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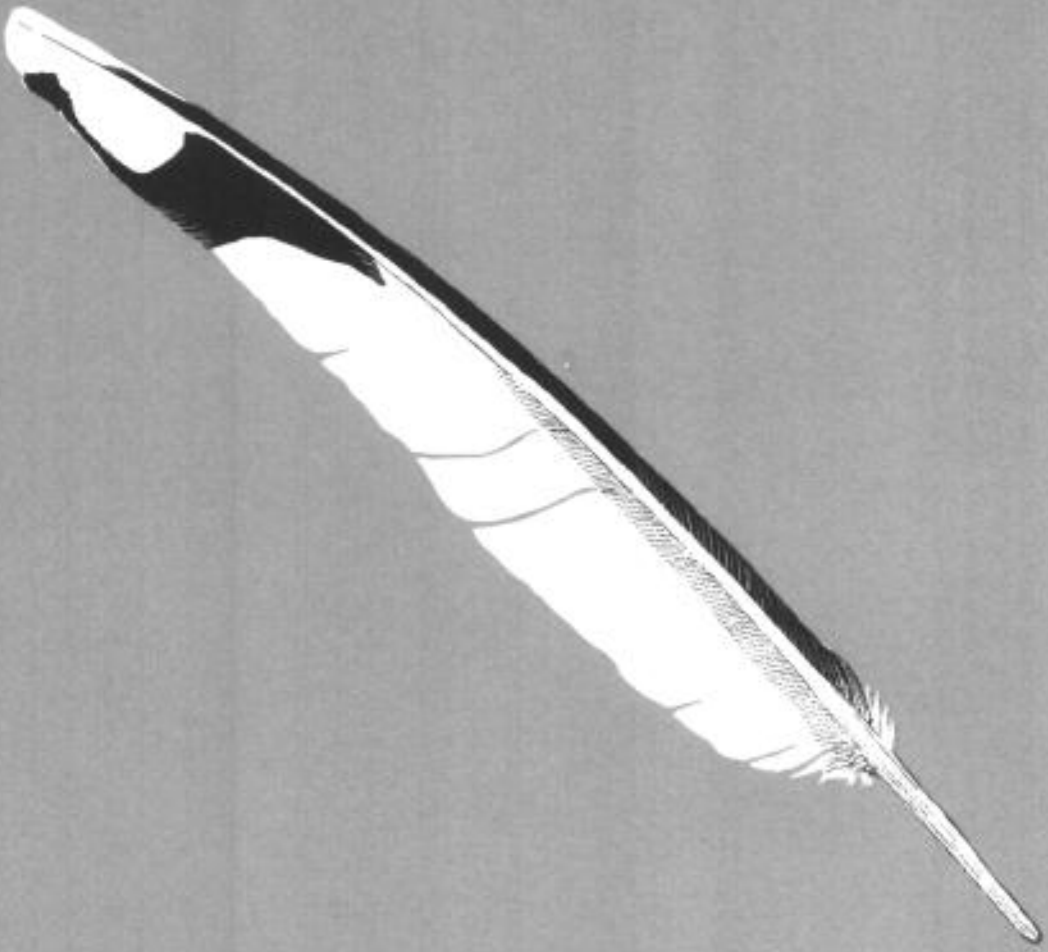

Recent Advances in the Study of Neogene Fossil Birds

I. The Birds of the Late Miocene-Early Pliocene Big Sandy Formation, Mohave County, Arizona

by

K. Jeffrey Bickart

II. Fossil Birds of the San Diego Formation, Late Pliocene, Blancan, San Diego County, California

by

Robert M. Chandler

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ORNITHOLOGICAL MONOGRAPHS

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FOREWORD

STORRS L. OLSON

The papers in the present volume represent major additions to our knowledge of two of the larger avifaunas of the North American Neogene, that is, the last half of the Tertiary Period, comprising the Miocene and Pliocene epochs spanning the period from about 22.5 million to 1.8 million years ago. Bickart treats an extremely large collection of bones from a Mio-Pliocene lake deposit, the Big Sandy Formation, in Arizona. This collection, made primarily in the 1940s, had lain unstudied for decades, so that virtually nothing was known of the birds from this locality. By contrast, Chandler's study of the late Pliocene San Diego Formation in California continues the elucidation of an avifauna, the studies of which began in 1933 and to which several workers have contributed periodically for half a century. Even so, the number of species in this avifauna is now more than doubled by Chandler's efforts. Each of these fossil avifaunas comprises nearly 40 species. The number of specimens studied was 2,000+ for the San Diego Formation, and to over a thousand in the case of the Big Sandy Formation. Most of the species described are known from many or most of the major skeletal elements, and in some cases, especially in the Big Sandy Formation, from partial or nearly complete associated skeletons.

There are strong biases in the species composition of all North American Neogene avifaunas, as may be seen from Becker's valuable compilation (J. J. Becker, 1987, *Neogene Avian Localities of North America*. Washington, D.C.: Smithsonian Institution Press). In contrast to Pleistocene avifaunas, which are mainly from cave and tarpit deposits and are heavily influenced by the actions of predators and scavengers, most Neogene fossil birds occur in aquatic or marine deposits. These avifaunas are overwhelmingly dominated by waterbirds, with diurnal raptors and Galliformes frequently present but other terrestrial or arboreal birds nearly always lacking. For example, in each of the extensive avifaunas described here, only a single bone of a passerine was reported. The San Diego avifauna, from a marine formation, is composed almost exclusively of pelagic and nearshore birds, with scant representation even of littoral species, to say nothing of terrestrial or arboreal ones.

In addition to the biases introduced by depositional environments, Bickart suggests another possible source of bias in his avifauna—differential susceptibility of wetland species to disease. The preponderance of individuals in the Big Sandy Formation is of Anatidae and the whole accumulation rather closely resembles the pattern of mortality that might be observed in a modern outbreak of botulinal poisoning. Further taphonomic bias in this fauna is shown by the great underrepresentation of hindlimb elements of ducks, geese, and swans, suggesting that in most instances the legs fell off before the decomposing carcasses accumulated along the lee shore of the lake and were buried.

The Big Sandy avifauna illustrates additional problems facing avian paleontologists. Frequently it was deemed expedient not to apply specific names to various taxa in the fauna but to refer them only to genus, a practice usually resorted to when material is too scanty or poorly preserved to be more certainly identified or diagnosed. But some of the Big Sandy species, such as the two teal-sized species of *Anas*, are represented by dozens of fossils of most of the major skeletal elements, including some associated material, so that they are much better known than any previously described pre-Pleistocene species of *Anas*. Despite the abundance of material, however, specific identification is still problematic. Even modern species of *Anas* are difficult to separate on criteria other than size. Furthermore, there are several previously named fossil species of North American teal-sized ducks that might be related to one or the other of the Big Sandy teals, but all are based on such fragmentary material that their identity will probably be forever uncertain. Although such taxa might eventually have to be discarded as *nomina vana*, they emphasize the need for some degree of circumspection in assigning specific names to fossil populations.

Although faunal surveys have now generally fallen into disfavor in ornithology, in part, one assumes, because they are inherently descriptive and nonexperimental, they are still absolutely essential to avian paleontology, where so much remains unknown. The two studies here well illustrate the fact that avian paleontology has progressed beyond the game of creating new names for isolated fragments of bone. The next logical step will be to track the history of entire continental or regional avifaunas, to see when certain species, genera, or even families appear and others disappear, or to compare a fossil avifauna with that occurring in the same area today. Fortunately, we are now reaching the point where such comparisons are possible, especially in North America and Europe, where the greatest numbers of paleontologists are concentrated.

California, for example, is rich in fossil marine avifaunas, of which that from the San Diego Formation is the largest. These range in age from early Miocene to Pleistocene (see Becker *op. cit.*). Similarly rich avifaunas are known from the east coast of North America, especially the mid-Miocene Calvert Formation of the Chesapeake Bay region and the early Pliocene Yorktown and Bone Valley Formations in North Carolina and Florida. These will offer interesting future comparisons between the east and west coasts of North America and between contemporaneous large marine avifaunas from South Africa (S. L. Olson, 1983, *S. Afr. J. Sci.* 79:399–402) and Peru (C. de Muizon, 1985, *Geologische Rundschau*, 74:547–563).

With the gift of human imagination we can use studies such as these to take us back millions of years to a California coastline with even more diverse birdlife than today, one with gannets, boobies, and several species of flightless auks. And even farther back in time we find a lakeshore in Arizona where the members of a waterbird assemblage not unlike that of the American West today might have suffered the same ravages of botulinal poisoning that plague their modern counterparts. Yet among the carcasses that accumulated were flamingos, Old World vultures, geese with the diving adaptations of a merganser, and other unusual waterfowl. We are fortunate at least to have the bones of these long-vanished birds to provide us with an ornithological perspective through evolutionary time. Without them, all would be conjecture.

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PART I

THE BIRDS OF THE LATE MIOCENE-EARLY PLIOCENE BIG SANDY FORMATION, MOHAVE COUNTY, ARIZONA

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INTRODUCTION

The Big Sandy Formation of western Arizona spans the boundary of the Miocene and Pliocene, from 6.1 to 4.6 mybp. Its lacustrine deposits have produced one of the largest pre-Pleistocene avifaunas known from North America. With 38 species in 13 families, represented by over 1,000 specimens, the diversity of the fauna is exceeded in North America only by that of the late Miocene Love Bone Bed and the late Miocene and early Pliocene Bone Valley faunas of Florida, the early Pliocene Lee Creek fauna of North Carolina, the mid-Pliocene Rexroad fauna of Kansas, and the Pliocene San Diego Formation of California, treated in this monograph by Chandler. When marine taxa are excluded, the Big Sandy Formation birds comprise the second most diverse avifauna, next to the Rexroad, from the pre-Pleistocene of North America.

Little has previously been written on these birds. The literature includes only a note on a fossil swan (Wetmore 1943) and a description of a new rail (Wetmore 1957). In this paper, several new species of anatids, a new stilt, and a new crow are named. The rest of the avifauna, identified to genus, provides some significant temporal and geographical extensions for various taxa.

At the end of the Miocene, western Arizona was rich with life. The birds included ducks, geese, and swans; a stork; grebes; rails; a crane; a flamingo; various shorebirds; a gull; several species of hawks, eagles, and vultures; a dove; and a crow. The mammals are similarly diverse, with 25 species in 12 families (MacFadden et al. 1979; R. H. Tedford pers. comm.). These have been termed the "Wikieup Local Fauna" (MacFadden et al. 1979). They include a rabbit; unidentified rodents; dogs and a fox; a bear; a procyonid; wolverines (including *Plesiogulo lindsayi* Harrison 1981, described from the Big Sandy Formation) and a badger; various cats; a horse (*Onohippidium galushai* MacFadden and Skinner 1979, described from the formation); five camelids; and several antilocaprids.

MATERIALS AND METHODS

For this study I examined approximately 1,200 specimens and ultimately assigned 1,036 to taxa. About 200 specimens in the Frick Collection remain unstudied. Almost all of these are phalanges of wings and legs, carpals, or similarly undiagnostic or less useful specimens.

The greater number of fossil specimens is from the Frick Collection, American Museum of Natural History (F:AM). Most of these specimens were collected from 1939 to 1941 by William Klaus and Guy E. Hazen, working for Childs Frick. A smaller number of AMNH specimens was collected in 1955–1956 by Ted Galusha, and in 1961–1962 by Robert J. Emry. The other fossils were made available for study by the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution (USNM). These include the type of *Rallus phillipsi,* a single end of a sandpiper humerus also collected by Allan Phillips, and several dozen specimens collected from spoil piles in 1976 by P. V. Rich and donated to the Smithsonian Institution.

All modern skeletons used for comparison are from the collections of the Division of Birds, National Museum of Natural History.

Anatomical terminology is from Howard (1929).

Measurements of specimens with dimensions less than 170 mm were taken with dial calipers to the nearest 0.05 mm. Measurements of larger specimens were taken with oversize sliding wooden calipers to the nearest 1 mm. Definitions of the measurements will be found in Appendix I; the measurements taken are illustrated in the Appendix figures.

In the "Systematic Paleontology" section below, I give for each taxon the specimens I have assigned to that taxon, with element and catalog number; a brief explanation for assignment to that taxon; comparison to previously named or otherwise recognized fossils in that taxon; and other pertinent comments. Most of the specimens are damaged in some way, but for the sake of brevity I have not usually described the damage.

In naming new species I have been relatively conservative. Although many of the bird fossils from the Big Sandy Formation undoubtedly come from species not previously named, and although most of the fossils are in very good condition, little is accomplished by attaching a name to one or two bones of a bird's body unless the fossils are particularly remarkable in themselves or provide important new information on the distribution of a group in time or space. For many purposes generic assignment is sufficient. The proliferation of names attached to undiagnostic material continues in avian paleontology despite the cautions by Olson (1985) and others on its lack of usefulness. I have no doubt that with more collecting much more complete material, including in many cases nearly complete skeletons, could be obtained for most of the taxa included here.

In several cases, notably with the ducks, I have not described species because of unresolved taxonomic complexities in the modern and fossil forms and because of the difficulty of determining whether a bird in the Wikieup fauna has already been named elsewhere on other elements of the skeleton.

As noted above, controversy has existed over the limits of the Miocene, Pliocene, and Pleistocene. My use of "Miocene" below in designating the age of a fossil bird from North America, includes time through all but the latest Hemphillian land mammal age; "Pliocene" means latest Hemphillian, and Blancan; "Pleistocene" to subsequent time. Thus, my designations of the ages of North American fossil birds differ in several cases from those of the original authors or Brodkorb's *Catalogue of Fossil Birds* (1963a, 1964b, 1967, 1971, 1978). These corrections are based on the work of Becker (1987). Ages given for birds from other parts of the world are those reported by the original author or in Brodkorb's *Catalogue.*

GEOLOGY

The Big Sandy Formation is chiefly a lacustrine deposit of late Miocene-early Pliocene age that crops out over an area of about 50 square kilometers near the town of Wikieup, Arizona (Fig. 1). It is exposed on the valley of the Big Sandy River, both in steep bluffs east of the river, and in the walls of many washes which head eastward from the river (Sheppard and Gude 1972). Outcrops vary in thickness from several meters to about 65 m; the total amount of Big Sandy Formation exposed is about 80 m (MacFadden et al. 1979; Sheppard and Gude 1972). The following summary of the geology of the deposits is taken from Sheppard and Gude (1972: pp. 5–9):

> The Big Sandy Formation consists chiefly of green and brown lacustrine mudstone or a calcareous silty or sandy variant.... These rocks grade laterally into coarser

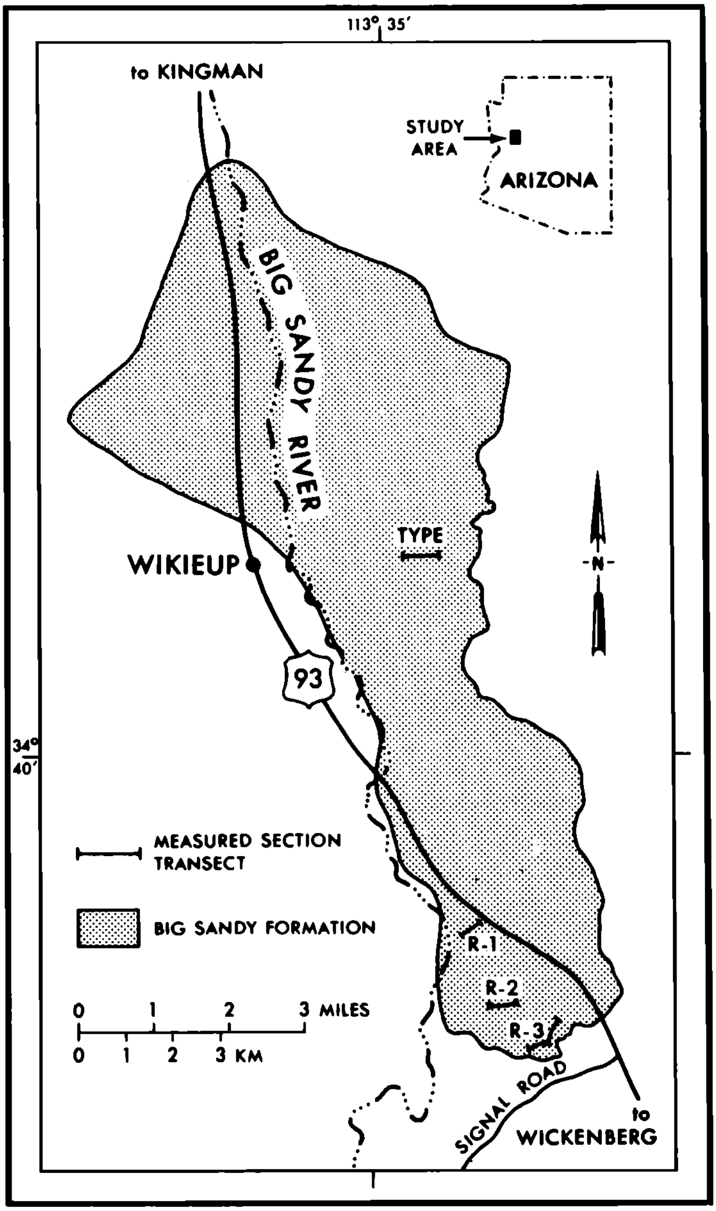


FIG. 1. Location of Big Sandy Formation, Mohave County, Arizona. "Type," "R-1," "R-2," and "R-3" refer to the type and reference sections of MacFadden et al. (1979), from which this map is taken.

> clastic rocks, including conglomerate. The coarse-grained rocks are probably a marginal facies of the mudstone; however, some sandstone and conglomerate included in the formation may be of fluviatile origin. . . . Tuffs are the most conspicuous and continuous strata in the formation. At least 13 tuffs [are] recognized, and they make up about 2–3 percent of the exposed formation. . . . Erosion and dissection of the nearly flat formation have proceeded to such a degree that most of the formation is characterized by badlands or dissected gravel-capped pediments. . . . Much of the formation is concealed by either gravel-capped pediments or relatively recent allu-

> vium of the Big Sandy River and its tributaries. The Big Sandy Formation unconformably overlies unnamed Tertiary sedimentary and volcanic rocks to the east and Tertiary volcanic rocks and Precambrian granitic rocks to the south. Small remnants of basalt crop from beneath the Big Sandy Formation. . . . These older rocks were probably islands in the lake during much of the deposition of the Big Sandy Formation. . . . Dips in the Big Sandy Formation are generally less than 2 degrees, but steeper dips have been recorded. . . . Normal faults of slight displacement cut the formation. . . .

Sheppard and Gude give detailed descriptions of one type and three reference sections in the formation. One of the reference sections, R-3, includes the fossil localities. It is located ". . . along a wash that parallels Signal Road about 2,600 ft northwest of the road, from NW¼ NW¼ SW¼ sec. 29 to NE¼ SE¼ NW¼ sec. 29, T. 15 N., R. 12 W., Greenwood Peak quad." (Sheppard and Gude 1972: p. 6).

The position of the Miocene/Pliocene boundary is controversial. Berggren and Van Couvering (1974) discuss this and conclude that the boundary is within the interval of 4.9 to 5.1 mybp. The Big Sandy Formation runs from late Epoch 6 to early Gilbert time on the magnetic polarity time scale, or from about 6.1 to 4.6 mybp (MacFadden et al. 1979), and thus spans the Miocene/Pliocene boundary as given by Berggren and Van Couvering (1974). The mean age of the formation as given by MacFadden et al. (1979) is 5.5 ± 0.2 mybp based on fission-track (zircon) dating of tuffs from three out of four of Sheppard and Gude's sections, including the one with the fossil localities. MacFadden et al. (1979) bracket the fossil quarries at between 5.12 and 5.29 mybp, based on correlation of their composite magnetic polarity zonation of the Big Sandy Formation with the magnetic polarity time scale of LaBreque et al. (1977). Thus, the quarries and their fauna may be considered as late Miocene.

