutrient foramen, whereas on the specimen from San Miguel Island this line crosses distal to the nutrient foramen. The nutrient foramen is 155 mm from the distal end of the ulna on SBMNH 81, as

compared with 122–146 mm in Recent material. Although the differences from Recent material noted here may merit at least subspecific rank, not enough material exists to warrant taxonomic designation.

This species, although previously unknown from marine Pleistocene deposits (Brodkorb, 1963:284), is not unexpected because it nests on San Miguel Island.

Family Plataliidae

*Plegadis chihi* (Vieillot 1817)

**MATERIAL.** Distal end of left humerus, SBMNH 100.

**REMARKS.** This species, unknown from marine deposits (Brodkorb, 1963:284), is present in the Pleistocene deposits at Rancho La Brea.

Order Anseriformes

Family Anatidae

*Chen caerulescens*  
(Linnaeus 1758)

**MATERIAL.** Proximal end of left humerus and phalanx 1 of digit 2, SBMNH 27; right mandible and carpometacarpus, SBMNH 41; proximal end of right humerus, SBMNH 54; right carpometacarpus and proximal end of left radius, SBMNH 66.

**REMARKS.** This species wintered regularly on the northern Channel Islands prior to 1900 (Guthrie, 1980).

*Branta canadensis*  
(Linnaeus 1758)

**MATERIAL.** Cranium, SBMNH 99; proximal end of left humerus, SBMNH 101.

**REMARKS.** The impressions of the salt glands above the orbit and overall size of the cranium are most like those in the small race of Canada Goose, *Branta canadensis minima* Ridgway 1885. Larger races of this species are common in the Pleistocene deposits of Santa Rosa Island (Orr, 1968).

*Melanitta perspicillata*  
(Linnaeus 1758)

**MATERIAL.** Distal end of left humerus, SBMNH 10.

**REMARKS.** This bone is slightly more robust than Recent material of this species, but it is not as large as in *Melanitta fusca*.

*Melanitta fusca*  
(Linnaeus 1758)

**MATERIAL.** Proximal end of right humerus, SBMNH 11; right coracoid, SBMNH 58.

**REMARKS.** This species is known from the Pleistocene of Newport Bay and San Pedro (Brodkorb, 1964:246).

*Mergus serrator* Linnaeus 1758

**MATERIAL.** Distal end of right ulna, SBMNH 12.

**REMARKS.** This species is previously unknown from the Pleistocene of California (Brodkorb, 1964:248), but it has been recovered from Pleistocene deposits at Fossil Lake, Oregon (Howard, 1946).

Table 2. Frequency of skeletal elements of *Chendytes lawi* from SMI-V-12.

Bone	Number	Percent
Femur	104	42.8
Tibiotarsus	30	12.3
Tarsometatarsus	13	5.3
Humerus	5	2.1
Ulna	2	0.8
Pelvis	9	3.7
Sternum	2	0.8
Coracoid	4	1.6
Scapula	1	0.4
Vertebra	71	28.8
Skull	3	1.2
Total	244	100.0

### *Chendytes lawi* L. Miller 1925

**MATERIAL.** Humeri, 29; ulnae, 4; coracoids, 5; scapulae, 5; femora, 186; fibulae, 26; tibiotarsi, 101; tarsometatarsi, 40; phalanges, 22; pelvi and sacra, 29; sterna, 6; vertebrae, 423; skull fragments, 36; mandibulae, 8; quadrates, 12; pterygoids, 3; SBMNH 5, 35, 45, 49, 54, 59, 68, 70, 71, 73-75, 79, 82, 87, 94-96. Egg shell fragments, SBMNH 55, 69.

**REMARKS.** Bones of *Chendytes lawi* were found in small numbers at almost every locality. At two localities (V-10, V-12), *Chendytes* was very abundant and was the only species recovered at the latter site. Eggshell fragments of a thickness and curvature expected for a bird the size of *Chendytes* are abundant at both localities. This, and the recovery of numerous bones of immature individuals, indicates that these sites once hosted breeding colonies. Bones of *C. lawi* from locality V-12, radiocarbon (<sup>14</sup>C) dated at 12,000 B.P., are the same size as material from northern California dated at 6000 B.P. (Morejohn, 1976) but slightly larger than the sample from San Miguel Island localities dating from 25,000 to 39,000 B.P. Measurements of specimens from various Pleistocene localities in California presented by Howard (1955) agree with those from the older San Miguel Island localities.