FOSSIL DEPOSITS

The Big Sandy Formation is largely devoid of fossils. In the winter of 1955–1956, Ted Galusha and an assistant, working for Childs Frick and the American Museum of Natural History, prospected the entire formation very thoroughly, and, according to Galusha, the two adjacent quarries that produced the fossils considered here are the only productive localities in the formation. He writes (unpublished field notes for 1955–1956 season; at AMNH), "Under systematic prospecting I found the Big Sandy beds to be some of the most unfossiliferous beds in which I have worked. Of course, a few quarries have been worked in the past and have produced a marvelous collection, but in general the bulk of the beds do not carry fragments, and we have on occasion prospected for days without seeing a single fragment."

The two quarries, the Bird Bone Quarry and the Clay Bank Quarry (also known as "Gray's Ranch Quarry"), are found in the southernmost exposed part of the formation, west of Route 93. MacFadden et al. (1979) give their location as SW¼, NE¼, sect. 29, T. 15N, R. 12W, Greenwood Peak Quadrangle, Mohave County, Arizona. The Bird Bone Quarry is about 100 m west of the Clay Bank Quarry, and the two are about 1.8 m apart stratigraphically (Galusha 1955–1956 field notes). MacFadden et al. (1979) have estimated a mean sedimentation rate at the

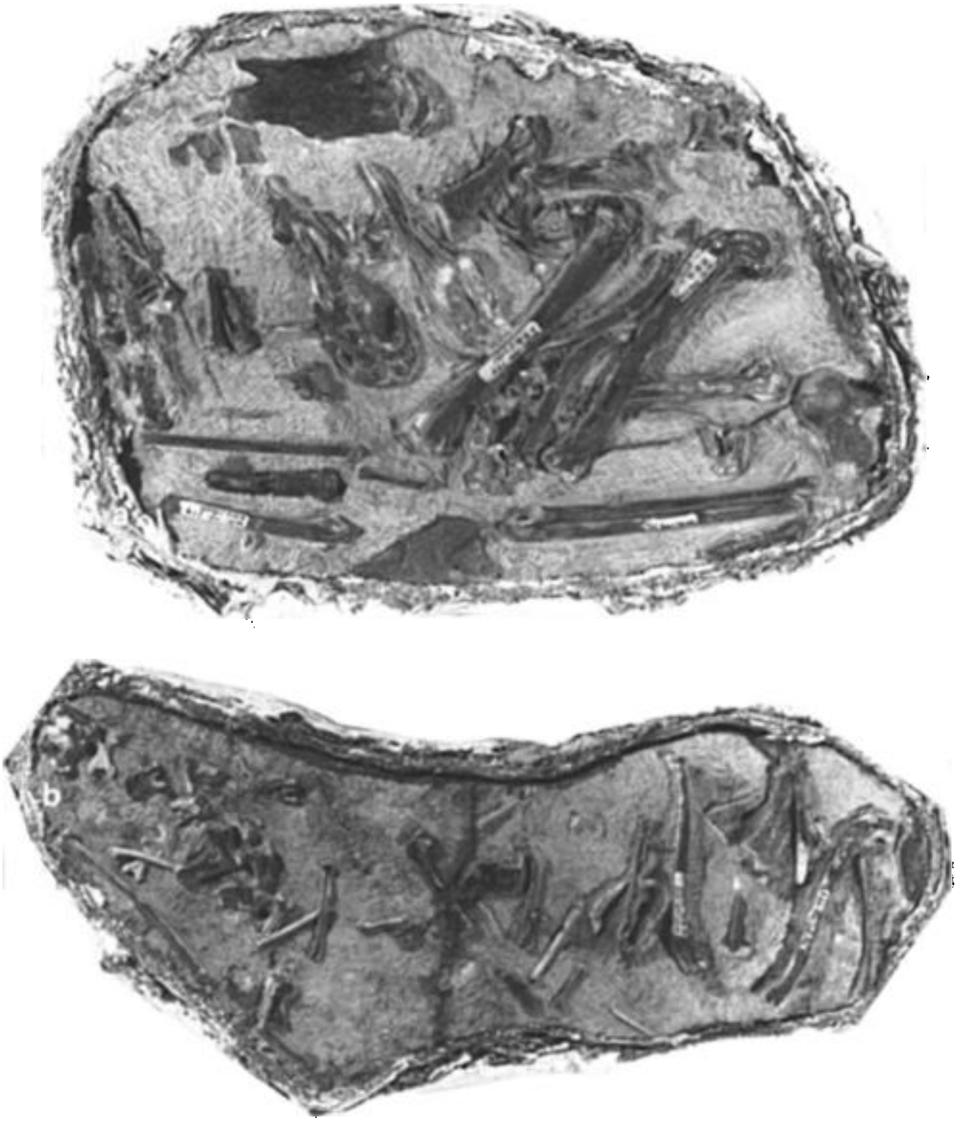


FIG. 2. a. Partially prepared block with partial skeleton of *Anser arizonae* sp. nov., F:AM 18000. b. Partially prepared block with partial skeletons of *Branta woolfendeni* sp. nov., F:AM 20889, and *Anas* sp. B, F:AM 20100.

type section of 88 mm/1,000 years. Based on this the separation of the two quarries is about 21,000 years. At their present stage of excavation, the quarries cover about 18,000 square feet. Worked out areas are covered with talus.

The fossils are found in an interval of about 15 feet of green siltstone, sandy siltstone, and mudstone, with tuffs and gray or green sandstone and siltstone above and below (Galusha 1955–1956 field notes). Judging from the several fossiliferous blocks from the American Museum collection that I prepared (Fig. 2), the concentration of fossils at the quarries is high. The quarries have not been worked out, and would still yield large numbers of fossils, but further work would require the removal of a very large amount of overburden (Robert J. Emry pers. comm.).

In addition to the Clay Bank and Bird Bone Quarries, four other localities in the formation have produced fossils, but only in very small numbers. No fossils from these quarries have contributed to the present study. Their localities are given in MacFadden et al. (1979).

SYSTEMATIC PALEONTOLOGY

Order PODICIPEDIFORMES (Fürbringer) 1888

Family PODICIPEDIDAE (Bonaparte) 1831

Tribe PODILYMBINI Storer 1963

Genus *Podilymbus* Lesson 1831

Podilymbus sp.

Referred material: right coracoid F:AM 20305; scapular end of right coracoid USNM 407747; proximal end of right tarsometatarsus F:AM 20775; proximal end of left tarsometatarsus F:AM 20778; distal end of left tarsometatarsus F:AM 20001.

Remarks: The proximal ends of tarsometatarsi have the separate canal for the tendon of insertion of flexor perforatus digiti II described by Storer (1963) as distinguishing his tribe Podilymbini, which includes the genera *Rollandia, Tachybaptus,* and *Podilymbus.* The proximal end of the tarsometatarsus in these genera cannot be separated except by size, the species of *Rollandia* and *Tachybaptus* being smaller than *Podilymbus.* The fossils fall within the size range of *Podilymbus podiceps* (see Storer 1976) to which they are also similar in details.

The assignment of the coracoids to tribe and genus is based strictly on size, because of the similarity of the elements in modern grebes. I do not agree with Murray (1967) that the coracoids of the two tribes can be separated reliably on qualitative characters. The two coracoids here differ greatly in size, but both fall within the range for *Podilymbus podiceps* as reported by Storer (1976), and almost certainly represent the same species as the tarsometatarsi.

Three extinct species of *Podilymbus* have been named, all from North America. *P. magnus* Shufeldt 1913 (late Pleistocene, Oregon) has been synonymized with *P. podiceps* (Storer 1976). *P. wetmorei* Storer 1976 (late Pleistocene, Florida) was distinguished from all other *Podilymbus* by the much heavier shaft of the tarsometatarsus (Storer 1976). *Podilymbus majusculus* (Murray 1967), based on a tarsometatarsus and referred material from the early Pliocene of Idaho, was diagnosed as being similar to *P. podiceps* but larger. Of the 10 specimens in Murray's hypodigm, three, the holotype and a referred femur and quadrate, are larger than *P. podiceps.* The other referred specimens fall within the size range of males of *P. podiceps,* and Murray suggested that they represent females of *P. majusculus.* The Wikieup *Podilymbus* may also represent females of *P. majusculus,* but cannot definitely be referred to the species by use of Murray's diagnosis.

Tribe PODICIPEDINI Storer 1963
Genus *Podiceps* Latham 1787
Podiceps sp.

Referred material: distal end of left humerus USNM 407749; proximal end of left ulna USNM 407748; proximal end of right tibiotarsus USNM 407750.

Remarks: The end of the ulna is referable to *Podiceps* by the characters given in Howard (1929) and Murray (1967). The other two specimens are tentatively referred to *Podiceps* on the basis of size. The specimens are similar in size and details to the comparable elements in *P. auritus.*

The fossil record of grebes is in great need of revision. A number of species have been named in *Podiceps* and allied extinct, possibly invalid, genera. The bones of the modern *Podiceps*-type grebes are all very similar in morphology, and the extinct forms are little different. The distal end of a humerus listed here is indistinguishable from a plastotype of *Podiceps pisanus* (Portis) 1889 (Pliocene, Italy), and from undescribed specimens from the early Pliocene Lee Creek fauna of North Carolina.

Order CICONIIFORMES Garrod 1874
Family CICONIIDAE (Gray) 1840
Genus *Ciconia* Brisson 1760
Ciconia sp.

Referred material: mandible F:AM 7095; retroarticular process of mandible F:AM 20609; partial furculae F:AM 8612, 11292, 20374; anterior end of sternum F:AM 11290; anterior ends of right scapulae F:AM 7093, 11287; anterior end of left scapula F:AM 7094; right coracoids F:AM 7096, 7097, 7099, 7102, 7103, 7109; left coracoids F:AM 7098, 7100, 7101, 7105, 7106; left coracoid missing scapular end F:AM 7104; scapular end of left coracoid F:AM 11295; right humeri (all damaged) F:AM 7023, 7024, 7025, 7030; distal end of right humerus F:AM 7031; left humerus (damaged) F:AM 7027; proximal end of left humerus F:AM 20856; right ulnae F:AM 7083, 7084, 7085; distal end of right ulna F:AM 7086; proximal ends of left ulnae F:AM 7087, 7088; distal end of left ulna F:AM 20316; right radii F:AM 7089, 7092; right carpometacarpi F:AM 7069, 7071, 7072, 7075, 7077, 7079; partial right carpometacarpus F:AM 11296; proximal ends of right carpometacarpi F:AM 7061, 7064, 7078, 7081; distal ends of right carpometacarpi F:AM 7060, 7082, 20474; left carpometacarpi F:AM 7067, 7074, 7076, 7082, 11288; distal halves of left carpometacarpi F:AM 7078, 20476; left digit II phalanx I (carpometacarpus) F:AM 8608; proximal right femur F:AM 20654; left femora F:AM 7057 (crushed), 7059; proximal left femur F:AM 20655; right tibiotarsus F:AM 7056; right tibiotarsus, missing distal end, F:AM 7054; right tibiotarsus, missing proximal end, F:AM 11285; distal ends of right tibiotarsi F:AM 7051, 7052, 7053; left tibiotarsus F:AM 7055; distal ends of left tibiotarsi F:AM 7049, 7050; right tarsometatarsi F:AM 7043, 7048, 19990; proximal end of right tarsometatarsus F:AM 7034; distal ends of right tarsometatarsi F:AM 7035, 7036, 7037, 7038, 7039, 7040; left tarsometatarsi F:AM 7042, 7045, 7046, 7047; proximal half of left tarsometatarsus F:AM 7036; proximal end of left tarsometatarsus F:AM 7041; left tarsometatarsus missing proximal end F:AM 20860.

Remarks: This species is a giant, equaling in size large individuals of the extant

Jabiru mycteria of Central and South America. The specimens fall in the high end of the size range for the Pleistocene *Ciconia maltha* (Howard 1942), and otherwise resemble that species. It seems likely that the Wikieup stork is ancestral to *Ciconia maltha.* The Wikieup stork might be related to a large, unnamed *Ciconia* from Bone Valley of Florida (Becker 1985).

Order ANSERIFORMES (Wagler) 1831

Family ANATIDAE Vigors 1825

Remarks: The fossil record of the family Anatidae is extensive, with some 80 named fossil species. Many or most of these are based on fragments of single bones that simply are not diagnostic; Woolfenden (1961) shows that genera and even tribes of living anatids often cannot be characterized on the basis of single post-cranial elements. I name a new swan, *Cygnus,* and three new geese, two in *Anser* and one in *Branta. Cygnus* is poorly represented in the fossil record of North America, and the relationships of the few modern taxa are fairly clear. Similarly, *Anser* and *Branta* are relatively uncommon in the fossil record of the family, and the Wikieup material includes associated material, with most of the elements, for two of the species. I consider it imprudent to name at this time the three species of ducks in the fauna, in light of the great number of extinct taxa already named and the great need for complete revision of the whole family based on actual examination of the types and a more complete quantitative study of the modern forms than has yet been published.

I have relied heavily on Woolfenden's (1961) invaluable work on the post-cranial osteology of the waterfowl. For the most part I agree with his observations; where I differ I have made note.

Subfamily ANSERINAE Vigors 1825

Remarks: Woolfenden (1961) gives characters by which the subfamilies of Anatidae can be separated. He did not study the radius and ulna; both are of little taxonomic value. Here, I note that the subfamilies Anserinae (including the tribes Dendrocygnini and Anserini) and Anatinae (including the tribes Tadornini, Anatini, Cairini, Aythyini, Somateriini, Mergini, and Oxyurini) can be distinguished by characters of the ulna. In both subfamilies, the articular surface of the external cotyla extends distally farther than does the articular surface of the internal cotyla, so that distally the plane of the external cotyla is parallel with the shaft. In the Anserinae, the medial border of this part of the cotyla is only slightly distinct from the proximal radial depression. In the Anatinae, including the Tadornini (except for *Cereopsis*), it is raised, very distinct, and more extensive distally.

Tribe ANSERINI Vigors 1825

Genus *Cygnus* Bechstein 1803

Subgenus *Olor* Wagler 1832

Remarks: All swans are currently placed in the single genus *Cygnus,* in which I also place the following new species. Nevertheless, the swans formerly included in the genus *Olor* (*O. buccinator* and *O. columbianus*) are quite distinct osteologically in most of the skeletal elements (Woolfenden 1961 and pers. obs.) from typical *Cygnus* and the two groups should be recognized at least at the subgeneric level.

In addition to the characters given by Woolfenden (1961), I note that the coracoid in the *Olor* group has a deep, strongly bordered groove in the triosseal canal, running from the top edge of the scapular facet about halfway to the brachial tuberosity, whereas in *Cygnus* this groove is absent. *Olor* resembles geese in this respect, although the shape of the groove or depression is different in the two groups. The ulna in *Olor* has the area of the proximal radial depression very distinct from the shaft, with a strong, pronounced border, especially on the external side, whereas in *Cygnus,* the depression blends smoothly with the shaft, except on the external edge, where there is a slightly raised border.

Cygnus (*Olor*) *mariae* sp. nov.

Fig. 3

Holotype: left humerus F:AM 7021, broken in several places and repaired. Collected in 1941 by William Klause.

Type locality: Bird Bone Quarry, SW¼, NE¼, sect. 29, T. 15N, R. 12W, Greenwood Peak Quadrangle, Mohave County, Arizona.

Horizon and age: Big Sandy Formation, late Hemphillian, late Miocene. Dated (fission-track, zircon) at 5.12–5.29 mybp.

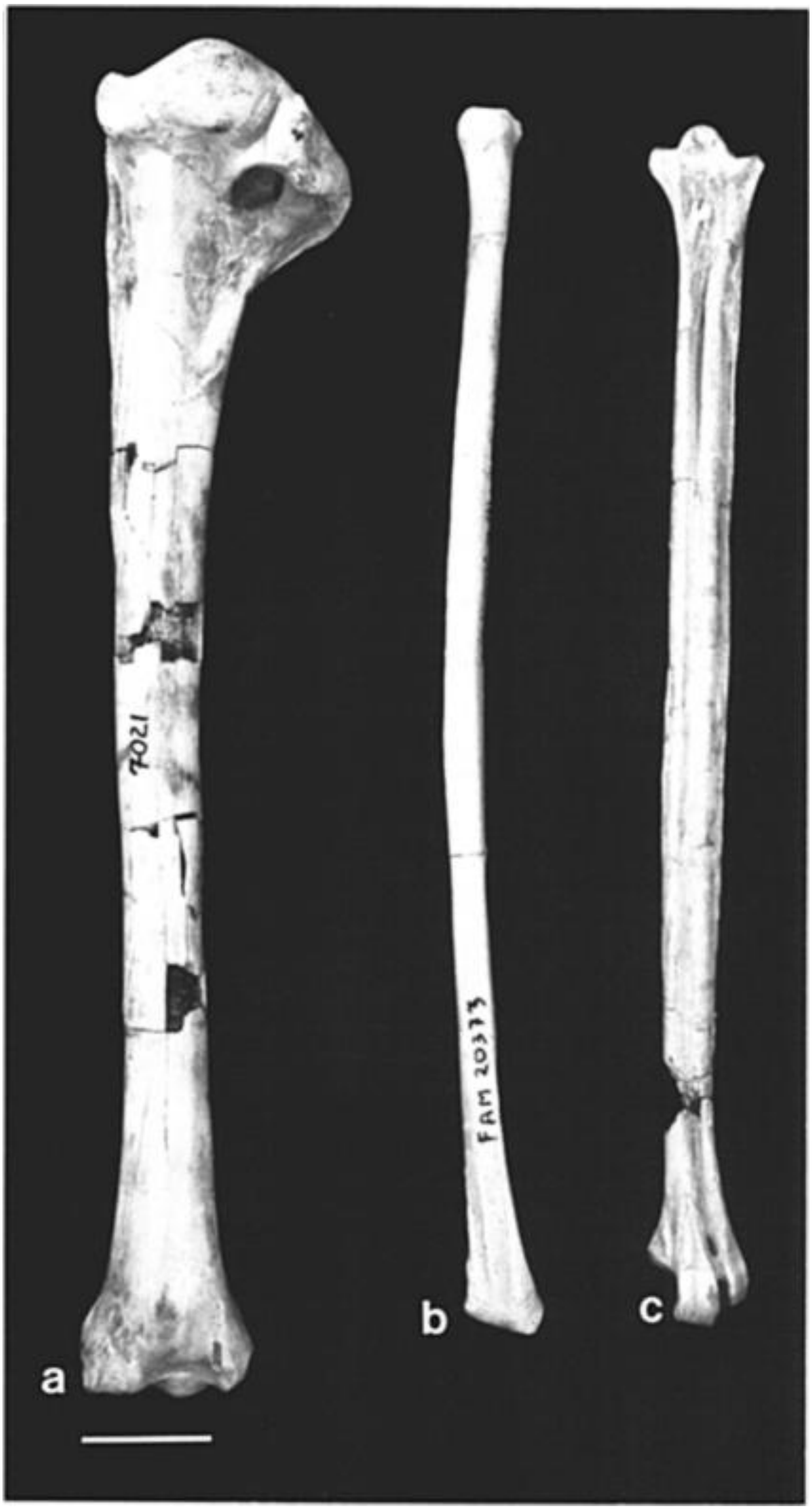
Measurements of holotype: see Table 1.

Paratypes: From Bird Bone Quarry: associated material F:AM 20017, including fragments of a furcula, a scapula, and a cervical vertebra, right humerus, right ulna, partial right radius; right coracoids F:AM 19985, 20264, USNM 407751; scapular end of right coracoid F:AM 7108; sternal ends of right coracoids F:AM 20268; left coracoids F:AM 19962, 19964, 19965, 19966; scapular end of left coracoid F:AM 7107; right humeri F:AM 7019, 7020, 7022, 7026, 7029, 19988; distal end of right humerus USNM 407757; left humerus F:AM 7028; proximal end of right ulna F:AM 19986; distal end of right ulna F:AM 20312; left ulnae F:AM 19911, 19912; proximal end of left ulna F:AM 20134; distal ends of left ulnae F:AM 19987, 20310; right radius F:AM 20373; proximal end of right radius F:AM 20372; distal end of right radius F:AM 20381; left radii F:AM 20020, 20375, 20376, 20377; proximal ends of right carpometacarpi F:AM 19955, 19956, 20208, 20473; distal end of right carpometacarpus F:AM 7080; left carpometacarpi F:AM 7068, 7070; distal end of left carpometacarpus F:AM 7066; distal right and left tibiotarsi (associated) F:AM 19973.

From Clay Bank Quarry: anterior end of right scapula F:AM 19982; sternal end of right coracoid F:AM 19963; distal end of right ulna F:AM 19913; distal end of left ulna F:AM 20313; proximal end of right radius F:AM 20380; right carpometacarpus, missing distal end, F:AM 7073; distal ends of right carpometacarpi F:AM 7062, 20470.

Additional Big Sandy Formation specimens: partial cranium F:AM 20607; partial pelvis F:AM 20588; anterior ends of right scapulae F:AM 19983, 20187; left femur F:AM 19971; left femur missing distal end F:AM 19972.

Measurements of paratypes: see Table 1.

Etymology: named for Mary Katherine Johns, a talented student of the geological sciences.


7021
FAM 20373
a
b
c

Diagnosis: In comparison with *Cygnus* (*Olor*) *cygnus buccinator* and *C.* (*Olor*) *columbianus, Cygnus mariae* has the humerus with (1) capital shaft ridge more pronounced, (2) ligamental furrow narrower and deeper, (3) impression of brachialis anticus shallower, not so broad at proximoexternal edge, and not so strongly outlined, and (4) area of attachment of M. scapulohumeralis cranialis rounded (oval in *C. buccinator,* pointed in *C. columbianus*).

Description: Scapula: Similar to extant *Olor. Coracoid:* Scapular facet deep and round, intermediate between extant species of *Olor* and of *Cygnus.* Groove of triosseal canal generally deeper than in extant *Olor. Humerus:* In addition to characters given above, more like species of *Cygnus* in having the impression for brachialis anticus not distinctly outlined (Woolfenden 1961: p. 9). *Ulna:* Similar to the ulna in extant *Olor. Radius:* Similar to the radius in extant swans (*Olor* and *Cygnus* not separable). *Carpometacarpus:* The Wikieup swan more closely resembles *Olor* than *Cygnus* in having the external crest of the trochlea larger and the lobe at its distal edge more developed (Woolfenden 1961). It more closely resembles *Cygnus* in having ". . . the process [of metacarpal I] inclining more definitely toward the inner side . . ."; in having ". . . the area below the pisiform process excavated into a distinct pitlike depression, the posterior rim of which is prominent."; and in having ". . . the cuneiform fossa . . . deeper, [with] a distinct proximal and medial rim." (Woolfenden 1961: p. 9). *Cygnus mariae* is further characterized by (1) having a very long intermetacarpal space: metacarpals II and III are separated much farther proximally than in any other swans, (2) having the internal rim of the carpal trochlea more evenly rounded, less pointed along the proximalmost edge, and (3) having the distance between the internal rim of the carpal trochlea and the pisiform process relatively less than in other swans. *Tibiotarsus:* similar to modern swans (*Olor* and *Cygnus* not separable).

The available specimens of the other skeletal elements (cranium, pelvis, femur) are too damaged for adequate comparison, although they clearly belong to a swan.

In the elements of the pectoral girdle and wing, *Cygnus mariae* is intermediate in size between living *Cygnus cygnus buccinator* and *C. columbianus.* The distal ends of tibiotarsi and referred femur are, however, smaller than in female *C. columbianus.*

Remarks: A number of species of swans have been described in extinct genera and in *Cygnus.* Those described in the extinct genera *Cygnopterus* and *Cygnavus* are quite distinct from modern swans (pers. obs.). *Paracygnopterus scotti* Harrison and Walker 1979 (Oligocene, England), if it is a swan at all, is extremely small. *Guguschia nailiae* Aslanova and Burchak-Abramovich 1968 (Oligocene, Azerbaidzhan) appears to be distinct from all modern swans. It was smaller than the Wikieup swan. *Cygnus herrenthalsi* (Van Beneden 1871a, b) (Miocene, Belgium) should be regarded as a *nomen dubium,* based as it is on a single pedal phalanx. *Cygnus pristinus* Kurochkin 1971 (Pliocene, Mongolia) appears to lack the groove in the triosseal canal of the coracoid; the other material of that species is inadequate

←

FIG. 3. a. *Cygnus mariae* sp. nov., holotype, left humerus F:AM 7021. b. *Cygnus mariae* sp. nov., paratypical right radius F:AM 20373. c. *Grus haydeni,* referred left tarsometatarsus F:AM 20858. Scale bar = 25 mm.

TABLE 1

Measurements (mm) of Holotype and Descriptive Statistics for Hypodigm of *Cygnus mariae* sp. nov., from the Late Miocene–Early Pliocene Big Sandy Formation, Mohave County, Arizona

Element		N	Min.	Max.	$\bar{X}$	s.d.
Coracoid						
HEAD-IDA		5	75.50	87.00	83.04	–
HEAD-SF		5	36.25	40.60	38.80	–
D-HEAD		5	9.25	11.20	10.40	–
W-SHAFT		4	11.95	13.40	12.40	–
Humerus	Holotype					
LENGTH	259	8	254	280	266	9
W-SHAFT	17.75	5	17.35	18.10	17.65	–
D-SHAFT	12.90	5	12.90	14.75	13.55	–
W-PROX	50.85	5	49.85	54.90	51.90	–
D-PROX	16.05	7	16.05	18.95	17.50	0.89
W-DIST	33.70	8	33.25	35.30	34.30	0.73
D-DIST	20.25	5	19.90	21.10	20.35	–
Ulna						
LENGTH		3	237	257	248	–
W-SHAFT		2	11.85	12.50	12.15	–
D-SHAFT		2	11.75	12.70	12.20	–
W-PROX		5	21.45	23.20	22.30	–
D-PROX		4	17.45	20.00	18.70	–
ECON		3	16.60	19.95	18.70	–
CPTB		5	18.90	21.00	19.70	–
Radius						
LENGTH		2	238	242	240	–
W-SHAFT		3	6.80	7.30	7.05	–
D-SHAFT		3	8.45	9.15	8.70	–
W-PROX		6	10.50	11.65	11.35	–
D-PROX		6	11.25	13.40	12.70	–
W-DIST		6	14.40	16.00	15.55	–
D-DIST		6	7.00	8.10	7.70	–
Carpometacarpus						
LENGTH		2	124.70	129.80	127.25	–
W-SHAFT		4	9.75	10.70	10.15	–
D-SHAFT		4	8.15	10.30	9.50	–
W-CARPAL		7	11.55	13.65	12.45	0.80
D-PROX		6	27.40	33.35	30.20	–
W-DIST		5	6.75	11.50	9.50	–
D-DIST		4	13.45	14.40	14.00	–
Tibiotarsus						
W-DIST-CR		2	22.5	22.8	22.65	–
D-ICON		1	13.30	–	–	–

for comparison. *Cygnus falconeri* Parker 1865 (Pleistocene, Malta) came from a much larger species than the Wikieup swan; Northcote (1982) has also recently shown it to have been flightless or nearly so. *Cygnus equitum* Bate 1916 (Pleistocene, Malta) appears actually to be a goose (Brodkorb 1964b). *Cygnus lacustris* (De Vis) 1906 (Pleistocene, Australia) and *Cygnus sumnerensis* (Forbes) 1890 (Quaternary, New Zealand), are both close to, or synonymous with, *Cygnus atratus*

(Millener 1981). Brodkorb (1958) described a swan, *Cygnus hibbardi*, from the early Pliocene of Idaho based on a tarsometatarsus missing the distal end and a referred femur missing the distal end. In his *Catalogue of Fossil Birds:* Part 2 (1964b), it appears as *Olor hibbardi* with no explanation for the changed genus. Brodkorb's type and referred specimen are not only incomplete, but so worn (judging from the illustrations) that I do not consider it possible to assign them to either the *Olor* or the *Cygnus* group. As noted above, the femur is scarcely different in the two groups, and I agree with Woolfenden's (1961) assessment that (p. 80) "... consistent criteria [to separate the two] of a qualitative nature are nonexistent." Thus, I regard *Cygnus hibbardi* as a swan of indeterminate affinities. In the collections of the Department of Paleobiology, Smithsonian Institution, there are several proximal ends of carpometacarpi and the distal end of a humerus from the Upper Pliocene near Hagerman, Idaho, that are referable to the subgenus *Cygnus*. If these bones and Brodkorb's *Cygnus hibbardi* belong to the same species, then that swan cannot be closely related to *C.* (*Olor*) *mariae.*

Other swans named from North America include *Cygnus paloregonus* Cope 1878 (Pleistocene, Oregon), which is based on most of the elements of the skeleton and belongs with the *Cygnus* group; and *Paracygnus plattensis* Short 1969 (late Miocene, Nebraska), based on the humeral end of a coracoid. Like *Cygnus mariae, Paracygnus plattensis* has a deep depression in the triosseal canal, but this is shaped differently from *Cygnus mariae,* which also differs in having the head of the coracoid wider, viewed internally, and in having the furcular facet undercut for its entire length.

There seem to have been three lineages of swans in the Miocene, Pliocene, and Pleistocene of North America. Two of these, as represented by *Cygnus paloregonus* and *Paracygnus plattensis* are now extinct on this continent; the third, the subgenus *Olor,* as represented by *Cygnus mariae,* survives in *Cygnus buccinator* and *Cygnus columbianus.*

Genus *Anser* Brisson 1760

Remarks: The genus is best characterized by the following characters: (1) coracoid with furcular facet undercut only at brachial tuberosity (completely undercut in *Branta*), (2) humerus with impression for external head of triceps indistinctly bordered (distinctly bordered in *Branta*), (3) sternum with ventral manubrial spine rounded (flattened laterally in *Branta*), (4) bill long (short in *Branta*), mandibular symphysis small and narrow (larger and broader in *Branta*).

Anser arenosus sp. nov.

Fig. 4

Holotype: right coracoid F:AM 18030. Collected in 1939 by Guy E. Hazen.

Type locality: Bird Bone Quarry, SW¼, NE¼, sect. 29, T. 15N, R. 12W, Greenwood Peak Quadrangle, Mohave County, Arizona.

Horizon and age: Big Sandy Formation, late Hemphillian, late Miocene. Dated (fission-track, zircon) at 5.12–5.29 mybp.

Measurements of holotype: see Table 2.

Paratypes: From Bird Bone Quarry: anterior end of left scapula F:AM 20536; right coracoids F:AM 18028, 18029, 18030, 18032; partial scapular end of right coracoid F:AM 20306; left coracoids F:AM 18031, 19967; scapular end of left

FIG. 4. Paratypes of *Anser arenosus* sp. nov. a. Left humerus F:AM 19777. b. Anterior end of left scapula F:AM 20536. c. Left coracoid F:AM 18031. d. Left radius F:AM 20311. e. Proximal end of left ulna F:AM 20311. f. Distal end of left ulna F:AM 19915. g. Right carpometacarpus F:AM 20210.

coracoid F:AM 20269; right humeri F:AM 19775, 19776, 20220; distal end of right humerus F:AM 19817; left humerus F:AM 19777; proximal end of left ulna and distal end of left ulna F:AM 19915; proximal end of left ulna and left radius F:AM 20311; right radius F:AM 20019; left radius F:AM 20384; right carpometacarpi F:AM 20210, 20212; proximal end of right carpometacarpus F:AM 20211; distal end of right carpometacarpus F:AM 19928; left carpometacarpi F:AM 20204, 20209; right first phalanges of second digit (carpometacarpus) F:AM 20172, 20174; left femur F:AM 18026.

TABLE 2

MEASUREMENTS (MM) OF HOLOTYPE AND DESCRIPTIVE STATISTICS FOR HYPODIGM OF *Anser arenosus* SP. NOV., FROM THE LATE MIOCENE–EARLY PLIOCENE BIG SANDY FORMATION, MOHAVE COUNTY, ARIZONA

Element		N	Min.	Max.	X̄
Scapula					
W-NECK		1	8.65	—	—
W-PROX		1	17.35	—	—
Coracoid	Holotype				
HEAD-IDA	72.70	5	71.00	76.25	72.90
HEAD-SF	30.80	6	30.10	32.40	31.15
D-HEAD	9.00	6	7.70	9.30	8.60
W-SHAFT	10.70	5	9.15	10.70	9.85
Humerus					
LENGTH		3	175	180	177
W-SHAFT		4	11.85	13.10	12.50
D-SHAFT		4	10.70	12.50	11.80
W-PROX		3	36.60	37.75	37.25
D-PROX		4	13.00	14.65	13.60
W-DIST		4	24.35	26.85	25.40
D-DIST		4	14.60	16.20	15.25
Ulna					
W-PROX		1	17.35	—	—
D-PROX		1	14.85	—	—
ECON		2	14.90	15.30	15.10
CPTB		2	15.00	15.25	15.10
Radius					
LENGTH		3	158.85	160.85	160.10
W-SHAFT		3	4.80	5.45	5.10
D-SHAFT		3	6.05	6.40	6.20
W-PROX		3	8.80	9.45	9.20
D-PROX		3	10.15	10.90	10.55
W-DIST		3	6.50	7.30	6.70
D-DIST		3	6.45	7.40	6.95
Carpometacarpus					
LENGTH		4	90.70	101.00	97.75
W-SHAFT		4	7.35	8.15	7.70
D-SHAFT		4	8.00	8.50	8.20
W-CARPAL		4	10.35	10.85	10.60
D-PROX		4	22.75	25.20	23.65
W-DIST		5	8.75	9.65	9.20
D-DIST		5	11.05	12.25	11.70
Femur					
W-SHAFT		1	8.70	—	—
D-SHAFT		1	8.70	—	—
W-PROX		1	20.60	—	—

From Clay Bank Quarry: distal end of right ulna F:AM 20315; distal end of left ulna F:AM 11297; proximal end of right carpometacarpus F:AM 20214.

From 400 ft west of Bird Bone Quarry: distal end of right humerus F:AM 19818.

Measurements of paratypes: see Table 2.

Etymology: arenosus, Latin for "sandy," in reference to the Big Sandy Formation.

Diagnosis: coracoid with (1) anterior half of the furcular facet deeply depressed toward the shaft, (2) pneumatic fossae underlying the brachial tuberosity separated by a distinct bony strut from the depression in the triosseal canal between the procoracoid and the brachial tuberosity.

Description: Scapula: The scapulae assigned to this species have a relatively undeveloped pneumatic foramen in the humeral end. Otherwise they are similar to the scapulae of extant *Anser* and *Branta* (which have a large foramen). *Coracoid:* Most individuals of the extant species of *Anser* examined have a very slight depression on the anterior half of the furcular facet (character 1, above), but it is far less deep and strongly bordered than in the fossils. This depression is found in all of the species of Tadornini, subfamily Anatinae, except *Cereopsis*; the depression is most similar in extent and shape to the Wikieup *Anser* in the genus *Tadorna.* All living geese have pneumatic fossae underlying the brachial tuberosity, that tend to be continuous with the depression in the triosseal canal, rather than separated by a bony strut as in the fossil. Some of the tadornines (*Alopochen, Neochen*) also have fossae under the brachial tuberosity. *Humerus:* The fossil humeri resemble extant *Anser* in all respects except for having a somewhat deeper, narrower, and longer brachial depression. *Ulna and radius:* Similar to extant geese (*Anser* and *Branta* not separable). *Carpometacarpus:* Similar to extant *Anser,* but with (1) the internal ligamental fossa deeper and (2) the fossa distal to the pisiform process deeper. *Femur:* Similar to modern geese but with a distinct groove running from the proximal end of the obturator ridge to the head where the head joins the neck. A slight tendency toward this condition is seen in the living *A. caerulescens* and *A. rossi.*

Remarks: Fossil geese are reviewed below in the descriptions of two new species of *Anser* and *Branta. Anser arenosus* is not conspecific with any of the previously named species.

Anser arizonae sp. nov.

Fig. 5

Holotype: partial associated skeleton F:AM 18000, including: cranium, rostrum, right and left mandibles, right and left quadrates, several cervical and thoracic vertebrae, rib fragments, sternum, furcula, pelvis, right and left scapulae, right and left coracoids, right and left humeri, right ulna missing middle section, left ulna, right radius lacking distal end, left radius, fragments of right carpometacarpus, left carpometacarpus, right digit 2 phalanx 1. Collected in 1939 by Guy E. Hazen.

Type locality: Bird Bone Quarry: SW¼, NE¼, sect. 29, T. 15N, R. 12W, Greenwood Peak Quadrangle, Mohave County, Arizona.

Horizon and age: Big Sandy Formation, late Hemphillian, late Miocene. Dated (fission-track, zircon) at 5.12–5.29 mybp.

Measurements of holotype: see Table 3.

Paratypes: From Bird Bone Quarry: anterior ends of right scapulae F:AM 20534, 20535; right coracoids F:AM 19979, 19981, 20029, 20034, 20270; sternal ends of right coracoids F:AM 20112, 20887; left coracoids F:AM 19976, 19977; scapular end of left coracoid F:AM 20110; sternal end of left coracoid F:AM 20274;

FIG. 5.1. Parts of the holotype of *Anser arizonae* sp. nov., F:AM 18000. a. Cranium and rostrum. b. Mandible. Scale bar = 10 mm.

right humeri F:AM 18050, 19778; distal end of right humerus USNM 407768; left humerus F:AM 18043; right ulna F:AM 19914; proximal end of left ulna USNM 407769; right radii F:AM 20018, 20169; distal end of right carpometacarpus F:AM 20468; left carpometacarpi F:AM 20205, 20206; left first phalanx of second digit (carpometacarpus) F:AM 20173; right femur F:AM 18025; left femora F:AM 20002, 20657; proximal end of left femur F:AM 20658.

From Clay Bank Quarry: associated material F:AM 20200, including: several vertebrae, rib scraps, anterior end of right scapula, posterior end of left scapula, proximal ends of right and left humeri, distal end of left humerus, distal end of left ulna, left carpometacarpus; sternum, F:AM 20562; furcula, missing ends of each clavicle, F:AM 18027; sternal end of right coracoid F:AM 20038; sternal end of left coracoid F:AM 20040; scapular end of left coracoid F:AM 20068; proximal end of right humerus F:AM 19946; distal end of left ulna F:AM 20122; proximal end of left radius F:AM 20386; proximal end of left carpometacarpus F:AM 20215.

Additional Big Sandy Formation specimens: anterior ends of sterna F:AM 20563, 20572, 20573, 20577; coracoidal ends of furculae F:AM 20546, 20547; partial pelves F:AM 20589, 20590, 20599; left tarsometatarsus F:AM 19991.

Measurements of paratypes: see Table 3.

Etymology: In reference to Arizona, the state from which the new species is known.