Although most skeletal elements are present, the frequency of different elements (Table 2) varies greatly. This variation is related to susceptibility to destruction by abrasion from wind-blown sand and to the collecting bias of surface collecting (Rich and Baird, 1986). Both of these biases favor preservation of thicker-walled and larger bones. In the case of *Chendytes*, these are leg bones. The preponderance of *Chendytes* leg bones found in midden sites was considered by Morejohn (1976) to indicate human-use patterns, but it is similar to that seen in deposits from San Miguel that were formed earlier than the oldest date for cultural material from the island.

## Order Falconiformes

### Family Vulturidae

#### *Gymnogyps californianus amplus* (L. Miller 1911)

**MATERIAL.** Right humerus and tibiotarsus, left radius and ulna, and partial cranium, SBMNH 97.

**REMARKS.** This material is similar to the specimens reported from Santa Rosa Island by Howard (Orr, 1968). Measurements

Table 3. Comparison of measurements (mm) of condor bones from San Miguel Island with Recent and Pleistocene samples.

	Origin of sample		
	Recent <sup>a</sup>	Rancho La Brea <sup>a</sup>	San Miguel Island
Humerus (maximum length)	262-274	260-292	300
Ulna (maximum length)	305-320	304-345	338
Tibiotarsus (maximum length)	208-213	212-244	245
Occipital (width)	22.5-24.9	25.6-30.2	28.4

<sup>a</sup> Data from Fisher, 1944, 1947.

are within the range of the Rancho La Brea species *Gymnogyps amplus*, or slightly larger (Table 3). However, recent work on condors by Emslie (1988) has indicated that there is much overlap between the Rancho La Brea sample of *G. amplus* and *G. californianus*. Emslie's assignment of all late Pleistocene material to the Recent species, with *amplus* retained as a subspecific designation, is followed here.

### Family Accipitridae

#### *Haliaeetus leucocephalus* (Linnaeus 1766)

**MATERIAL.** Distal end of left tibiotarsus, SBMNH 9; distal end of left tibiotarsus, SBMNH 24; right tarsometatarsus and distal end of right tibiotarsus, SBMNH 43; distal end of left tarsometatarsus, SBMNH 50; left tarsometatarsus and proximal left radius, SBMNH 62.

**REMARKS.** Prior to 1950 this species nested on San Miguel Island.

#### *Buteo jamaicensis* (Gmelin 1788)

**MATERIAL.** Claw and phalange, SBMNH 17; proximal left ulna, SBMNH 37; left humerus and distal right tibiotarsus, SBMNH 38; right humerus, SBMNH 46.

**REMARKS.** This species nests irregularly on San Miguel Island.

### Family Falconidae

#### *Polyborus plancus prelutosus* Howard 1938

**MATERIAL.** Distal right tibiotarsus, SBMNH 36; pelvic fragments, SBMNH 80; proximal end of right tibiotarsus, SBMNH 84; distal end of left tibiotarsus, SBMNH 90; right tarsometatarsus, SBMNH 92; right radius, SBMNH 93; proximal end of right tarsometatarsus, SBMNH 98.

**REMARKS.** Maximum length of the measurable material from San Miguel is as follows: radius, 106.6 mm; tarsometatarsus, 93.5 mm; tibia, 110 mm. Howard (1938) described the Rancho La Brea caracara as a new species, *Polyborus prelutosus*, and more recently (Howard, 1962) assigned material from the upper Pleistocene of Santa Rosa Island to this species. She noted that *P. prelutosus* was "a link between the other known species" (Howard, 1938:238-39), i.e., *P. cheriway* (Jacquin 1784) of Central America and northern South America, *P. plancus* (J.F. Miller 1777) of southern South America, and *P. lutosus* Ridgway 1876 of Guadalupe Island. All three of these Recent forms are now

considered of subspecific rank within *P. plancus* (American Ornithologists' Union, 1983).