Diagnosis and description: Skull: Nares narrower, more elongate than in modern

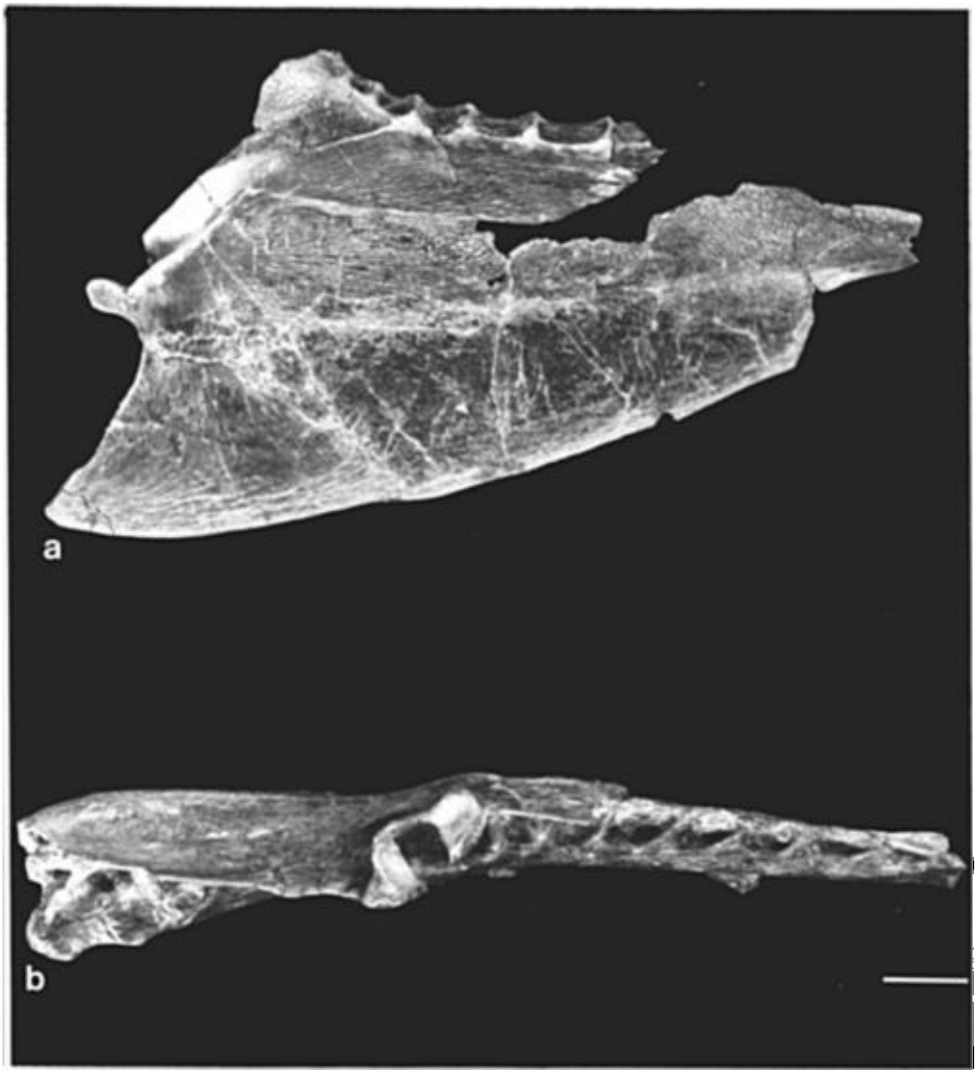


FIG. 5.2 Parts of the holotype of *Anser arizonae* sp. nov., F:AM 18000. a. Sternum. b. Pelvis. Scale bar = 10 mm.

species of *Anser,* tomial edges of upper mandible straight rather than concave, but bill still much more similar to the *Anser* type than to the *Branta* type. *Mandible:* Compared to modern species of *Anser,* surangular low, dentaries straight and shallow; symphysis larger and broader, more like *Branta* in this respect. *Vertebrae:* Similar to modern *Anser. Furcula:* Similar to modern *Anser. Sternum:* Quite distinct from extant species of both *Anser* and *Branta*: relatively long, with the carinal apex projecting far forward of the ventral manubrial spine and the carina itself shallower anteriorly, but deeper posteriorly, than in modern geese. Ventral manubrial spine a knob, as in *Anser,* rather than a laterally flattened plate, as in *Branta. Pelvis:* Similar to modern *Anser. Scapula:* As in *Anser arenosus* above,

FIG. 5.3. Parts of the holotype of *Anser arizonae* sp. nov., F:AM 18000. a. Furcula. b. Left and right scapulae. c. Left and right coracoids. Scale bar = 20 mm.

this species has the pneumatic fossa of the scapula less developed than in modern geese. *Coracoid:* The coracoid of this species has a depression in the furcular facet that is far less pronounced than in *Anser arenosus,* but still deeper and more distinct than in extant *Anser.* The coracoid also has a notch between the depression of the furcular facet and the brachial tuberosity. These features are quite similar to the depression and notch in *Tadorna,* but the coracoid is clearly that of a goose by Woolfenden's (1961) characters. The depression in the triosseal canal is not as deep as that in *Anser arenosus,* but as in that species, there is a separation between the triosseal canal depression and the pneumatic fossae that undercut the brachial tuberosity. *Humerus:* Resembles extant *Anser* but with (1) external tuberosity/pectoral attachment relatively large, and (2) internal tuberosity more squared, less triangular in outline (viewed from the side), and longer, projecting farther beyond the head. *Ulna:* Similar to modern *Anser. Radius:* Similar to modern *Anser. Carpometacarpus:* As in *Anser arenosus,* similar to modern *Anser* but with fossa distal to pisiform process slightly deeper and longer. *Alar phalanges:* Similar to modern *Anser. Femur:* As in extant geese, but with ridge on proximal end that borders trochanter more developed. *Tarsometatarsus:* A single tarsometatarsus is only tentatively referred to this species because of its poor preservation and because, although from an anatid, and of a length not improbable for this species, it is unusually stout, casting doubt on its generic affinities.

Remarks: A number of extinct species of geese have been named in the genera *Anser* and *Branta,* and several in allied extinct genera. All are dissimilar in size or proportions to either *Anser arenosus* or *Anser arizonae.* Those from the Miocene include *Presbychen abavus* Wetmore 1930 (California), larger than any of the

FIG. 5.4. Holotypical left and right humeri of *Anser arizonae* sp. nov., F:AM 18000. Scale bar = 20 mm.

FIG. 5.5. Parts of the holotype of *Anser arizonae* sp. nov., F:AM 18000. a. Left carpometacarpus. b. Right digit II, phalanx I of carpometacarpus. c. Proximal ¾ of right radius. d. Left radius. e. Left ulna. f. Right ulna. Scale bar = 20 mm.

TABLE 3

MEASUREMENTS (MM) OF HOLOTYPE AND DESCRIPTIVE STATISTICS FOR HYPODIGM OF *Anser arizonae* SP. NOV., FROM THE LATE MIOCENE–EARLY PLIOCENE BIG SANDY FORMATION, MOHAVE COUNTY, ARIZONA

Element		N	Min.	Max.	X̄	s.d.
Scapula	Holotype (r/l)					
W-NECK	8.50/8.20	5	7.90	8.50	8.20	–
W-PROX	14.65/15.00	3	14.55	15.00	14.75	–
Coracoid						
HEAD-IDA	69.05/67.90	7	63.00	70.20	66.50	2.44
HEAD-SF	27.95/28.05	6	26.60	29.55	28.00	–
D-HEAD	7.50/6.95	7	6.75	8.00	7.25	0.38
W-SHAFT	9.85/9.15	8	8.70	9.85	9.35	0.35
Humerus						
LENGTH	161.75/162.25	5	151.35	163.70	158.50	–
W-SHAFT	11.80	3	11.40	11.80	11.55	–
D-SHAFT	9.45	3	9.15	9.90	9.50	–
W-PROX	34.30/30.95	8	30.95	35.70	33.15	1.54
D-PROX	11.75/11.80	8	10.55	12.70	11.95	0.59
W-DIST	23.25/23.20	7	22.85	23.65	23.30	0.23
D-DIST	14.55/13.65	7	13.00	14.75	14.10	0.55
Ulna						
LENGTH	153.25	2	150.65	153.25	151.95	–
W-SHAFT	8.45/8.75	2	8.45	8.75	8.60	–
D-SHAFT	8.50/8.40	2	8.40	8.50	8.45	–
W-PROX	15.45/15.85	3	15.30	15.85	15.55	–
D-PROX	13.00/12.75	3	12.75	13.05	12.95	–
ECON	13.95/13.30	2	13.30	13.95	13.65	–
CPTB	13.50/13.90	2	13.50	13.90	13.70	–
Radius						
LENGTH	144.55	3	142.00	147.05	144.55	–
W-SHAFT	5.10/4.90	3	4.90	5.15	5.05	–
D-SHAFT	6.05/5.60	3	5.55	6.05	5.75	–
W-PROX	8.05/8.05	4	8.05	8.35	8.15	–
D-PROX	9.45/9.05	4	9.05	9.75	9.40	–
W-DIST	10.35	3	10.35	11.20	10.80	–
D-DIST	5.80	3	5.65	6.40	5.95	–
Carpometacarpus						
LENGTH	89.05	4	83.70	89.05	85.85	–
W-SHAFT	7.00	4	6.80	7.30	7.00	–
D-SHAFT	7.36	4	7.30	7.70	7.45	–
W-CARPAL	8.85	5	8.65	9.20	8.90	–
D-PROX	22.00	5	20.70	22.00	21.20	–
W-DIST	8.15/8.10	6	7.90	8.25	8.10	–
D-DIST	10.85/10.30	6	10.10	10.85	10.45	–
Furcula						
LENGTH	60.40	1	–	–	–	–
D-PROX	7.65	2	7.65	8.15	7.90	–
Femur						
LENGTH		2	75.65	79.20	77.40	–
W-SHAFT		2	8.35	8.75	8.55	–
D-SHAFT		1	–	–	–	–
W-PROX		3	17.00	19.50	18.25	–
W-DIST		2	17.55	17.75	17.65	–

TABLE 3
CONTINUED

Element		N	Min.	Max.	X̄	s.d.
Cranium	Holotype					
LENGTH	63.5	1	–	–	–	–
INT-ORB	9.9	1	–	–	–	–
Rostrum						
LENGTH	61.2	1	–	–	–	–
ANT-LENGTH	29.90	1	–	–	–	–
W-NARES	5.50	1	–	–	–	–
L-NARES	22.40	1	–	–	–	–
WIDTH	17.3	1	–	–	–	–
DEPTH	23.5	1	–	–	–	–
Mandible						
LENGTH	112.50	1	–	–	–	–
L-SYMPH	11.95	1	–	–	–	–
W-SYMPH	14.00	1	–	–	–	–
D-SUR	10.60	1	–	–	–	–
Sternum						
D-CARINA	31.90	2	31.90	31.90	31.90	–
VMS-COST	49.70	1	–	–	–	–
Pelvis						
L-SYNSAC	124.23	1	–	–	–	–
L-ANT	49.75	1	–	–	–	–
W-TROCH	47.20	2	35.70	47.20	41.45	–

Wikieup geese; *Anser scaldii* (Van Beneden 1871a, b) (Belgium), smaller than any of the geese from the Big Sandy Formation; and *Anser atavus* (Fraas) 1870 (Germany), *Anser cygniformis* (Fraas) 1870 (Germany), and *Anser oeningensis* (Von Meyer) 1865 (Switzerland), all birds with unusually stout limb proportions. *Eremochen russelli* Brodkorb 1961 (Oregon) was quite different in the shape of the head of the humerus and, as in the Wikieup *Branta,* lacks the pneumatic foramen of the scapula. *Branta esmeralda* Burt 1929 (Nevada) is correctly assigned to that genus. The generic assignment of *Branta howardae* L. Miller 1930 (California), based on the distal end of a carpometacarpus, is questionable, but in any case it differs from the various Wikieup geese in shapes of the facets for digits II and III.

Quite a few species have been named from the Pliocene, many in recent years from Mongolia. These Pliocene geese include the following forms. *Anser eldaricus* Burchak-Abramovich and Gadzyev 1978 (Georgia, USSR), was larger than all extant geese and, thus, the Wikieup birds. *Anser devjatkini* Kurochkin 1971 (Mongolia), was about the size of *Anser arizonae,* but is based only on the distal end of a tibiotarsus which is an insufficient piece of the skeleton for diagnosis. *Anser tchikoicus* Kurochkin 1985 (Mongolia), was intermediate in size between the two Wikieup species of *Anser,* and also differs in the shapes of the articular surfaces of the carpometacarpus. *Anser liskunae* Kurochkin 1976 (Mongolia) was the same size as *Anser arizonae,* but is based on undiagnostic material, an abraded left humerus. *Anser udabnensis* Burchak-Abramovich 1957 (Mongolia), based on the proximal end of an ulna, is also indeterminate. *Anser pressus* (Wetmore) (1933), from the Pliocene of Idaho, was smaller in size than either of the Wikieup *Anser* and larger than the Wikieup *Branta*, differing also in the shape of the popliteal area of the distal end of the holotypical femur. *Anser thompsoni* Martin and Mengel 1980, from the Pliocene of Nebraska, was about the same size as *Anser arizonae*, and is the only extinct goose besides the Wikieup species that is based on truly diagnostic material, a nearly complete, although crushed, skeleton. It differs from *Anser arizonae* and *Anser arenosus* in the following characters: (1) furcula disproportionately small, (2) coracoid with less depression of the furcular facet, no separation of groove in triosseal canal from pneumatic fossa under brachial tuberosity; (3) humerus with impression of M. brachialis anticus markedly elongate and parallel with the shaft; (4) skull with bill relatively short; and (5) carpometacarpus with process of metacarpal I longer and narrower. It is interesting that, as in the Wikieup geese, *Anser thompsoni* had the pneumatic foramen of the scapula relatively very small in comparison to modern geese.

From the Pleistocene are the following species. *Anser azerbaidzhanicus* Serebrovsky 1940 (Azerbaidzhan, USSR), is based on a cranium that appears to have been about 1½ times larger than in extant geese. *Anser equitum* (Bate) 1916 (Malta) had very stout wing bones and apparently reduced powers of flight. *Anserobranta tarabukini* Kurochkin and Ganya 1972 (Moldavia, USSR) has as a type an obviously pathological proximal end of a carpometacarpus; the other specimens are so worn as to be undiagnostic. *Branta dickeyi* L. Miller 1924 (California) was huge, the size of *Cygnus columbianus*. *Branta propinqua* Shufeldt 1892 (Oregon) was smaller than any of the Wikieup geese.

Genus *Branta* Scopoli 1769

Remarks: The genus is best characterized in the post-cranial skeleton by the following characters that are found in the following species: (1) coracoid with entire furcular facet undercut, and (2) humerus with impression of external head of triceps distinctly bordered.

Branta woolfendeni sp. nov.
Fig. 6

Holotype: right tarsometatarsus F:AM 20888. Collected in 1976 by Pat V. Rich.

Type locality: Bird Bone Quarry, SW¼, NE¼, sect. 29, T. 15N, R. 12W, Greenwood Peak Quadrangle, Mohave County, Arizona.

Horizon and age: Big Sandy Formation, late Hemphillian, late Miocene. Dated (fission-track, zircon) at 5.12–5.29 mybp.

Measurements of holotype: see Table 4.

Paratypes: From Bird Bone Quarry: associated material F:AM 20889, including: sternum fragment, furcula, right and left scapulae, left coracoid, right and left humeri, distal end of right ulna, left ulna, proximal end of right radius, left femur; associated material F:AM 20202, including: sternal fragments, part of head of left humerus, distal end of left humerus and part of shaft, right ulna missing center section of shaft, right carpometacarpus; associated material F:AM 20325, including: distal end of right ulna, proximal end of right carpometacarpus; furculae F:AM 20550, 20552; associated material F:AM 20681, including: distal end of right tibiotarsus, distal end of right tarsometatarsus; associated material F:AM 20887, including: nearly complete furcula, radius without distal end; anterior ends of right and left scapulae F:AM 20189, 20880 (part); anterior end of right scapulae F:AM 20197, 20219, 20520; anterior ends of left scapulae F:AM 20196, 20198, 20199, 20524, 20526, 20528, USNM 407770, 407771, 407772, 407773; right coracoids F:AM 19889, 20021, 20028, 20030, 20031, 20032, 20033, 20048, 20049, 20050, 20051, 20053, 20054; scapular end of right coracoid F:AM 19980; left coracoids F:AM 20022, 20023, 20024, 20028, 20043, 20044, 20045, 20046, 20047, 20059; scapular ends of left coracoids USNM 407774, 407775; right humeri F:AM 18045, 18048, 18049, 18051, 19781; proximal end of right humerus F:AM 19920; distal ends of right humeri F:AM 19784, 19918, USNM 407776; left humeri F:AM 18046, 18047, 18052, 18053, 18054, 18055, 18056, 19779, 19780, 19782, 19783, 19786, 19790, 20203; distal ends of left humeri F:AM 20102, 20259; fragments of proximal and distal ends of left humerus F:AM 20268; right ulnae F:AM 18038, 18042, 20127, 20128, 20129, 20130, 20141, 20143; proximal end of right ulna F:AM 20131; left ulnae F:AM 18036, 18037, 18039, 18040, 18041, 20123, 20124, 20125, 20132, 20135, 20143, 20330; proximal end of left ulna F:AM 20327; distal ends of left ulnae F:AM 20121, 20126, 20145, 20322, 20339; right radii F:AM 20389, 20392, 20393, 20409; proximal and distal ends of right radius F:AM 20406; proximal ends of right radii F:AM 20407, 20414; distal ends of right radii F:AM 20408, USNM 407777; left radii F:AM 18034, 18035, 20390; proximal ends of left radii F:AM 20410, 20422; distal end of left radius F:AM 20402, USNM 407778; right carpometacarpi F:AM 19870, 19872, 19873, 19877, 19878, 19879, 19880, 19881, 19882, 19883, 19884, 19885, 19886, 19887, 19904, 19905, 19906, 19910, 19929, 20052, 20117, 20472; proximal ends of right carpometacarpi F:AM 19957, 20469, USNM 407779; distal ends of right carpometacarpi F:AM 20171, 20460, 20464, 20465, 20466; left carpometacarpi F:AM 19869, 19888, 19890, 19895, 19896, 19897, 19898, 19899, 19900, 19901, 19902, 19908, 19989; partial left carpometacarpus 20207; proximal ends of left carpometacarpi F:AM 18017, 19958, 20113, USNM 407780; distal ends of left carpometacarpi F:AM 19814, 19891; right first phalanges of second digit (carpometacarpus) F:AM 20178, 20179, 20180, 20182, 20183, 20185; left first phalanx of second digit (carpometacarpus) F:AM 20181; right femora F:AM 20664, 20667; proximal end of right femur F:AM 20675; left femora F:AM 20003, 20004, 20661, 20662, 20665, 20666; distal end of left femur F:AM 20674; right tibiotarsus F:AM 20009; distal end of right tibiotarsus F:AM 18016; left tibiotarsi F:AM 18001, 18002, 18003, 18004; right tarsometatarsi F:AM 18005, 18006, 18008; proximal end of right tarsometatarsus USNM 407781; distal end of right tarsometatarsus F:AM 19996; left tarsometatarsi F:AM 18007, 18033.

From Clay Bank Quarry: anterior end of right scapula F:AM 20525; anterior ends of left scapulae F:AM 20193, 20194, 20195, 20217; right coracoids F:AM 19978, 20026, 20027; scapular ends of right coracoids F:AM 20037, 20039, 20041, 20271; left coracoids F:AM 20036, 20042; scapular end of left coracoid F:AM 20035; proximal ends of right humeri F:AM 19916, 19947, 19948, 20252; distal ends of right humeri F:AM 19820, 19821, 19951, 19952, 19953; left humerus F:AM 18044; proximal ends of left humeri F:AM 19816, 19917; distal ends of left humeri F:AM 19923, 20254; proximal ends of right ulnae F:AM 20138, 20139, 20140; distal ends of right ulnae F:AM 20144, 20147, 20336; proximal ends of left ulnae F:AM 20137, 20326; distal ends of left ulnae F:AM

FIG. 6.1. Paratype specimens of *Branta woolfendeni* sp. nov. Associated material F:AM 20889. a. Left femur. b. Furcula. c. Left and right scapulae. d. Proximal end of right radius. e. Left ulna and distal end of right ulna. f. Left and right humeri. Scale bar = 10 mm.

20145, 20146; proximal ends of right radius F:AM 20416; proximal ends of left radii F:AM 20395, 20399; distal ends of left radii F:AM 20396, 20397; right carpometacarpus F:AM 19876; proximal ends of right carpometacarpi F:AM 19903, 19931; distal ends of right carpometacarpi F:AM 19874, 20467; left carpometacarpus F:AM 19892; proximal ends of left carpometacarpi F:AM 18017, 19894, 19930; distal ends of left carpometacarpi F:AM 19893, 19934, 20213; right first phalanx of second digit (carpometacarpus) F:AM 20176; left first phalanx of second digit (carpometacarpus) F:AM 20177; right femur F:AM 20007; proximal ends of right femora F:AM 20670, 20671; distal ends of right femora F:AM 20672, 20673; left femur F:AM 20660; left femur missing part of distal end F:AM 20668; proximal end of left femur F:AM 20669; distal ends of left femora F:AM 20659, 20663; proximal end of right tibiotarsus F:AM 20013; distal ends of right tibiotarsi F:AM 18015, 20014, 20713; distal ends of left tibiotarsi F:AM 18012, 18013, 18014; proximal ends of right tarsometatarsi F:AM 19922, 19994; distal ends of right tarsometatarsi F:AM 18009, 18021, 18023; proximal end of left tarsometatarsus F:AM 19993; distal ends of left tarsometatarsi F:AM 10381, 18010, 19997.