Howard (1938:239), in describing *Polyborus preltosus*, noted that "were it not for the time element involved, all the caracaras might be thought of as purely subspecific divisions of one form." She went on to say, however, that "The idea of possible subspecific relationship between Pleistocene and Recent species seems to me to be wholly untenable" (Howard, 1938:239). Later, following the discussion of taxonomic approaches to chronocline variation by Simpson (1943), Howard (1947) and other avian paleontologists (e.g., Wetmore, 1959) recognized the applicability of subspecific names to fossil forms. Today the tendency is to identify fossil samples that differ slightly in size or robustness from Recent material of the same lineage simply as variant populations of the Recent species without a separate taxonomic designation (e.g., Howard, 1947). Even in cases where some bones are distinctly separable, if these bones are minor components, taxonomic designation is not made. However, in cases where such fossil samples were previously designated as separate species, the former species name is retained at the subspecific level, as was suggested by Wetmore (1959:12) and finally formally done by Emslie (1988) for *Gymnogyps californianus amplus*.

Given the range of variation in the Recent and Pleistocene samples of the genus *Polyborus* mentioned here and the lack of any single character where overlap between the samples does not occur, I consider designation of the Pleistocene population as a subspecies of the living caracara the best approach.

#### *Falco sparverius* Linnaeus 1758

**MATERIAL.** Proximal end of left humerus, SBMNH 19.

**REMARKS.** This species is a regular visitor to the northern Channel Islands.

### Order Charadriiformes

#### Family Scolopacidae

##### *Charadrius* sp. cf.

##### *C. alexandrinus* Linnaeus 1758

##### or *C. semipalmatus*

##### Bonaparte 1825

**MATERIAL.** Right femur, SBMNH 83.

**REMARKS.** The femur is identical in size and configuration in these two small plovers. Although neither species is known from the North American fossil record, both species have been recovered from the South American Pleistocene (Campbell, 1976, 1979).

#### Family Laridae

##### *Larus californicus*

##### Lawrence 1854

**MATERIAL.** Right tibiotarsus and tarsometatarsus, SBMNH 64; left humerus, SBMNH 67; right coracoid, SBMNH 28.

**REMARKS.** The coracoid and humerus are identical to Recent material of this species, whereas the tibiotarsus and tarsometatarsus are slightly shorter and more robust than Recent material. This species is also known from Pleistocene deposits at Fossil Lake, Oregon (Brodkorb, 1967:209).

#### *Larus* sp.

**MATERIAL.** Anterior sternal fragment, SBMNH 29.

**REMARKS.** This fragment could belong to any of four species of gulls (*Larus occidentalis* Audubon 1839, *L. argentatus* Pontoppidan 1763, *L. glaucescens* Naumann 1840, or *L. thayeri* Brooks 1915) present along the Pacific Coast.

#### *Rissa tridactyla* (Linnaeus 1758)

**MATERIAL.** Left coracoid, SBMNH 76.

**REMARKS.** The curvature of the sternal facet is identical to that of Recent material of this species and unlike that of other gulls of similar size (*Larus canus* Linnaeus 1758, *L. delawarensis* Ord 1815). This species is questionably recorded for Rancho la Brea (Howard, 1936:36).

### Family Alcidae

#### *Uria aalge*

#### (Pontoppidan 1763)

**MATERIAL.** Right ulna, SBMNH 2; left ulna and carpo-metacarpus, SBMNH 8; proximal end of right humerus, right ulna, and sacral fragment, SBMNH 14; left coracoid and femur, proximal end of left humerus, and premaxillary bones, SBMNH 42; right humerus, SBMNH 72.

**REMARKS.** Whereas the limb bones are identical to Recent material of this species, the premaxilla is slightly more robust. This species is also known from the Pleistocene of Santa Rosa Island (Orr, 1968).

#### *Cepphus columba*

#### Pallas 1811

**MATERIAL.** Anterior portion of upper bill, SBMNH 15.

**REMARKS.** This specimen is slightly larger than Recent material of this species but the distance from the tip of the bill to the opening of the nares makes it clearly referable here and not to *Uria aalge*, with which it otherwise might be confused because of size. *Cepphus columba* nests on San Miguel Island, but it is previously unrecorded in Pleistocene deposits (Brodkorb, 1967:219).

#### *Synthliboramphus hypoleucus*

#### (Xantus de Vesey 1860)

**MATERIAL.** Bill tip, SBMNH 164; right humerus, SBMNH 165.

**REMARKS.** Both bones are slightly smaller than Recent material of *Synthliboramphus antiquus*, from which they are nearly indistinguishable in form. This species, which breeds today in small numbers on Prince Island just off the north shore of San Miguel Island (Sowls et al., 1980), has not been previously recorded in the Pleistocene of California (Brodkorb, 1967:219).

#### *Synthliboramphus antiquus*

#### (Gmelin 1789)

**MATERIAL.** Humeri, 102; ulnae, 58; radii, 12; carpometacarpi, 37; coracoids, 38; furculae, 10; scapulae, 2; femora, 5; tibiotarsi, 23; tarsometatarsi, 17; sacra; pelvi, 2; sterni, 4; vertebrae, 6; skull fragment; quadrate; SBMNH 166-176.

**REMARKS.** The bones referred to *Synthliboramphus antiquus* are slightly larger than Recent material of this species. Bones of this species are separable on the basis of size from *S.*

**Table 4. Measurements of depth of maxilla in puffins. All measurements taken at anterior edge of external nares. All samples represent both sexes.**

Species	N	Range	Mean	SD
<i>Cerorhinca monocerata</i>	12	5.91-7.70	7.09	0.46
<i>Fratercula</i> sp.	12	8.86-10.34	9.52	0.40
<i>Fratercula cirrhata</i>	11	12.40-16.60	14.61	1.18

*hypoleucus*, which they otherwise resemble in all respects. The presence of bones from immature individuals, as indicated by degree of ossification, and of eggshell fragments assignable to this species on the basis of curvature and thickness suggest that a breeding population is sampled by this collection. This species is an uncommon wintering species south of central California today, but it is present in upper Pleistocene deposits at San Pedro (Brodtkorb, 1967:219).

*Ptychoramphus aleuticus*  
(Pallas 1811)

**MATERIAL.** Humeri, 289; ulnae, 203; radii, 58; carpometacarpus, 118; coracoids, 135; furculae, 9; scapulae, 7; femora, 59; tibiotarsi, 82; tarsometatarsi, 48; sacra, 3; pelvi, 2; sterni, 14; vertebrae, 18; skull fragments, 10; mandible; quadrates, 4; SBMNH 177-190.

**REMARKS.** As an estimated 20,000 *Ptychoramphus aleuticus* nest on Prince Island and another 2,000 on Castle Rock, both just off the north shore of San Miguel Island (Sowls et al., 1980), the presence of this species in San Miguel Island deposits is not unexpected. As with the previous species, the presence of bones from immature birds and of eggshell fragments referable to this species indicate that it nested on San Miguel Island. The bones referred here are slightly larger than Recent material of this species from southern California.

*Fratercula* sp.

**MATERIAL.** Humeri, 501; ulnae, 381; radii, 97; carpometacarpus, 256; coracoids, 373; furculae, 41; scapulae, 43; femora, 181; tibiotarsi, 107; tarsometatarsi, 124; phalanges, 103; claws, 21; sacra, 27; pelvi, 11; sterni, 52; vertebrae, 227; skull fragments, 67; mandibuli, 28; quadrates, 29; SBMNH 141-144, 147-160.

**REMARKS.** This species, which is being described elsewhere, is the most abundant species in the upper Pleistocene deposits on San Miguel Island, the bones of this puffin literally forming a pavement at locality 7. The presence of eggshell fragments, remains of immature individuals, and complete articulated skeletons, which apparently are the remains of animals that died in burrows, all indicate that these remains are from a breeding colony. At first, the postcranial bones were thought to belong to the living species *Cerorhinca monocerata* (Pallas 1811), from which they are almost indistinguishable on the basis of size and form. It was not until a skull was recovered that a significant difference from *C. monocerata* in the height of the mandibles and maxillaries became apparent. Because all maxillae recovered from the upper Pleistocene deposits on San Miguel Island are referable to *Fratercula* sp. on the basis of size (Table 4), all postcranial material is also referred to that genus here, despite the fact that many elements are inseparable from *C. monocerata*.