From between Bird Bone Quarry and Clay Bank Quarry: anterior end of right scapula F:AM 20188; left coracoid F:AM 20055; left ulna F:AM 20319. From Big Sandy Formation, quarry unknown: distal end of left ulna F:AM 20322.

Additional Big Sandy Formation specimens: partial crania F:AM 20600, 20601, 20602, 20604; carina of sternum F:AM 20554.

FIG. 6.2 Holotype and paratype specimens of *Branta woolfendeni* sp. nov. a. Right tarsometatarsus, holotype, F:AM 20888. b. Right femur, paratype, F:AM 20664. c. Left carpometacarpus, paratype, F:AM 19895. d. Right radius, paratype, F:AM 20389. e. Left tibiotarsus, paratype, F:AM 18001.

Measurements of paratypes: see Table 4.

Etymology: Named for Dr. Glen E. Woolfenden, in recognition of his outstanding contribution to our knowledge of the postcranial anatomy and the relationships of waterfowl.

Diagnosis: The tarsometatarsus of this species may easily be distinguished from that of all other anatids by the following combination of characters: (1) very long and slender, (2) trochleae laterally compressed rather than spread, (3) trochlea for digit II long (length parallel to shaft), and (4) median ridge of trochlea for digit II reaching the level of the proximal end of the facet for digit III on trochlea III, not extending past it.

All four of these characters (which are from Woolfenden 1961) distinguish the tarsometatarsus of this species from those of geese and swans. Characters 1, 3, and 4 distinguish it from the non-diving ducks, and character 1 from the divers.

TABLE 4

MEASUREMENTS (MM) OF HOLOTYPE AND DESCRIPTIVE STATISTICS FOR HYPODIGM OF *Branta woolfendeni* SP. NOV., FROM THE LATE MIOCENE–EARLY PLIOCENE BIG SANDY FORMATION, MOHAVE COUNTY, ARIZONA

Element	N	Min.	Max.	$\bar{x}$	s.d.
Scapula					
W-NECK	11	5.85	12.10	8.05	2.07
W-PROX	18	10.30	13.00	11.65	0.78
Coracoid					
HEAD-IDA	22	54.25	61.40	56.90	1.72
HEAD-SF	32	20.35	24.40	22.85	0.98
D-HEAD	31	5.10	6.55	5.95	0.29
W-SHAFT	27	6.85	8.75	7.80	0.48
Humerus					
LENGTH	16	123.80	151.45	141.15	8.42
W-SHAFT	11	8.60	10.00	9.15	0.45
D-SHAFT	9	6.95	7.55	7.15	0.19
W-PROX	23	25.00	29.80	27.45	1.48
D-PROX	26	8.90	10.75	9.75	0.53
W-DIST	34	16.85	20.90	18.75	1.02
D-DIST	28	10.05	12.15	11.05	0.55
Ulna					
LENGTH	19	118.95	135.15	128.00	5.87
W-SHAFT	11	6.30	7.80	6.85	0.38
D-SHAFT	11	6.70	8.00	7.05	0.37
W-PROX	23	11.85	13.20	12.55	0.35
D-PROX	26	9.55	12.10	10.60	0.56
ECON	25	8.90	11.20	10.35	0.54
CPTB	25	9.70	11.95	10.63	0.55
Radius					
LENGTH	4	120.05	127.90	122.15	—
W-SHAFT	4	3.85	4.55	4.15	—
D-SHAFT	4	4.05	4.70	4.25	—
W-CARPAL	14	5.80	6.60	6.20	0.22
D-PROX	14	6.40	7.75	7.25	0.23
W-DIST	13	8.15	9.15	8.60	0.35
D-DIST	13	4.30	5.50	4.85	0.27
Carpometacarpus					
LENGTH	33	68.20	81.05	73.80	3.34
W-SHAFT	29	4.20	6.40	5.15	0.51
D-SHAFT	30	4.85	6.05	5.65	0.26
W-CARPAL	49	6.30	8.90	7.10	0.46
D-PROX	40	15.20	17.75	16.40	0.76
W-DIST	30	6.05	7.40	6.60	0.31
D-DIST	29	8.10	9.60	8.80	0.42
Furcula					
LENGTH	2	45.65	55.00	50.30	—
D-PROX	4	5.15	6.20	5.85	—
Femur					
LENGTH	5	58.65	63.50	60.80	—
W-SHAFT	5	5.55	6.05	5.86	—
D-SHAFT	5	5.65	6.60	6.15	—
W-PROX	12	8.00	9.95	8.70	0.58
W-DIST	7	12.25	14.35	13.25	0.65

TABLE 4
CONTINUED

Element		N	Min.	Max.	X̄	s.d.
Tibiotarsus						
LENGTH		4	117.30	135.65	124.30	—
W-SHAFT		1	6.80	—	—	—
D-SHAFT		1	4.90	—	—	—
W-PROX-M		3	10.90	11.75	11.30	—
W-DIST-CR		8	11.45	12.70	12.05	0.41
D-ICON		11	6.15	8.90	7.30	0.66
Tarsometatarsus	Holotype					
LENGTH	75.85	5	70.80	79.90	76.45	—
W-SHAFT	5.10	5	4.65	5.15	4.87	—
D-SHAFT	5.70	5	5.20	6.30	5.75	—
W-PROX	12.90	7	12.15	13.45	13.05	0.41
D-PROX	8.55	4	8.25	8.55	8.28	—
TRII-TRIV	11.85	9	11.30	13.05	11.90	0.46

In characters 3 and 4 it closely resembles the diving ducks. Diving ducks vary in character 2, the spread of the trochleae, with the eiders having the trochleae spread. In addition to these distinguishing characters, the tarsometatarsus has the depression below the head on the anterior side (containing the inner and outer proximal foramina) deep, as is the outer extensor groove.

Description: Scapula: The scapula of this species of *Branta* completely lacks the pneumatic fossa found in all modern species of geese in the humeral end of the scapula. Because of the reduced pneumatic fossae in the scapulae of the species of *Anser* discussed above, the large pneumatic fossa in the scapulae of modern geese has probably developed within the past five million years. Steadman (1980) noted the similar development of a pneumatic fossa in the scapula in fossil turkeys during the Pleistocene. *Coracoid:* All of the fossil specimens have a slight depression in the furcular facet. This is also found in extant *Branta,* but does not occur with regularity in all individuals of a particular species, and the size and shape within a species are not as consistent as in the fossils. *Humerus, ulna, and radius:* Similar to extant species of *Branta. Carpometacarpus:* Similar to extant *Branta,* but with (1) metacarpal I, viewed externally or internally, more triangular, less elongate than extant species; this is due both to its being shorter and to the proximal, external edge (which adjoins the external rim of the carpal trochlea) being straight, rather than concave; and (2) fossa distal to pisiform process deeper. *Femur:* The femur of *Branta woolfendeni* is distinct from that of all living geese. In proportions it is relatively very long and slender. The lengths of several of the fossil femora are greater than the femora of *Branta canadensis taverneri,* and the others are at the upper end of the size range of that species, although the wing elements of *Branta woolfendeni* average smaller than in *B. c. taverneri.* Viewed laterally, the long axis of the shaft of the femur is curved, and the narrowest part of the shaft is about at its midpoint. In this, the new species agrees with the Anatinae and differs from the geese and swans, in which "... the long axis of the shaft is virtually a straight line. The bone also tapers markedly from the wide trochanteric end to the thinnest part, which lies immediately proximal to the condyles." (Woolfenden 1961: p. 67). Within the Anatinae, the femur of *Branta woolfendeni* is more similar to those of the Tadornini, Anatini, and Cairini than to those of the diving tribes, which show marked modifications on the femur. As described below, the rest of the hindlimb of *Branta woolfendeni* is also like that of anatines, suggesting a more aquatic way of life in this species than in modern geese. *Tibiotarsus:* As with the femur, the tibiotarsus of this species is exceedingly long and slender. The five fossil specimens all are greater in length than male *B. c. taverneri.* Using the tibiotarsus Woolfenden (1961) was unable to define the Anserinae and Anatinae. He separated swans and geese from other waterfowl by their lacking a distally directed hook on the lateral tip of the outer cnemial crest that is ". . . characteristic of other waterfowl." (p. 74). The one specimen of *Branta woolfendeni* that has the outer cnemial crest preserved has this "hook," but this character is not entirely reliable: most geese and swans lack it, but some individuals do have it. In addition to the length and slenderness of the tibiotarsus, *Branta woolfendeni* is unusual among geese in having a relatively long, very proximally directed inner cnemial crest. Among the waterfowl, this condition is most similar to the inner cnemial crest in the diving ducks.

Remarks: The fossil record of the geese has been discussed above in the description of the new species *Anser arizonae. Branta woolfendeni* does not resemble *Branta esmerelda* or *Branta howardae* from the Miocene of Nevada and California respectively, or *Branta dickeyi* or *Branta propinqua* from the Pleistocene of California and Oregon, respectively. Of those forms, it is probably closest in morphology to *Branta esmerelda,* which is middle Miocene in age.

This is the most abundant species in the collection of Big Sandy Formation birds.

Genus *Anabernicula* Ross 1935

This genus and its correct subfamilial placement are problematical. The genus was erected by Ross (1935) for several tarsometatarsi from the Pleistocene McKittrick asphalt deposits of California. Ross named *Anabernicula gracilenta,* and placed the genus in the Anserinae, calling it a "pigmy goose." Howard (1936) lumped Ross's *A. gracilenta* and *Branta minuscula* Wetmore 1924 (Blancan, Arizona) as *Anabernicula minuscula,* also adding some specimens from Rancho La Brea. Howard (1964) subsequently named a new species of the "pigmy goose," *Anabernicula oregonensis,* on most of the limb elements, from the Pleistocene Fossil Lake deposits of Oregon. She also decided that Wetmore's material from Arizona was in fact specifically distinct, and restored *Anabernicula gracilenta* Ross, for the pygmy goose from the McKittrick and Rancho La Brea sites in California; *Anabernicula minuscula* remains for Wetmore's pygmy goose humerus from the older deposits in Arizona. Finally, Short (1970) named a fourth species, *Anabernicula robusta,* on a humerus from the Pleistocene of Nebraska. Short noted (1970: p. 148): "The new fossil humerus does not fit within the closely similar *A. oregonensis-A. gracilenta* complex . . . nor is it in any way intermediate between the humeri of those late Pleistocene species and the Pliocene *A. minuscula.* It appears to represent a rather stockier "pygmy goose" of a size similar to these species." Short accepted Howard's (1964) removal of *Anabernicula* from the subfamily Anserinae to the tribe Tadornini in the subfamily Anatinae, and his comparisons of *A. robusta* are primarily with genera in that tribe; he considered *A. robusta* closest to *Chloephaga, Alopochen,* and *Neochen,* whereas Howard considered *A. oregonensis* closest to *Tadorna.*

The subfamilial position of *Anabernicula gracilenta* and *A. minuscula* is ambiguous. I have examined the holotypical proximal end of a humerus of *A. minuscula,* and I cannot find diagnostic characters for placing it with either geese (Anserinae) or sheldgeese (Anatinae). It strongly resembles *Tadorna* (Anatinae) in both size and details, but in the prominence of the capital shaft ridge, one of the distinguishing points of anserine humeri, it is closer to *Branta.* Ross (1935), although he placed *A. gracilenta* in the Anserinae, noted similarities in the tarsometatarsi to the Anatinae. The most taxonomically useful element, the humerus, has a weak capital shaft ridge, with the ridge directed toward the external tuberosity, which is characteristic of most Tadornini but not *Tadorna.* Howard (1964), as noted above, moved the genus to the Tadornini; she gave an emended diagnosis for the genus, but her diagnosis scarcely mentions *Branta* or other geese, and primarily treats similarities and differences with *Tadorna.* She does not clearly state her reasons for placement of the genus in the Tadornini.

I have not examined any of the material of *A. oregonensis,* but the humerus as illustrated (Howard 1964: p. 6) more closely resembles the geese than the shelgeese or shelducks, in its prominent capital shaft ridge directed toward the head rather than toward the external tuberosity. Howard (1964) notes that in *A. oregonensis* the ridge is more pronounced than in *A. gracilenta.*

A. robusta is rather different from the other three named species of *Anabernicula,* as Short (1970) noted. The humerus (the only known element of the species) is much more robust, the capital groove strongly undercuts the head, and it lacks the capital shaft ridge which is present to varying degrees in the other three species. Judging from the illustrations, it clearly belongs in the Tadornini, and within that tribe, Short seems to have correctly allied it with the *Chloephaga-Alopochen-Neochen* group rather than with *Tadorna.* I doubt strongly, however, that it is congeneric with the other *Anabernicula.*

Thus, the extinct genus *Anabernicula,* and the four included species, is in great need of re-evaluation based on all available specimens. It seems that it might include some species that properly belong with the Anserinae, and others with the Tadornini of the Anatinae.

I tentatively refer the Wikieup goose to this genus, although if the genus did not exist, I would unquestionably refer the material to *Branta* in the Anserinae, even though it is so much smaller than any extant goose.

cf. *Anabernicula* sp.

Referred material: associated material F:AM 20880 (in part), including: nearly complete sternum, furcula missing ends of clavicles, proximal end of left radius; right coracoids F:AM 20057, 20061, 20062, 20063, 20064, 20065, 20066, 20067; scapular ends of right coracoids F:AM 20038, 20040; sternal end of right coracoid F:AM 20279; left coracoids F:AM 20056, 20058, 20170, 20265; scapular end of left coracoid F:AM 20107; right humeri F:AM 19787, 19788, 19789; left humeri F:AM 11314, 19792, 19793, 19794; right ulnae F:AM 20136, 20142; right carpometacarpi F:AM 19857, 19860, 19867, 19868, 19875; left carpometacarpi F:AM 19861, 20166; right femur F:AM 20006; left femur F:AM 20005; right tibiotarsus F:AM 20008; left tibiotarsus F:AM 20010; distal half of left tibiotarsus F:AM 20703; proximal end of right tarsometatarsus F:AM 18018; distal ends of right tarsometatarsi F:AM 18020, 18022, 20772; left tarsometatarsi F:AM 19998, 19999; proximal end of left tarsometatarsus F:AM 18011.

Remarks: Sternum: Has the characters of the Anserinae as given by Woolfenden (1961). Ventral manubrial spine rounded, like *Anser,* rather than flattened laterally, like *Branta*; quite unlike the elongate spine of *Tadorna. Coracoid:* The coracoid has all the characters of the coracoids of the Anserinae and more specifically of geese as given by Woolfenden (1961). It is similar to the coracoids of extant *Branta,* but smaller. *Humerus:* Resembles the humeri of living species of *Branta.* Similar to the humerus of extinct *Anabernicula minuscula* in size and in having a quite distinct impression for the external head of the triceps, but the Wikieup bird differs in having a much stronger capital shaft ridge, which is directed more to the head than to the external tuberosity, as in living *Branta.* Wetmore (1924) stated that the impression for the external head of the triceps is more distinct in *Branta canadensis* than in brants (e.g., *Branta bernicla*) (and he allied his *Branta minuscula* more closely with the former species for that reason). I disagree and so cannot make a more specific statement about the relationships of the Wikieup bird within the genus *Branta,* based on the humerus, although small size alone would suggest closer relationships with brants. *Ulna:* The medial border of the distal portion of the external cotyla is more prominent than in geese, but less prominent than in anatines. Otherwise similar to extant *Branta.* The paratypical ulna of *A. oregonensis* illustrated by Howard (1964) seems to be more of the anatine type. *Radius:* Similar to extant *Branta. Carpometacarpus:* The Wikieup bird resembles both *Branta* and *Tadorna.* It differs from both of those genera and resembles *Anabernicula oregonensis* and *A. gracilenta* in the character by which Howard (1964: p. 4) distinguishes *A. oregonensis*: ". . . process of metacarpal I prominent and more attenuated than in *Tadorna.* . . ." The carpometacarpus is smaller than that of *A. oregonensis* and larger than that of *A. gracilenta. Femur:* Agrees with the diagnosis of the femur of *Anabernicula* as given by Howard (1964). The shaft is straight (as in other *Anabernicula*), and this is the primary character by which Woolfenden (1961) distinguishes geese and swans from ducks. The external condyle of the femur of the Wikieup bird also has the distinct anserine condition noted by Woolfenden (1961, p. 67): "The external condyle [with] the anterior ridge elevated from the trend of the shaft." *Tibiotarsus:* This element in the Wikieup bird seems to be relatively long and slender. The overhanging of the proximal articular surface is intermediate between *Branta* and *Tadorna* (*Anabernicula* said to be like *Tadorna* in Howard 1964), and the supratendinal bridge is like *Branta* (not tipped posteriorly, as in *Anabernicula*). The outer cnemial crest is long and proximally directed, unlike geese and like diving ducks. *Tarsometatarsus:* All of the specimens are only very tentatively referred; they are rather larger and stouter than one would expect from the other elements, and the tarsometatarsi known for other species of *Anabernicula* are diagnosed as being relatively slender.

Anserinae genus indeterminate sp. A

Referred material: proximal end of left humerus F:AM 7032.

Remarks: This specimen is from an anserine bird smaller than *Cygnus mariae* and larger than *Anser arenosus.* It is too damaged for further comparison, but definitely represents an additional species in the fauna.

Anserinae genus indeterminate sp. B

Referred material: proximal end of left humerus F:AM 11307.

Remarks: This specimen is probably from a goose similar in size to *Anser arenosus,* but the specimen is distinct from humeri of that species in the shape of the pneumatic fossa.

Subfamily Anatinae (Vigors) 1825
Tribe Anatini (Vigors) 1825
Genus *Anas* Linnaeus 1758

The assignment of the following three species to the tribe Anatini (dabbling ducks) is based primarily on the most taxonomically useful element, the humerus, which is the only skeletal element by which the closely related tribes of Anatini and Cairinini (perching ducks) can be separated. The other pectoral and forelimb elements are of much less use in defining the tribes of ducks (Woolfenden 1961), and the allocation of the fossil elements to the several species is based primarily on size.

The characters of the humerus for the modern Anatini and for the fossils are (from Woolfenden 1961: p. 12): "(1) the capital shaft ridge is obsolete, in contrast with the sheldrakes. (2) The pneumatic fossa is ovaloid and unrimmed with heavy bone, in contrast with the perchers [= Cairinini] . . . (3) The pneumatic fossa is open and contains bony struts . . . instead of being closed as in the pochards (except *Netta* and usually *Metopiana*), eiders, sea ducks (except *Mergus* and *Lophodytes*), and stiff-tailed ducks." The humeri are distinguished from the above pochard genera by having the facet for the anterior articular ligament less elevated (Woolfenden 1961: p. 17) and from the above sea duck genera by having the olecranal fossa shallower (Woolfenden 1961: p. 16).