The great similarity of the postcranial elements of *Cerorhinca monocerata* to those of *Fratercula* sp. and the age of the deposits

on nearby Santa Rosa Island make it likely that postcranial elements from Santa Rosa Island referred to *C. monocerata* by Howard (in Orr, 1968) belong to *Fratercula* sp. With this reassignment, *Cerorhinca monocerata* is completely absent from the fossil record and is known back to only 2,000 B.P. in midden deposits on San Miguel Island (Guthrie, 1980).

The great skeletal similarities between *Fratercula* sp. and *Cerorhinca monocerata* lead me to consider it highly likely that the former was ancestral to the latter. This view, if correct, calls into question the assignment of Miocene and Pliocene material to *Cerorhinca* (L. Miller, 1925; Howard, 1971).

Order Strigiformes

Family Tytonidae

*Tyto alba* (Scopoli 1769)

**MATERIAL.** Proximal end of right femur, SBMNH 6; shaft of left humerus, SBMNH 30.

**REMARKS.** These bones are identical to Recent material of this species.

Family Strigidae

*Asio* sp. cf.

*A. priscus* Howard 1964

**MATERIAL.** Distal end of left femur, SBMNH 86.

**REMARKS.** Howard (1964) described *Asio priscus* based on a tibiotarsus from the upper Pleistocene of Santa Rosa Island. Her diagnosis indicated that *A. priscus* was generally distinguishable from *A. flammeus* Pontoppidan 1763 by size, the fossil bone being 6 mm (7 percent) longer than that of Recent *A. flammeus* and also longer than specimens assigned to *A. flammeus* from upper Pleistocene deposits of Rancho La Brea. The femur from San Miguel Island is slightly larger than material of Recent *A. flammeus* available to me, and it also has a straighter shaft. Although *A. flammeus* is a regular visitor to the Channel Islands during migration (Garrett and Dunn, 1980) and is also known from midden deposits on San Miguel Island (Guthrie, 1980), this specimen seems best assigned to the slightly larger island species *A. priscus*.

Order Passeriformes

Family Alaudidae

*Eremophila alpestris*  
(Linnaeus 1759)

**MATERIAL.** Right tarsometatarsus, SBMNH 88.

**REMARKS.** This species nests on San Miguel Island.

Family Corvidae

*Corvus corax* Linnaeus 1758

**MATERIAL.** Left femur and right radius, SBMNH 39; proximal left humerus, right and left tarsometatarsi, and fragment of left carpometacarpus, SBMNH 31.

**REMARKS.** This species nests on San Miguel Island.

Table 5. Avifauna from upper Pleistocene deposits on San Miguel Island. Numbers indicate identifiable bones from each locality.