Anas sp. A

Referred material: associated material F:AM 19798, including: right coracoid, right scapula, right and left humeri, left ulna, proximal end of left radius; furcula, missing the ends of the clavicles, F:AM 20549; coracoidal ends of furculae F:AM 20539, 20540, 20542, 20544; anterior ends of right scapulae F:AM 20216, 20218, 20521, 20533; anterior end of left scapula USNM 407784; right coracoids F:AM 20066, 20069 20070, 20071, 20072, 20073, 20074, 20080; scapular ends of right coracoids F:AM 20110, 20275, 20281, 20282; sternal end of right coracoid F:AM 20886; left coracoids F:AM 20075, 20077, 20078, 20081, 20272; scapular ends of left coracoids F:AM 20076, 20086, 20273, 20280; sternal end of left coracoid F:AM 20079; right humeri F:AM 19791, 19804, 19805, 19806, 19807, 19808, 19809, 19810, 19811, 19812, 19813, 19814; proximal ends of right humeri F:AM 19921, 19922, 20247; distal ends of right humeri F:AM 19803, 19924, 19954, 20120; left humeri F:AM 19795, 19796, 19797, 19799, 19800, 19801, 19823, 19919; proximal ends of left humeri F:AM 19949, 20098; distal ends of left humeri F:AM 19802, 20103, 20236; right ulnae F:AM 20155, 20156, 20332; proximal ends of right ulnae F:AM 20328, 20334; distal ends of right ulnae F:AM 20157, 20163; left ulnae F:AM 20152, 20153, 20154; proximal ends of left ulnae F:AM

20151, 20323; distal ends of left ulnae F:AM 20148, 20149, 20337, 20340; right and left radii F:AM 20167; proximal ends of right radii F:AM 20412, 20419, 20430; distal ends of right radii F:AM 20425, USNM 407785; left radii F:AM 20400, 20401; proximal end of left radius USNM 407786; right carpometacarpi F:AM 19856, 19858, 19859, 19943; proximal end of right carpometacarpus USNM 407787; distal end of right carpometacarpus F:AM 20457; left carpometacarpi F:AM 19864, 19865, 19866, 19871, 19944 (two specimens); proximal ends of left carpometacarpi F:AM 19862, 19863, 20471; distal ends of left carpometacarpi F:AM 20462, 20463, USNM 407788; proximal end of left femur F:AM 20724; right tibiotarsus F:AM 20011; proximal half of right tibiotarsus F:AM 20701; distal half of right tibiotarsus F:AM 20012; distal end of right tibiotarsus F:AM 20015; right tarsometatarsus F:AM 20000.

Remarks: A medium-sized *Anas,* similar in size and details to modern Holarctic *A. strepera.* All other fossil species of *Anas* named from the New World are teal-sized, smaller than this species.

Anas sp. B

Referred material: associated material F:AM 20100, including: partial cranium, partial sternum, right coracoid, right and left humeri, right ulna, right radius, proximal end of left radius, proximal end of right carpometacarpus, right and left tarsometatarsi, right tibiotarsus; anterior ends of right scapulae F:AM 20190, USNM 407789, 413602; anterior ends of left scapulae F:AM 20516, 20517, 20518, 20519, USNM 413603; right coracoids F:AM 20082, 20087, 20088, 20090, 20091, 20097, 20277, 20285; scapular ends of right coracoids F:AM 20109, 20283, USNM 413604, 413605; left coracoids F:AM 20083, 20084, 20085, 20089, 20096, 20108, 20286, 20308; scapular end of left coracoid USNM 413606; right humeri F:AM 19824, 19825, 19832, 19834, 19835, 19836; distal ends of right humeri F:AM 20243, 20244; left humeri F:AM 19826, 19828, 19831, 19832, 19925, 20119, 20230, 20238; proximal ends of left humeri F:AM 19827, 19926, 19950, 20245, 20246, 20262; distal ends of left humeri F:AM 20111, 20242; right ulna F:AM 20344; proximal ends of right ulnae F:AM 20114, 20342, USNM 413607; distal ends of right ulnae F:AM 20341, 20349; left ulnae F:AM 20343, 20350, 20359; proximal ends of left ulnae F:AM 20346, 20347; distal end of left ulna F:AM 20348; right radii F:AM 20432, 20653; proximal and distal ends of right radius F:AM 20429; left radii F:AM 20420, 20433; proximal and distal ends of left radius F:AM 20434; proximal ends of left radii F:AM 20435, USNM 413608; distal ends of left radii F:AM 20427, 20428; right carpometacarpi F:AM 19933, 19959, 20164; proximal ends of right carpometacarpi F:AM 19960, 19961, 20461, USNM 413609; distal ends of right carpometacarpi F:AM 19942, USNM 413610; left carpometacarpi F:AM 19936, 19937, 19938, 19939, 20165, 20450, 20455; proximal ends of left carpometacarpi F:AM 19940, 19941, USNM 413611; distal ends of left carpometacarpi F:AM 20451, 20458, 20459; left tarsometatarsus F:AM 19995.

Remarks: A small duck, closest in size to, but averaging somewhat larger than, *Anas discors.* Limbs comparatively stout. Several teal-sized ducks have been named from the New World. Two are approximately the size of *A. discors.* These are *Anas pullulans* Brodkorb 1961 (late Miocene, Oregon), based on the proximal end of a carpometacarpus, and *A. itchtucknee* McCoy 1963 (late Pleistocene, Florida), based on a coracoid. I have not examined the material of either species. This Wikieup bird might be referable to either one; it is closest in age to *A. pullulans,* and, from the illustrations, generally resembles that species.

Anas sp. C

Referred material: associated material F:AM 20444, including: right humerus, right ulna, and right radius; anterior end of left scapula USNM 413612; right coracoids F:AM 20092, 20093, 20095, 20298; scapular ends of right coracoids F:AM 20287, 20293, USNM 413613; left coracoids F:AM 20094, 20288, 20289, 20290, 20292, 20295, 20297; scapular ends of left coracoids F:AM 20294, 20296, 20726; sternal end of left coracoid F:AM 20291; right humeri F:AM 19834, 19846, 19847, 19848, 19849, 19850, 19852, 19853, 19854; proximal ends of right humeri F:AM 20116, 20226, 20233, 20237; distal ends of right humeri F:AM 19851, 20104, 20105; left humeri F:AM 19829, 19830, 19839, 19840, 19841, 19843, 19844, 20101, 20225; proximal ends of left humeri F:AM 19842, 19855, 19927; distal ends of left humeri F:AM 20240, 20241, 20263, USNM 413614; right ulnae F:AM 20352, 20353, 20355; distal ends of right ulnae F:AM 20284, 20358, 20365; left ulnae F:AM 20345, 20351, 20356, 20370; proximal ends of left ulnae F:AM 20357, USNM 413615; distal ends of left ulnae F:AM 20354, 20362; right radius F:AM 20441; proximal ends of right radii USNM 413616, 413617; left radii F:AM 20382, 20438, 20440; right carpometacarpus F:AM 11280; distal end of right carpometacarpus USNM 413618; left carpometacarpi F:AM 11281, 20449, 20454; proximal end of left carpometacarpus F:AM 20475; distal end of left carpometacarpus F:AM 20456 (all carpometacarpi are tentatively referred, because they are somewhat smaller than I would expect relative to the sizes of the other elements); distal end of left tibiotarsus F:AM 20719.

Remarks: A small duck, closest in size to, but somewhat larger than, living *Anas carolinensis.* Limbs comparatively slender. This species from the Big Sandy Formation is similar in size to two previously named species from North America: (1) *Anas bunkeri* Wetmore 1944 (Middle Pliocene to Lower Pleistocene deposits in Oregon, Texas, Kansas, Arizona, and Idaho; type and only illustrated specimen a carpometacarpus); (2) *Anas greeni* Brodkorb 1964a (Lower Pliocene, South Dakota), based on a worn distal end of a femur. These two might represent the same species. Brodkorb (1964a, p. 57) stated that *A. bunkeri* was a "relatively large species of teal," but in fact the holotypical carpometacarpus falls at the low end of the size range of *A. carolinensis,* and, thus, is very close in size to *A. greeni.* Because of the uncertainty of the relationships of the two, I do not refer this Wikieup bird to either.

Anatinae, tribe indeterminate, sp. A

Referred material: right ulna, lacking distal end, F:AM 19815; distal ends of right ulnae F:AM 20158, 20159, 20160, 20161, 20163; left ulnae F:AM 20150, 20331; distal end of left ulna F:AM 20378.

Remarks: It seems rather curious to have as the only specimens of another anatid species nine ulnae or pieces thereof and no other elements, but these definitely represent a species distinct from any of those discussed above. They belong to a duck, by the character of the proximal end of the ulna given above, but come from a very large species. They exceed in size the ulnae of all living

North American species of dabbling ducks, and fall within the size range of modern *Somateria mollissima,* an eider.

Anatidae, subfamily indeterminate

Remarks: Some two dozen specimens cannot be definitely referred to any of the species discussed above, or to any more specific category than waterfowl. They might represent as many as three or four additional forms.

Order ACCIPITRIFORMES (Vieillot) 1816
Family ACCIPITRIDAE (Vieillot) 1816
Subfamily BUTEONINAE (Vigors) 1824
Genus *Buteo* Lacepede 1799
Buteo sp. A

Referred material: right tibiotarsus F:AM 20702.

Remarks: This specimen can be referred to *Buteo* rather than to *Accipiter* by the rounder, less pronounced condyles, and the somewhat depressed supratendinal bridge. The specimen is similar in size and details to the tibiotarsus of females of *Buteo platypterus.*

All of the buteonine hawks listed in Brodkorb (1964b), which range from middle Oligocene to late Miocene, are much larger than this species, as are *B. hoffstetteri* Campbell 1976 (late Pleistocene, Ecuador), and *B. circoides* Kurochkin 1968 (Oligocene, Mongolia). *Buteo pusillus* Ballman 1969 (Miocene, France) is smaller than the Wikieup bird.

cf. *Buteo* sp. B

Referred material: distal end of right ulna F:AM 20725.

Remarks: This specimen generally resembles the distal end of the ulna of extant hawks, but is possibly distinct from the modern genera, so I have assigned it only tentatively to *Buteo.* It is from a large hawk, about the size of modern *Buteo jamaicensis,* and, thus, certainly represents a species distinct from the one noted above.

Genus *Aquila* Brisson 1760
Aquila sp. A

Referred material: right coracoid F:AM 19969; proximal end of left tarsometatarsus F:AM 11298.

Remarks: The coracoid is very similar to that of the living Palaearctic species *Aquila chrysaetos,* differing only in the lesser development of the bicipital attachment, the shape and size of the pneumatic foramina, and minor details of the sternal facet. It also agrees in size with that species, matching the female specimens available. The proximal end of tarsometatarsus is also very like that in *A. chrysaetos,* differing slightly in the shapes of the calcaneal ridges of the hypotarsus. It is from a larger individual than the one represented by the coracoid, being similar in size to males of *A. chrysaetos.*

Aquila sp. B

Referred material: right humerus (lacking proximal end) F:AM 20255; right radius F:AM 20385; left carpometacarpus F:AM 11284; right tarsometatarsus F:AM 11299.

Remarks: The humerus closely resembles *Aquila* in the large size of the entepicondyle and the ectepicondylar prominence, depth of olecranal fossa and internal tricipital groove, and in the degree of curvature of shaft and in proportions. The tarsometatarsus agrees with *Aquila* in its robust proportions (tarsometatarsus robust also in *Haliaeetus*), lack of a strong, sharp ridge extending from the proximal to distal end on anterior side, very deep metatarsal facet, location of the prominent, oval tubercle for tibialis anticus, and other features. The generic assignment of the radius and carpometacarpus is less certain because of the great similarities in these elements among different genera in the family, but they are of an appropriate size to go with the other elements above, and are generally quite like *Aquila,* especially in the shape of the humeral cotyla and bicipital tubercle (radius) and the process of metacarpal 1 and the extensor attachment (carpometacarpus). The various bones of this species are all smaller than the comparable elements in *A. chrysaetos.*

No valid, extinct species of *Aquila* have been named from North America, although the genus has been noted from several localities. There are, however, numerous unstudied Neogene accipitrids, including eagles, from North America in various collections.

Subfamily GYPAETINAE (Vieillot) 1816
Genus *Neophrontops* L. Miller 1916
Neophrontops sp.

Referred material: associated material F:AM 19909, including: left radius, left carpometacarpus; right coracoid F:AM 19968; left coracoid F:AM 20307; right humerus F:AM 11305; left ulna F:AM 20318; right carpometacarpus F:AM 19907; right tarsometatarsus F:AM 11300; left tarsometatarsus F:AM 11301.

Remarks: Howard (1932: p. 64) noted that "... the coracoid of *Neophrontops americanus* is individual and cannot be likened to that of any other genus." The genus is characterized by having the head of the coracoid square in outline viewed anteriorly, and having the head (viewed dorsally), rotated medially, so that the plane of the furcular facet is at right angles to the plane of the ventral end. The two Wikieup specimens are assigned on the basis of these characteristics. The humerus is clearly referable to the Gypaetinae by the shape of the distal end and the proportions of the shaft. The entepicondyle is very small, giving a curved outline (especially viewed palmarly) between the internal condyle and the entepicondyle. In the Accipitriformes, only the Pandionidae, Cathartidae, and the Gypaetinae have this characteristic. The specimen cannot be referred to *Pandion,* in which the shape of the deltoid crest is very different. Nor can it be from a New World vulture, in which there are large foramina in the brachial depression and capital groove that are lacking in the Wikieup specimen. The fossil also has the stoutness that helps to separate the Gypaetinae from other Accipitriformes. The fossil humerus is in general very similar to *Neophron,* differing chiefly in its greater length, the much deeper ligamental furrow, and the more greatly curved shaft.

The assignment of the ulna and radius above to this genus is tentative. The Gypaetinae cannot be distinguished as a group by the ulna. F:AM 20318 closely resembles *Neophron,* however, in (1) having a prominent, triangular proximal radial depression which is distinct from the shaft (depression not distinctly set off from the shaft in hawks and eagles; less distinct in other Gypaetinae); and (2) having the external condyle with its proximal articular surface blending smoothly into the shaft (as in other Gypaetinae) rather than being distinct from the shaft (as in hawks and eagles). The radius can definitely be assigned to the Gypaetinae by having a semicircular, rather than oval, humeral cotyla. Rich (1980) lists several other characters of the radius that she says distinguish the subfamily, but I have difficulty discerning them. Rich (1980) also gives several characters of the radius as distinctive of *Neophrontops.* Of these, the Wikieup specimen has neither a particularly pronounced ligamental prominence, nor an especially inflated distal end, but it does have the characteristic highly curved shaft and rounded palmar surface of the distal end of the shaft.

The carpometacarpi can be assigned to the Gypaetinae by two of the characters given by Rich (1980: p. 46): the contact of the ventral margin of the pollical facet and the dorsal margin of the shaft, and the rounded, rather than squared, shape of the process of metacarpal I. Her other characters for the subfamily are not consistently true in my series of specimens of the subfamily. The fossil carpometacarpus can be assigned to *Neophrontops* by the following characters: (1) internal ligamental fossa deeply excavated, (2) a deep fossa at the base of metacarpal I adjacent to the pisiform process, (3) a deep, round pit for the external ligamental attachment, and (4) a distinct furrow extending from the pisiform process to the intermetacarpal space. F:AM 19907 is larger than F:AM 19909, but otherwise the two are identical. The radius and ulna are both shorter than the radius and ulna of *Neophrontops americanus,* but the other elements assigned to the Wikieup bird are longer than in that species. Howard (1932) noted that the radius and ulna of *N. americanus* were smaller than in *Neophron,* although the other elements were larger, so perhaps these birds had a short forewing, and this was especially pronounced in the Wikieup bird.

Tarsometatarsi F:AM 11300 and 11301 are unmistakably gypaetine, and resemble most closely *Neophron* and *Neophrontops.* They are longer than, but otherwise almost identical in proportions and other details to, the tarsometatarsus of *Neophrontops americanus* Miller as illustrated in Howard (1932).

Eleven species, in four genera, have been named in the Gypaetinae from the New World. *Arikarornis, Neogyps,* and *Paleoborus* are apparently all more closely related to each other than to *Neophrontops,* which stands out as being very similar to the living genus *Neophron.* As noted above, the Wikieup specimens are also similar to *Neophron.* The six nominal species of *Neophrontops* are all from the western United States, ranging in age from mid-Miocene to late Pleistocene. The Wikieup bird, a large *Neophrontops,* was probably about the same size as *Neophrontops americanus,* but differs from that species in limb proportions. The fossil record of *Neophrontops* has been treated exhaustively by Rich (1980).

Subfamily CIRCINAE Bonaparte 1838
Genus *Circus* Lacepede 1799
Circus sp.

Referred material: anterior end of left scapula F:AM 20522.

Remarks: This specimen is immediately referable to the genus *Circus* by its having a very deeply incised, strongly bordered groove ventral to the acromium on the anterior/lateral aspect of the bone. It lacks the pneumatic foramen adjacent to the coracoidal articulation on the medial side of the bone that is found in modern members of the genus, but, as noted above in the discussion of the

Anatidae, pneumatic foramina seem to be relatively recent and quickly evolving characters in a number of groups. The specimen is about 75% larger than the scapula of the North American Northern Harrier, *Circus cyaneus.*

This specimen is the first extinct representative of the subfamily from North America. Two species of harriers have been named in the genus *Thegornis* from the Miocene of Argentina, and one in the genus *Circus* from the Quaternary of New Zealand.

Order GRUIFORMES (Bonaparte) 1854
Family GRUIDAE Vigors 1825
Genus *Grus* Pallas 1766

Remarks: Of the four living genera of cranes (*Grus, Anthropoides, Bugeranus,* and *Balearica*), only *Balearica* can be consistently distinguished on the wing elements. The Wikieup crane is definitely not referable to that African genus, and the assignment of the wing elements to *Grus* is based on their association with definitely assignable hindlimb elements. In the tibiotarsus, the specimens are referable to *Grus* rather than to *Anthropoides* or *Bugeranus* by having the internal condyle extending not so far medially; they are distinct from *Balearica* by having the process on the internal side of the tendinal groove less developed, and the prominence on the internal side of (anterior of) the groove for peroneus profundus less developed. The tarsometatarsi are referable to *Grus* and distinct from *Anthropoides* by having the distal end narrower (trochlea II flared less medially) and trochlea II produced farther posteriorly; from *Balearica* by having the distal end narrower (*Grus rubricunda* has distal end wide); and from *Bugeranus* by having the attachment for the external ligament more toward the anterior of the element, and by having the outer tubercle for tibialis anticus oval, not round, and the inner tubercle more developed.

Grus haydeni Marsh 1870
Fig. 3

Referred material: associated material F:AM 20859, including: distal end of right humerus, distal end of right ulna, right radius, right carpometacarpus, right phalanx I of digit II of carpometacarpus; distal end of right femur F:AM 7058; distal ends of right tibiotarsi F:AM 20704, 20705; proximal end of right tarsometatarsus F:AM 19974; distal end of right tarsometatarsus F:AM 19975; left tarsometatarsus F:AM 20858; proximal end of left tarsometatarsus F:AM 20727.

Measurements of referred material: see Table 5.

Amended Diagnosis: Humerus, ulna, radius and carpometacarpus: Similar to living North American *Grus americana* and *G. canadensis*; size of the largest specimens of *Grus canadensis* examined. *Femur:* The specimen is too damaged for adequate comparison. *Tibiotarsus:* Similar to modern *Grus,* but with the groove for peroneus profundus deeper and situated more distally. *Tarsometatarsus:* Distinct from living *Grus* in having a slightly more robust shaft and deeper, narrower anterior metatarsal groove. As with the wing elements, the hindlimb elements are intermediate in size between the two extant North American species.

Remarks: Marsh (1870) described this species on a somewhat worn distal end of left tibiotarsus, from "later Tertiary beds of the Niobrara River," Nebraska, now regarded as Pleistocene. His diagnosis of the species was inadequate, as he did not compare it to modern genera and species of cranes, but merely described the morphology of the specimen. Wetmore (1928) considered the species to be conspecific with *Grus canadensis,* the extant North American Sandhill Crane, stating (p. 4) that "... there are no valid characters to mark it from the sandhill crane." Brodkorb (1967) listed it as a Pleistocene example of *Grus canadensis.* I examined a cast of the type of *Grus haydeni,* and compared it with the distal ends of tibiotarsi of the Wikieup crane. They are similar to each other, and in my view, distinct from *Grus canadensis* and other extant cranes. In the Smithsonian collection of fossil birds from the late Miocene Lee Creek phosphate deposits of North Carolina (essentially contemporaneous with the Big Sandy Formation deposits) is the distal end of a right tarsometatarsus (USNM 210421) of a crane that is indistinguishable from the Wikieup tarsometatarsi, and, thus, also probably represents *Grus haydeni.*

The fossil record of the Gruidae is extensive. Most of the species belong to distinct, earlier Tertiary genera. Two species have been named in the genus *Grus* from North America, in addition to *Grus haydeni. Grus conferta* A. H. Miller and Sibley 1942 (late Miocene, California), based on the distal end of a left tarsometatarsus, came from a crane the size of *G. americana* and, thus, was larger than the Wikieup bird. The type is also very distinct in morphology from modern cranes (S. L. Olson, pers. comm.). *G. nannodes* Wetmore and Martin 1930 (late Miocene, Kansas), based on a left carpometacarpus lacking the proximal end, came from a bird "decidedly smaller" than *G. canadensis.* A second crane is known from the Lee Creek deposits, in addition to the one referred to *Grus haydeni* above. It is of truly great size, equalling the extant Sarus Crane (*Grus antigone*) of Asia.