Species	Locality number									
	2	4	5	6	7	8	10	11	12	
<i>Gavia arctica</i>	—	1	—	—	3	—	1	—	—	
<i>Podiceps nigricollis</i>	—	—	1	—	1	—	1	—	—	
<i>Aechmophorus</i> sp.	—	—	—	—	1	—	—	—	—	
<i>Diomedea albatrus</i>	—	1	1	3	1	—	—	—	—	
<i>Fulmarus glacialis</i>	—	1	—	—	3	—	—	—	—	
<i>Puffinus griseus</i>	—	6	1	—	8	—	—	—	—	
<i>Puffinus opisthomelas</i>	—	2	—	—	1	—	1	—	—	
<i>Oceanodroma homochroa</i>	—	—	—	—	1	—	—	—	—	
<i>Pelecanus occidentalis</i>	—	12	—	—	—	—	—	—	—	
<i>Phalacrocorax penicillatus</i>	—	4	—	1	1	—	—	—	—	
<i>Phalacrocorax pelagicus</i>	—	—	—	2	1	—	—	—	—	
<i>Ardea herodias</i>	—	4	—	—	—	—	—	—	—	
<i>Plegadis chibi</i>	—	—	—	—	1	—	—	—	—	
<i>Chen caerulescens</i>	—	—	—	—	4	1	1	—	—	
<i>Branta canadensis</i>	—	—	—	1	1	—	—	—	—	
<i>Melanitta perspicillata</i>	—	—	—	—	—	—	1	—	—	
<i>Melanitta fusca</i>	—	—	—	—	1	—	1	—	—	
<i>Mergus serrator</i>	—	—	—	—	—	—	1	—	—	
<i>Chendytes lawi</i>	1	1	1	3	4	—	667	16	244	
<i>Gymnogyps californianus</i>	—	—	—	—	—	—	6	—	—	
<i>Haliaeetus leucocephalus</i>	—	—	—	—	7	—	2	—	—	
<i>Buteo jamaicensis</i>	—	1	—	—	4	—	1	—	—	
<i>Polyborus plancus</i>	—	1	—	2	4	—	—	—	—	
<i>Falco sparverius</i>	—	—	—	—	1	—	—	—	—	
<i>Charadrius</i> sp.	—	—	—	—	—	—	1	—	—	
<i>Larus californicus</i>	—	—	—	—	2	—	—	2	—	
<i>Larus</i> sp.	—	1	—	—	—	—	—	—	—	
<i>Rissa tridactyla</i>	—	1	—	—	—	—	—	—	—	
<i>Uria aalge</i>	—	—	—	4	4	1	—	1	—	
<i>Cepphus columba</i>	—	—	—	—	1	—	—	—	—	
<i>Synthliboramphus hypoleucus</i>	—	—	—	—	1	—	1	—	—	
<i>Synthliboramphus antiquus</i>	—	15	—	34	161	15	87	7	—	
<i>Ptychoramphus aleuticus</i>	—	69	10	124	107	5	612	24	—	
<i>Fratercula</i> sp.	93	232	61	—	1,166	61	1,032	24	—	
<i>Tyto alba</i>	—	—	—	—	1	—	—	—	—	
<i>Asio</i> sp. cf. <i>A. priscus</i>	—	—	—	—	—	—	1	—	—	
<i>Eremophila alpestris</i>	—	—	—	—	—	—	1	—	—	
<i>Corvus corax</i>	—	—	—	—	2	—	4	—	—	
<i>Zonotrichia leucophrys</i>	—	—	—	—	1	—	—	—	—	
<i>Melospiza melodia</i>	—	—	—	—	1	—	—	—	—	
Passeriformes	—	—	—	—	2	—	—	—	—	

Family Emberizidae

*Zonotrichia leucophrys*  
(Forster 1772)

**MATERIAL.** Left tibiotarsus, tarsometatarsus, and proximal end of left ulna, SBMNH 145.

**REMARKS.** This species is a common winter visitor to San Miguel Island.

*Melospiza melodia* (Wilson 1810)

**MATERIAL.** Right ulna, left tibiotarsus, left mandible, and proximal end of left humerus, SBMNH 146.

**REMARKS.** This species nests on San Miguel Island.

Passeriformes indet.

**MATERIAL.** Distal tibia and pelvic fragment, SBMNH 77.

DISCUSSION

The upper Pleistocene terrestrial fossil-bearing deposits on San Miguel Island were formed by erosion from cliffs just inland from the shoreline and wind deposition of sand blowing inland from beaches. Thus, the deposits contain representatives of the avifauna that both nested on these cliffs and washed up on the beaches and were blown inland (Table 5). The terrestrial paleoavifauna consists of 11 species, seven raptors and four passeriforms. All but three of these species are present regularly on San Miguel Island today. Of the three species not present today,

two (*Haliaeetus leucocephalus*, *Gymnogyps californianus*) are known either historically or from archeological sites on San Miguel Island and one (*Polyborus plancus*) is known from fossil sites on nearby Santa Rosa Island. With the exception of *Gymnogyps californianus* and *Polyborus plancus*, all of the raptorial species in the paleoavifauna either nest on San Miguel Island or did so in historic time. *Polyborus plancus* has colonized islands elsewhere off the Pacific coast. The small number of bones recovered of these raptorial species is consistent with their small island populations. Bones of land birds are rare in the deposits. They tend to be associated with bones of mice and *Tyto alba*, and they probably represent the remains of owl pellets.

The marine paleoavifauna, with three exceptions, consists of species that either occurred in historic time or currently occur in the vicinity of San Miguel Island. As indicated here, all three of the exceptions apparently nested on San Miguel Island. One, *Chendytes lawi*, is extinct with no descendants. The other two species (*Synthliboramphus antiquus* and *Fratercula* sp.) or their descendants today breed well north of San Miguel Island.