Family RALLIDAE Vigors 1825
Subfamily RALLINAE (Vigors) 1825
Genus *Rallus* Linnaeus 1758
Rallus phillipsi Wetmore 1957

Holotype: complete right tarsometatarsus USNM 187424, collected in 1952 by Allan R. Phillips from "... Gray Ranch, near Wikieup post office, Mohave County, in northwestern Arizona." (Wetmore 1957: p. 267). A more exact locality is not given; presumably it is either the Bird Bone or the Clay Bank Quarry.

Referred material: distal ends of right ulnae F:AM 20364 and 20369; right carpometacarpus F:AM 20445; proximal end of left carpometacarpus USNM 407752; proximal end of right femur F:AM 20678; complete right tarsometatarsus F:AM 11303 (homeotype); left tarsometatarsus (damaged) F:AM 20770; right tibiotarsus F:AM 20706; distal ends of right tibiotarsi F:AM 20720, USNM 407753; distal end of left tibiotarsus USNM 407782. (All topotypes.)

Measurements of holotype and referred material: see Table 6.

Remarks: The homeotypical tarsometatarsus is slightly longer than the holotype of *Rallus phillipsi,* but is otherwise similar. The proximal end of a femur is similar in size to that of small *R. longirostris,* but differs in having the neck slightly shorter and in having a lip on the underside of the head. The distal ends of tibiotarsi are indistinguishable from those of small individuals of *Rallus longirostris* (and articulate well with the tarsometatarsus). The ulnae and carpometacarpus are also similar to small *R. longirostris.*

Rallus phillipsi is the only bird heretofore described from the Big Sandy For-

TABLE 5

MEASUREMENTS (MM) OF SPECIMENS REFERRED TO *Grus haydeni* MARSH 1870, FROM THE LATE MIOCENE–EARLY PLIOCENE BIG SANDY FORMATION, MOHAVE COUNTY, ARIZONA

Element	F:AM 20859			
Humerus				
W-DIST	33.60			
D-DIST	19.95			
Ulna				
ECON	16.20			
CPTB	16.25			
Radius				
LENGTH	252			
W-SHAFT	9.75			
D-SHAFT	7.25			
W-PROX	9.75			
D-PROX	9.95			
W-DIST	14.50			
D-DIST	8.35			
Carpometacarpus				
W-SHAFT	8.10			
D-SHAFT	7.35			
W-CARPAL	10.75			
D-PROX	24.30			
	F:AM 20704	F:AM 20705		
Tibiotarsus				
W-DIST-CR	19.95	21.45		
D-ICON	11.25	11.15		
	F:AM 20858	F:AM 19975	F:AM 20727	$\bar{X}$
Tarsometatarsus				
LENGTH	230	—	—	—
W-PROX	22.80	23.70	25.30	23.95
D-PROX	13.00	14.90	—	13.95
TRII-TRIV	19.95	—	—	—

mation deposits. Although Wetmore (1957) characterized it as "definitely smaller" than *R. longirostris,* Olson (1977) noted that with a larger comparative series, *R. phillipsi* falls into the small end of the size range of *R. longirostris. R. phillipsi* is in fact almost indistinguishable from modern *R. longirostris*; the ends of tibiotarsi, ulnae, and carpometacarpus now available agree with Olson's (1977) report.

Rallus sp.

Referred material: anterior half of right scapula F:AM 20514; anterior half of left scapula F:AM 20515; left coracoid F:AM 20300; right humerus F:AM 20221; left radius F:AM 20442; right tibiotarsus F:AM 20207; left tibiotarsus (missing proximal end) F:AM 20710; distal end of right tibiotarsus F:AM 20715.

Remarks: These bones all come from a typical, medium- sized *Rallus,* falling within the size range of *R. aquaticus* of Egypt, and intermediate in size between North American *R. longirostris* and *R. limicola.* Distinct in size from *R. phillipsi,*

TABLE 6

MEASUREMENTS (MM) OF HOLOTYPE AND SPECIMENS REFERRED TO *Rallus phillipsi* WETMORE 1957, FROM THE LATE MIOCENE–EARLY PLIOCENE BIG SANDY FORMATION, MOHAVE COUNTY, ARIZONA

Element		N	Min.	Max.	X̄
Ulna					
ECON		2	3.70	3.80	3.75
CPTB		1	3.68	—	—
Carpometacarpus					
LENGTH		1	25.65	—	—
W-SHAFT		2	1.95	1.95	1.95
D-SHAFT		2	1.80	1.85	1.83
W-CARPAL		2	2.55	2.75	2.65
W-DIST		1	3.00	—	—
Femur					
W-PROX		1	8.00	—	—
Tibiotarsus					
LENGTH		1	68.25	—	—
W-SHAFT		1	3.05	—	—
D-SHAFT		1	2.90	—	—
W-DIST-CR		2	5.65	5.80	5.70
D-ICON		3	3.75	4.10	3.95
Tarsometatarsus	Holotype				
LENGTH	47.35	2	47.35	48.65	48.00
W-SHAFT	3.00	2	3.00	3.15	3.10
D-SHAFT	2.60	2	2.60	2.95	2.75
W-PROX	5.75	2	5.75	6.10	5.90
D-PROX	4.70	2	4.70	5.15	4.90
TRIII-TRIV	4.45	2	4.45	5.10	4.75

these bones probably represent a second species of *Rallus,* but the material is too incomplete to name.

Besides *Rallus phillipsi,* two species of *Rallus* have been named from North America. The Wikieup *Rallus* sp. was approximately the same size as *Rallus prenticei* Wetmore 1944 (early Pliocene, Kansas) and, judging from Wetmore's illustrations (which are poor), appears to differ only slightly in the shape of the head of the humerus. The Wikieup *Rallus* sp. should perhaps be assigned to that species. It is smaller than *R. lacustris* (Brodkorb) 1958 (Pliocene, Idaho).

Genus *Coturnicops*

Coturnicops sp.

Referred material: distal end of left humerus F:AM 20223; proximal end of left tibiotarsus F:AM 20722; distal end of left tarsometatarsus USNM 407754.

Remarks: The humerus is clearly referable to *Coturnicops* rather than to *Laterallus* by its straighter shaft; within the genus, however, it cannot safely be distinguished from *C. noveboracensis,* with which it is similar in size. The other two bones are assigned strictly on the basis of general resemblance to *Coturnicops* and on being the right size to go with the humerus; *Laterallus* and *Coturnicops* are not actually separable on these elements.

These are the oldest specimens known of the smaller North American rails in general and of the genus *Coturnicops* in particular, the only other ones being *Laterallus insignis* Feduccia 1968 and *Coturnicops avita* Feduccia 1968 (both from the early Pliocene Glenns Ferry Formation of Idaho).

Rallidae genus and species indeterminate

Referred material: left humerus F:AM 20224; right ulna F:AM 20363; left ulna F:AM 20368.

Remarks: The humerus and ulnae listed are typically rallid except for the quality, especially pronounced in the humerus, of extraordinary stoutness; their robust nature is not approached by any living or extinct genus in the family.

Order CHARADRIIFORMES Huxley 1867

Family RECURVIROSTRIDAE Bonaparte 1831

Genus *Himantopus* Brisson 1760

Remarks: The fossil tarsometatarsi are clearly referable to the stilts, *Himantopus,* rather than to the avocets, *Recurvirostra,* or the Australian Banded Stilt, *Cladorhynchus leucocephalus,* by their very great length and relative slenderness. The paratypes, although not found in association with the holotype, also plainly belong to a stilt, by their small size and delicateness, compared to avocets.

Himantopus olsoni sp. nov.

Fig. 7

Holotype: left tarsometarsus, F:AM 20780, with hole in shaft, trochlea for digit II broken off (and reglued), and proximal end missing. Collected in 1939 by Guy E. Hazen.

Type locality: Bird Bone Quarry: SW¼, NE¼, sect. 29, T.15N, R.12W, Greenwood Peak Quadrangle, Mohave County, Arizona.

Horizon and age: Big Sandy Formation, late Hemphillian, late Miocene. Dated (fission track, zircon) at 5.12–5.29 mybp.

Measurements of holotype: see Table 7.

Paratypes: From Bird Bone Quarry: distal right humerus F:AM 20235; left humerus F:AM 20228; right ulna F:AM 20360; left ulna F:AM 20335; right femur F:AM 20229; distal ends of right tibiotarsi F:AM 20711, 20712, USNM 407755, 407756; distal ends of left tibiotarsi F:AM 20717, 20721; proximal end of right tarsometatarsus F:AM 20779; distal ends of left tarsometatarsi F:AM 11302, 20774, 20776. From Clay Bank Quarry: left coracoid F:AM 20303; dorsal end of left coracoid F:AM 20304; proximal end of right humerus F:AM 20227; left femur F:AM 20676.

Measurements of paratypes: see Table 7.

Etymology: named for Dr. Storrs L. Olson, in recognition of his contributions to avian paleontology and his insightful work on the evolutionary relationship of recurvirostrids and flamingos.

Diagnosis: Tarsometatarsus longer than that in any other species of *Himantopus,* being approached only by *H. knudseni* of the Hawaiian Islands.

Description: The humerus differs from that in other species of *Himantopus* in having (1) a pit in the pneumatic fossa; (2) the attachment to the shaft of the median crest of the pneumatic fossa closer to the capital shaft ridge; and (3) the

FIG. 7. a. *Corvus galushai* sp. nov., holotype left carpometacarpus, F:AM 11282. b–h. Specimens of *Himantopus olsoni* sp. nov. b. Left coracoid, paratype, F:AM 20303, c. Left ulna, paratype, F:AM 20335. d. Left humerus, paratype, F:AM 20228. e. Distal end of left tibiotarsus, paratype, F:AM 20717. f. Proximal end of right tarsometatarsus, paratype, F:AM 20779. g. Right femur, paratype, F:AM 20229. h. Left tarsometatarsus, holotype, missing proximal end, F:AM 20780. Scale bar = 10 mm.

head less undercut on the anconal side. The other skeletal elements (except the coracoid, discussed below) resemble the elements in extant *Himantopus*, but are larger.

Remarks: The assignment of the coracoid F:AM 20303 is somewhat uncertain.

TABLE 7

MEASUREMENTS (MM) OF HOLOTYPE AND DESCRIPTIVE STATISTICS OF HYPODIGM OF *Himantopus olsoni* SP. NOV., FROM THE LATE MIOCENE–EARLY PLIOCENE BIG SANDY FORMATION, MOHAVE COUNTY, ARIZONA

Element	F:AM 20303	F:AM 20304			
Coracoid					
HEAD-IDA	22.45	—			
HEAD-SF	8.20	—			
D-HEAD	3.40	3.55			
W-SHAFT	3.25	—			
	F:AM 20227	F:AM 20228			
Humerus					
LENGTH	—	61.20			
W-SHAFT	—	4.95			
D-SHAFT	—	3.20			
W-PROX	13.00	13.05			
D-PROX	—	6.15			
W-DIST	—	9.70			
D-DIST	—	5.75			
	F:AM 20335	F:AM 20360			
Ulna					
W-SHAFT	3.80	3.80			
D-SHAFT	3.70	3.75			
W-PROX	7.00	6.90			
D-PROX	6.05	5.85			
ECON	5.55	5.45			
CPTB	5.70	5.95			
	F:AM 20229	F:AM 20676			
Femur					
LENGTH	37.05	—			
W-SHAFT	3.55	—			
D-SHAFT	3.00	—			
W-PROX	7.90	8.05			
W-DIST	8.30	—			
		N	Min.	Max.	X̄
Tibiotarsus					
W-DIST-CR		5	5.80	6.05	5.90
D-ICON		6	4.60	4.95	4.70
Tarsometatarsus	Holotype				
W-SHAFT	3.05	1	—	—	—
D-SHAFT	3.10	1	—	—	—
W-D-SHAFT	2.75	2	2.75	2.80	2.77
TRIII-TRIV	5.60	2	5.50	5.60	5.55

It is clearly a charadriiform with a procoracoidal foramen, which eliminates all but the Recurvirostridae, Charadriidae, Stercorariidae, and Laridae. The last three can be eliminated by the shape of the sternal facet, which is evenly and gently curved in the fossil, but is greatly curved in the plovers, and with a small protrusion on the anterior end, externally, in the jaegers and gulls. The coracoid, although the right length for *Himantopus olsoni*, is stouter than the coracoids in modern species of *Himantopus* examined.

This is the first extinct species described in the genus *Himantopus*. The only other records for the Recurvirostridae are discussed below.

Genus *Recurvirostra*
Recurvirostra sp.

Referred material: proximal end of right humerus F:AM 20227; left humerus F:AM 11308.

Remarks: Within the Recurvirostridae, the fossils are referable to *Recurvirostra* by their large size. They fall within the range of *R. americana*, and differ from that species only in the slightly more proximal position of the ectepicondylar prominence on the shaft.

Three other avocets have previously been noted in the fossil record. These are the late Eocene-early Oligocene *Recurvirostra sanctaeneboulae* Mourer-Chauvire 1978, known only from the proximal end of an ulna; an unidentified species of *Recurvirostra* from the Upper Middle Miocene of California (L. H. Miller 1961); and *Recurvirostra* "similar to extant *R. americana*" reported by Rogers et al. (1985) from the Pleistocene of Colorado.

Family PHOENICOPTERIDAE Bonaparte 1831
Genus *Phoenicopterus* Linnaeus 1758
Phoenicopterus sp.

Referred material: left femur F:AM 20656.

Remarks: This specimen closely resembles the femora in modern flamingos and in size is similar to *Phoenicopterus ruber.*

The fossil record of flamingos has been reviewed recently by Olson (1985) and Olson and Feduccia (1980). The femur of the Wikieup flamingo is badly worn and cannot be referred to any previously named species.

Family CHARADRIIDAE Vigors 1825
Genus *Charadrius* Linnaeus 1758
Charadrius sp.

Referred material: complete right humerus F:AM 11309.

Remarks: Within the Charadriidae, referable only by size and proportions to the genus *Charadrius*, which includes almost all of the very small charadriids; *Anarhynchus* of New Zealand has a humerus similar in length but much slenderer. Similar to *C. melodus* in size and morphology.

As noted by Olson (1985: p. 175), "The Tertiary record of the Charadriidae as reflected in Brodkorb (1967) proves to be entirely illusory"; of the four named taxa, none belong in the family. The specimen noted here is, thus, the first pre-Pleistocene record for the family.

Family SCOLOPACIDAE Vigors 1825
Genus *Limosa* Brisson 1760
cf. *Limosa* sp.

Referred material: right coracoid F:AM 20302.

Remarks: F:AM 20302 is from a large scolopacid, similar to modern *Limosa* and *Numenius*. In size it agrees with *Limosa fedoa* and *Numenius phaeopus.*

Two paleospecies of *Limosa* have been named from North America, *Limosa vanrossemi* L. Miller 1925 (middle Miocene, California), and *Limosa ossivallis* Brodkorb 1967 (early Pliocene, Florida). Both were also similar in size to *L. fedoa*, but their preservation (the first, a skeletal impression, the second, the distal end of a tibiotarsus) prevents comparison with the Wikieup specimen.

Genus *Tringa* Brisson 1760

Tringa sp. A

Referred material: proximal end of left tarsometatarsus USNM 407758.

Remarks: In proportions (smallish head, long, slender shaft) and details most closely resembles *Tringa*. It is similar in size to *T. flavipes*. This specimen has a peculiar lateral bulge in the shaft below the head, which I discount as an individual peculiarity (the tibiae and tarsae of shorebirds are often somewhat deformed).

cf. *Tringa* sp. B

Referred material: left radius F:AM 20439.

Remarks: Tentatively assigned. The specimen represents a scolopacid somewhat larger than *Tringa melanoleuca*.

Brodkorb (1967) lists a number of species of *Tringa* (including *Totanus*), all of which are from Europe, and all, except the very small *Totanus lartetianus* Milne-Edwards 1863 (Lower Miocene, France) are based on very fragmentary material. Feduccia (1970) named the one valid species of *Tringa* from North America, *Tringa antigua* (Pliocene, Kansas), based on a complete humerus which is slightly smaller than in *T. solitaria*. Thus, it was smaller than either of the Wikieup species of *Tringa*.

Genus *Calidris* Merrem 1804

Remarks: The following three species are all referred to *Calidris* for ease in future reference. Several genera of small scolopacids are indistinguishable in the post-cranial skeleton, and the forms below might actually represent any of these genera.

cf. *Calidris* sp. A

Referred material: right ulna F:AM 20367; distal end of left carpometacarpus USNM 407759.

Remarks: These specimens represent a scolopacid the size of the largest *Calidris* (e.g., *C. canutus*); they are also similar in size to *Arenaria interpres* or *Heteroscelus incanus*.

cf. *Calidris* sp. B

Referred material: right coracoid F:AM 20611; distal end of right humerus USNM 407760; proximal end of left humerus F:AM 20222; right ulna F:AM 20366; distal end of right ulna USNM 407761; right carpometacarpus USNM 407762; distal end of right carpometacarpus USNM 407763; distal end of right tibiotarsus F:AM 20723.

Remarks: These specimens might come from one or more small scolopacids of several genera: *Calidris, Actitis, Xenus* (all sandpipers), or *Phalaropus* (phalaropes).

cf. *Calidris* sp. C

Referred material: distal ends of right humeri USNM 407764, 407765; proximal end of right ulna USNM 407766; proximal end of right carpometacarpus USNM 407767.

Remarks: These specimens are indistinguishable in size and details from several modern species, including, for example, *Calidris pusilla* and *C. mauri.*

Several small sandpiper-like scolopacids have been named from North American deposits. Weigel (1963) erected the new genus and species *Paractitis bardi* for the scapular end of a coracoid from the Lower Oligocene of Saskatchewan; this is a ridiculous example of naming fragmentary specimens. Brodkorb (1955) named *Calidris pacis* on the proximal end of a humerus from the Lower Pliocene of Florida; it came from a bird larger than any of the forms recorded here. Brodkorb (1963b) also named *Calidris rayi* on part of a coracoid, about which it is difficult to say anything because of the extremely fragmentary nature of the specimen.

Family LARIDAE Vigors 1825

Subfamily LARINAE (Vigors) 1825

cf. *Larus* sp.

Referred material: right ulna F:AM 20333; proximal end of right radius USNM 407783.

Remarks: Both specimens are referable to the Larinae rather than to the Sterninae; the ulna by (1) the longer olecranon, (2) the longer humero-ulnar depression, and (3) the convex and oval shape of the prominence for the anterior articular element; the radius by (1) the flattened outline (viewed proximally) of the proximal articular end. Referred to *Larus* only tentatively; the several genera of gulls are difficult to separate on these elements. The ulna is approximately the same length as that of *Larus pipixcan,* but is proportionately stouter.

Five extinct species of gulls have been named from North America. *Gaviota niobrara* A. H. Miller and Sibley 1941 (late Miocene, Nebraska) is quite distinct from all other larines (Olson 1985). *Larus pristinus* Shufeldt 1915 (early Miocene, Oregon) is of indeterminate affinities (Olson 1985). *Larus elmorei* Brodkorb 1953 (early Pliocene, Florida), *L. robustus* Shufeldt 1891, and *L. oregonus* Shufeldt 1891 (both Pleistocene, Oregon), are all based on elements other than the radius and ulna, and all came from birds much larger than the Wikieup species.