The abundance of three species of alcids (*Fratercula* sp., *Synthliboramphus antiquus*, and *Ptychoramphus aleuticus*) and the duck *Chendytes lawi* as well as eggshells and bones of immature individuals referable to these species indicates presence of nesting colonies on San Miguel Island. Variation in the numbers of these four species among the various fossil localities is probably a reflection of the nearness of the colonies to the different localities and an indication that each species nested in a slightly different area. These colonies may have suffered predation by the Pacific rattlesnake [*Crotalus viridis* (Rafinesque 1818)] and island fox [*Urocyon littoralis* (Baird 1858)], both of which were present on San Miguel as well as from raptorial birds. The dwarf mammoth [*Mammuthus exilis* (Stock and Furlong 1928)] may also have affected nesting success by walking on nests and collapsing burrows. These factors may have been partially responsible for the large numbers of these species in the deposits.

Marine species that did not nest on San Miguel Island in large colonies are rare in the deposit. Bones of most of these species are incorporated in the deposit either because they served as food for raptorial birds nesting on San Miguel Island or because their bones blew inland from beached carcasses. *Phalacrocorax pelagicus* and *Cephus columba* nest on San Miguel Island in sea caves overhanging the sea. Both species are rare in San Miguel Island deposits, as would be expected because incorporation of bones from these species into the deposits would have been primarily from beached birds rather than directly from nesting colonies.

Two of the species in the San Miguel Island paleoavifauna (*Oceanodroma homochroa*, *Cephus columba*) are recorded for the first time in the late Pleistocene. Four additional species (*Mergus serrator*, *Larus californicus*, *Charadrius* sp., and *Synthliboramphus hypoleucus*) are new to the California Pleistocene.

Only two species in the San Miguel Island paleoavifauna represent extinct lineages. One, *Chendytes lawi*, was a flightless duck that became extinct only after human occupation of the northern Channel Islands (Guthrie, 1980). The other, *Asio priscus*, is an extinct island endemic closely related to the mainland *Asio flammeus*. In the approximately 30,000 years since the formation of the San Miguel Islands upper Pleistocene deposits, one species (*Fratercula* sp.) has changed at the generic level and an additional two species (*Gymnogyps californicus amplus*, *Polyborus plancus prelutosus*) have changed at the subspecific level. Both these latter subspecies were once considered separate species.

The number of extinct species from the upper Pleistocene of San Miguel Island (2 of 41 or 5 percent) is low compared to the Pleistocene terrestrial deposits, which contain large numbers of extinct raptors (Selander, 1965), but it agrees with the number of extinct forms (3 of 41 species) from other upper Pleistocene marine deposits in California (Howard, 1949).

Although only three of the species of late Pleistocene birds from San Miguel Island that belong to extant lineages are taxonomically separated from Recent populations, 13 of 41 species in the paleoavifauna are separable on the basis of size or configuration. Of these, 12 are larger than their modern representatives and 1 is smaller. Zink and Remsen (1986) recently reviewed the application of Bergman's rule to birds and found few species that supported the rule and two alcids that contradicted it. However, R. Storer (pers. comm., 1988) has found north-south clinal variation in birds to be more prevalent than previously thought. He also finds significant clinal variation in two alcids, a guillemot and a murre. The larger size of many of the late Pleistocene birds on San Miguel Island may be correlated with cooler climates at the time of deposition. The one species that is smaller in the late Pleistocene than its Recent descendants (*Synthliboramphus hypoleucus*) had a larger member of the same genus also present on the island. Smaller size here may be the result of interspecific competition. That five of the six species of alcids from the upper Pleistocene of San Miguel Island are separable from Recent forms suggests a high rate of evolution in the group.

## SUMMARY

Previously known Pleistocene deposits from offshore California are either marine with few birds, or, as is the case with the extensive deposits on Santa Rosa Island, they contain a mainly terrestrial and lagoonal avifauna (Orr, 1968). The upper Pleistocene deposits along the northwestern coast of San Miguel Island contain a well-preserved and incredibly abundant avifaunal assemblage with 41 species and provide us with our most complete record of a coastal avifauna in southern California during the late Pleistocene.

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