Order COLUMBIFORMES (Latham) 1790

Family COLUMBIDAE (Illiger) 1811

Genus *Zenaida* Bonaparte 1838

Zenaida cf. *Zenaida prior* Brodkorb 1969

Referred material: left tarsometatarsus F:AM 20777.

Remarks: A dove, generally similar in proportions and details to any of the genera of small New World doves (*Claravis, Columbina, Scardafella, Zenaida, Zenaidura*), and to the Old World doves of the genus *Streptopelia,* but closest to *Zenaida* and *Streptopelia.* Within those genera, which are very similar, the size, proportions, and details of the fossil fall in the ranges of variation of both *Zenaida macroura* and *Streptopelia turtur.* It might be conspecific with *Zenaida prior* Brodkorb 1969 (Pliocene, Kansas), based on the proximal end of a humerus, and

TABLE 8

MEASUREMENTS (MM) OF HOLOTYPE OF *Corvus galushai* SP. NOV., FROM THE LATE MIOCENE–EARLY PLIOCENE BIG SANDY FORMATION, MOHAVE COUNTY, ARIZONA

Element	F:AM 11282
Carpometacarpus	
LENGTH	33.05
W-SHAFT	3.15
D-SHAFT	2.50
W-CARPAL	4.40
D-PROX	8.20
W-DIST	7.70
D-DIST	4.10

said to be very similar to *Z. macroura. Columba* (= *Chloroenas*) *micula* (Wetmore) 1924 (Pleistocene, Arizona), and *Geotrygon* (= *Oreopelia*) *larva* (Wetmore) 1920 (Quaternary, Puerto Rico) are both larger than the Wikieup fossil. Small, *Columbina*-sized doves from the Thomas Farm local fauna (early Miocene, Florida) are as yet unnamed (Olson 1985).

Order PASSERIFORMES (Linnaeus) 1758
Family CORVIDAE Vigors 1825
Subfamily CORVINAE (Vigors) 1825
Genus *Corvus* Linnaeus 1758

Remarks: A medium-sized corvid, clearly referable to the genus *Corvus,* the crows and ravens, as opposed to the various genera of magpies, jays, treepies, the nutcracker (all subfamily Garrulinae), etc., by the following characters: (1) metacarpal 3 relatively straight, (2) distal end of metacarpal 3 wider dorsoventrally, and (3) distal metacarpal symphysis on the internal side with a very deep, distinct pit distally, and a corresponding ridge proximally, separating the pit from the intermetacarpal symphysis.

Corvus galushai sp. nov.
Fig. 7

Holotype: complete left carpometacarpus, F:AM 11282.

Type locality: Bird Bone Quarry, SW¼, NE¼, sect. 29, T.15N, R.12W, Greenwood Peak Quadrangle, Mohave County, Arizona.

Horizon and age: Big Sandy Formation, late Hemphillian, late Miocene. Dated (fission-track, zircon) at 5.12–5.29 mybp.

Measurements of holotype: see Table 8.

Etymology: named for the late Theodore Galusha, in recognition of his work on the Big Sandy Formation.

Diagnosis: The specimen is distinct from extant species of *Corvus* in the following characters: (1) external ligamental attachment more prominent, (2) external side of metacarpal 3 wider dorsoventrally, and intermetacarpal space narrower, (3) metacarpal 3 divided for entire length into distinct and clearly separated dorsal and external surfaces. In the other members of the genus and family, metacarpal 3 "twists" distally: the dorsal surface, proximally, becomes the external surface, distally. This specimen is from a very small crow; the carpometacarpus is identical in length with that of *Corvus imparatus* (the Mexican Crow, of Mexico and the southwestern United States), and it is shorter than those of almost all the other modern members of the genus.

Remarks: In the subfamily Corvinae there are seven extinct fossil species. Four are known from carpometacarpi. Three of these, *Corvus pliocaenus* (Portis) 1888, *Corvus wetmorei* Brodkorb 1959 (lately synonymized with extant *C. nasicus* (Olson and Hilgartner 1982) and *Corvus antecorax* Mourer-Chauvire 1975, from the Upper Pleistocene and Lower Pleistocene of France and Rumania, the Upper Pleistocene of the Bahamas, and the Middle and Upper Pleistocene of France, respectively, are larger than the form reported here. *Corvus larteti* Milne-Edwards 1871, from the Upper Miocene of France, is much smaller than the Wikieup specimen. It is so small, in fact, that one might reasonably wonder if it were correctly identified; it does, however, have characters (2) and (3) given above for *Corvus* (the shaft of metacarpal 3—character 1—is missing). The other three extinct corvines, none known from carpometacarpi, are *Corvus hungaricus* Lambrecht 1916 (Lower Pleistocene of France), *Corvus pumilis* Wetmore 1920 (Quaternary and Recent of Puerto Rico and the Virgin Islands), and *Corvus moriorum* Forbes 1892 (Quaternary of Chatham Islands and New Zealand). Comparison of the sizes of the known material of these species with the comparable elements of *Corvus imparatus* suggests that all were larger than the Wikieup crow.

Corvus galushai becomes the oldest known member of the genus, if the placement of *Corvus larteti* is regarded as uncertain.

DISCUSSION

In this section I will describe the composition of the avifauna, discuss possible reasons for the accumulation of such a great number of bird fossils, and offer explanations for such peculiarities of the fauna as the preponderance of fossils of ducks, geese, and swans, and the underrepresentation of hindlimb elements.

The Wikieup avifauna includes a minimum of 38 species in 13 families (Table 9). These have been identified from 1,036 specimens representing a minimum of 160 individuals (Table 9). The 11 species of ducks, geese, and swans make up by far the greatest proportion of the avifauna, 81% by number of specimens and 70% by minimum number of individuals (MNI) (Table 10). Following the family Anatidae in abundance is the Ciconiidae, represented by one species comprising approximately 9% by number of specimens and 7% by MNI. None of the other families make up more than 5% of the fauna, by either specimens or individuals, with rails and recurvirostrids being the most common of these, and the flamingo, plover, dove, and the new crow the least common.

It is highly unlikely, of course, that these proportions accurately reflect the composition of the original avifauna. Wolff (1975) has concluded that, for mammals, it is necessary to collect 12,000 to 25,000 specimens from a site, obtained by careful washing, screening, and sorting of all sediment samples, in order to obtain an accurate picture of the composition of a fauna. It is unlikely that it would take fewer specimens for birds. Given the absence of procedures designed to obtain bones of smaller vertebrates from the Big Sandy Formation quarries, small birds are certainly underrepresented in the collection. In addition, the bones of the smaller species are less likely to have been preserved, being more delicate and prone to destruction.

The preponderance in the fauna of anatids cannot, however, completely be attributed to these biases towards collection and preservation of birds of large size. The two smallest, teal-sized ducks (*Anas* spp. B and C) are the third and fourth most common species in the fauna. Their numbers greatly exceed those of the comparably sized stilt *Himantopus olsoni,* the godwit *Limosa* sp., and the gull *Larus* sp. Thus, the great number of anatids must be attributed either to their actually being the predominant birds in the fauna, or to some sort of preservational or depositional bias that selectively favored anatids.

It seems likely that the vertebrates preserved at the quarries were transported there after death, given the nearly complete absence of fossils in other, lithologically similar, parts of the formation. As the most aquatic of the taxa represented here, it might simply be that anatids were dying in more likely locations for subsequent transport of bodies. Obviously this is true when comparing the anatids to the terrestrial species, such as the accipitrids, the dove, and the crow. It might also be true when comparing the anatids to the other birds such as rails, stilts, and sandpipers. These birds, while associated with water, do not frequent the deeper, more open water where ducks are more likely to be found and where dead, bloated, and floating bodies would be less hindered by vegetation and easily moved by wind and waves to a distant point of accumulation. Interestingly, the most common anatids in the fauna are the ducks of the genus *Anas* and the unusual, possibly very aquatic, goose *Branta woolfendeni,* whereas the least common are the geese of the genus *Anser* and the swan *Cygnus* (Table 11). Today, geese and swans are relatively more terrestrial than ducks and they spend much time feeding and resting in fields. Thus, within the Anatidae, as in the avifauna as a whole, there is a pattern of greater preservation of the more aquatic forms. There is, however, little information available on just where birds actually die, and this correlation might be misleading—ducks, although more aquatic than, for example, stilts, might not die in water more frequently than stilts.

Another possible explanation for the greater numbers of anatids and of particular species of anatids might be differential mortality. From time to time today there are massive die-offs of various species of anatids from disease. The disease that takes the greatest toll of waterfowl populations is botulism, caused by ingestion of the neurotoxin produced during the metabolism of the bacterium *Clostridium botulinum* (*C. botulinum* Type C being the agent in most cases). The disease is most common in shallow, brackish, slightly alkaline marshes and lakes of the western United States, where it was first identified early in this century as a major cause of waterfowl mortality (Sciple 1953; Jensen and Williams 1964; Kalmbach 1968). Jensen and Williams (1964) noted the conditions associated with heavy mortality (p. 336):

> Reflooding of a gently sloping, moist shoreline exposed by receding water levels is commonly followed by botulism losses. A possible explanation for this apparent cause-and-effect relationship is that the moist mud between the water's edge and dry soil (the fringe area) serves as an incubator. Here, free of the diluting and heat

TABLE 9

NUMBER OF SPECIMENS OF EACH ELEMENT OF THE SKELETON, TOTAL NUMBER OF SPECIMENS, AND MINIMUM NUMBER OF INDIVIDUALS FOR EACH SPECIES IN THE FAUNA; TOTALS FOR EACH FAMILY; AND TOTALS FOR THE ENTIRE FAUNA

	Element															
Taxon	Skull	Furc	Ster	Pelv	Scap	Cora	Hum	Ulna	Radi	Carp	Carp Phal	Femu	Tibi	Tars	No. spec.	Min. no. inds.
Podilymbus sp.						2								3	5	2
Podiceps sp.							1	1					1		3	2
Podicipedidae TOTAL						2	1	1					1	3	8	4
Ciconia sp.	2	3	1		3	13	7	7	2	21	1	4	9	17	90	11
Cygnus mariae	1	1		1	4	11	9	9	9	11		2	1		59	5
Anser arenosus					1	8	6	4	3	7	2	1			32	6
Anser arizonae	1	4	6	4	6	16	9	6	5	7	1	4		1	70	6
Branta woolfendeni	4	4	3		23	38	43	43	23	64	9	20	14	18	306	31
cf. *Anabernicula*		1	1			16	7	2	1	7		2	3	7	47	10
Anserinae indet. sp. A							1								1	1
Anserinae indet. sp. B							1								1	1
Anas sp. A		5			6	24	34	17	11	18		1	4	1	121	17
Anas sp. B	1		1		8	22	26	13	12	23			1	3	110	15
Anas sp. C					1	17	33	15	7	7			1		81	14
Anatinae indet. sp. A								9							9	6
Anatidae TOTAL	7	15	11	5	49	152	169	118	71	144	12	30	24	30	837	112
Buteo sp. A													1		1	1
cf. *Buteo* sp. B								1							1	1
Aquila sp. A						1								1	2	1
Aquila sp. B							1		1	1				1	4	1
Neophrontops sp.						2	1	1	1	2				2	9	1
Circus sp.					1										1	1
Accipitridae TOTAL					1	3	2	2	2	3			1	4	18	6
Grus haydeni							1	1	1	1	1	1	2	4	12	2
Rallus phillipsi								2		2		1	4	2	11	3
Rallus sp.					2	1	1		1				3		8	2
Coturnicops sp.							1						1	1	3	1
gen. et sp. indet.							1	2							3	1
Rallidae TOTAL					2	1	3	4	1	2		1	8	3	25	7

TABLE 9
CONTINUED

	Element														
Taxon	Skull	Furc	Ster	Pelv	Scap	Cora	Hum	Ulna	Radi	Carp	Carp Phal	Femu	Tibi	Tars	No. spec.	Min. no. inds.
Himantopus olsoni						2	3	2				2	6	6	21	4
Recurvirostra sp.							2								2	1
Recurvirostridae TOTAL						2	5	2				2	6	6	23	5
Phoenicopterus sp.												1			1	1
Charadrius sp.							1								1	1
cf. *Limosa* sp.						1									1	1
Tringa sp. A														1	1	1
cf. *Tringa* sp. B									1						1	1
cf. *Calidris* sp. A								1		1					2	1
cf. *Calidris* sp. B						1	2	2		2			1		8	2
cf. *Calidris* sp. C							2	1		1					4	2
Scolopacidae TOTAL						2	4	4	1	4			1	2	17	8
cf. *Larus* sp.								1	1						2	1
Zenaida cf. *Zenaida prior*														1	1	1
Corvus galushai										1					1	1
TOTAL	9	18	12	5	55	175	193	140	79	176	14	39	52	71	1,036	160

TABLE 10

For Each Element in the Skeleton, Its Percentage of the Total Specimens in Each Family and in the Entire Collection; for Each Family, Its Percentage Representation in the Collection, Calculated by (1) the Number of Specimens from that Family, and (2) the Minimum Number of Individuals in that Family. For Example, for Podicipedidae, 25% of the Specimens are Coracoids. The Eight Grebe Bones Make Up 0.8% of the Total Collection of 1,036 Specimens; the Minimum of Four Grebe Individuals Makes Up 2.5% of the Total Minimum Number of Individuals, 160

	Element														
Family	Skull	Furc	Ster	Pelv	Scap	Cora	Hum	Ulna	Radi	Carp	Carp Phal	Feme	Tibi	Tars	No. spec.	Percent of inds.
Podicipedidae						25	12.5	12.5					12.5	37.5	0.8	2.5
Ciconiidae	2.2	3.3	1.1		3.3	14.4	7.8	7.7	2.2	23.3	1.1	4.4	10.0	18.8	8.7	6.9
Anatidae	0.8	1.8	1.3	0.6	5.9	18.2	20.2	14.1	8.5	17.2	1.4	3.6	2.9	3.6	80.8	70.0
Accipitridae					5.6	16.7	11.1	11.1	11.1	16.7			5.6	22.2	1.7	3.8
Gruidae							8.3	8.3	8.3	8.3	8.3	8.3	16.6	33.3	1.2	1.3
Rallidae					8.0	4.0	12.0	16.0	4.0	8.0		4.0	32.0	12.0	2.4	4.4
Recurvirostridae						8.7	21.7	8.7				8.7	26.1	26.1	2.2	3.1
Phoenicopteridae												100.0			0.1	0.6
Charadriidae							100.0								0.1	0.6
Scolopacidae						11.8	23.5	23.5	5.9	23.5			5.9	11.8	1.6	5.0
Laridae								50.0	50.0						0.2	0.6
Columbidae														100.0	0.1	0.6
Corvidae										100.0					0.1	0.6
Total	0.9	1.7	1.2	0.5	5.3	16.9	18.6	13.5	7.6	17.0	1.4	3.8	5.0	6.9	—	—

TABLE 11

RELATIVE ABUNDANCES OF THE 11 SPECIES OF ANATIDAE IN THE WIKIEUP AVIFAUNA, EXPRESSED AS PERCENTAGES OF TOTAL NUMBER OF SPECIMENS AND TOTAL MINIMUM NUMBER OF INDIVIDUALS OF ANATIDAE

Species	Percent of no. of specimens	Percent of minimum no. of inds.
Cygnus mariae	7.0	4.5
Anser arenosus	3.8	5.4
Anser arizonae	8.4	5.4
Branta woolfendeni	36.6	27.7
cf. *Anabernicula*	4.5	8.9
Anserinae indet. sp. A	0.1	0.9
Anserinae indet. sp. B	0.1	0.9
Anas sp. A	14.5	15.1
Anas sp. B	13.1	13.4
Anas sp. C	9.6	12.5
Anatinae indet. sp. A	1.0	5.1

> insulating effects of the water, *Clostridium botulinum* can grow and produce toxin in the entrapped organic materials. When subsequent reflooding covers such a fringe area with water and makes it attractive to waterfowl, toxin-containing materials are consumed when they feed.

Outbreaks of botulism occur most heavily in late summer and early fall (Sciple 1953; Jensen and Williams 1964). In addition, Sciple (1953) noted (p. 7) that "Migrant birds are particularly prone to intoxication, possibly because of heavy feeding activity after arrival from long flights" and "The malady is further associated particularly with highly organic old-lake-bottom soils."

Although any bird species living at or near a marsh or lake with botulism might be affected by the disease, a definite relationship exists between the mortality of a species and its feeding habits. Those species that find more of their food in the marsh mud where *C. botulinum* thrives are more common victims (Jensen and Williams 1964). Thus, mortality in outbreaks today is greatest among the "dabbling ducks" such as the Northern Pintail (*Anas acuta*), the Green-winged Teal (*A. crecca*), the Blue-winged Teal (*A. discors*), the Gadwall (*A. strepera*), and the Mallard (*A. platyrhynchos*) (Sciple 1953). Less common victims are geese, swans, and diving ducks, which do not typically feed in shallow water areas above mud, and species of other families. The mortality of the affected waterfowl species is tremendous. According to Sciple (1953: p. 3), "Some rough estimates of mortality in the enormous outbreaks in the vicinity of Great Salt Lake have placed the total number of dead at around 300,000 birds in a single year. During one of these serious years, workers picked up and buried nearly 47,000 carcasses from what must have been a relatively small area."

The species of the Wikieup avifauna occur in the proportions that one would expect if they represent mortality from botulism (Tables 9, 10, 11). Most common, of course, are waterfowl. Among the waterfowl, the most common are *Branta woolfendeni* and *Anas* spp. A, B, and C, all four of which were probably shallow water feeders. Much less common are the other geese, the swan *Cygnus mariae,* the two indeterminate anserines, and the indeterminate anatine, which was possibly a diving duck such as an eider (*Somateria* spp.).

Less common than *Branta woolfendeni* and the dabbling ducks, but more common than the other waterfowl is the stork, *Ciconia* sp. Storks do not occur today in the parts of North America where botulism is common, so there is no information on stork mortality from the disease. The only stork found in the United States today, *Mycteria americana* (not counting the accidental *Jabiru mycteria*), "prefers to feed in shallow, muddy ponds, marshes, and sloughs . . ." (Bent 1926: p. 62). This kind of area is similar to that preferred by dabbling ducks, and might also have been favored by the extinct Wikieup stork.

An ornithologist visiting that ancient lake of Arizona might have observed a scene like the one described by Jensen and Williams (1964: p. 333):

> We start off with a light heart, but as we near the marsh, we stop abruptly in shock and horror. The shoreline, where only last evening we saw thousands of sleek, apparently healthy birds, is now littered with their bodies. Most of them are ducks, but here and there we see a Canada goose, a gull, an avocet, a black-necked stilt. . . .

In light of these reports, it is interesting to note the difference in the nature of the fossil material between Bird Bone Quarry and Clay Bank Quarry. The specimens from the former consist mostly of entire elements with relatively minor damage, and there is some associated material. The specimens from the latter consist mostly of ends of limb bones, with greater damage than the Bird Bone Quarry specimens, and only one of the sets of associated material in the collection comes from this quarry. Possibly the bones from the two quarries accumulated in different ways: the Bird Bone Quarry material from a sudden massive die-off as a result of disease, with relatively little disarticulation of carcasses prior to transport, little damage to bones, and rapid burial; the Clay Bank Quarry material from normal mortality, with gradual accumulation of random skeletal elements transported to the site after disarticulation of carcasses and damage to the bones over time.

Very useful for corroboration of catastropohic vs. attritional death would be more information on the exact nature of the bird-bearing fossil deposits—the density of fossils, the frequency of associated material, whether the fossils occur in a distinct, shallow layer or layers, and so on. The bones in the blocks that I prepared (Fig. 2) were very closely packed, and all bones occurred on the same level in the block, no bones being found deeper. However, reliable answers to these questions can come only from further excavation of the quarries.

Although it seems likely that the avifauna of the Big Sandy Formation represents a catastrophic death assemblage, the actual cause will probably never be determined. I can think of no way to prove massive death from disease as opposed to, for example, a sudden winter storm such as has caused great mortality on the Great Lakes in winter (pers. obs.).

One must conclude that this collection of fossil birds does not accurately reflect the composition of the original avifauna as a whole because (1) there was probably some bias in favor of collection of large species, and (2) the Anatidae and possibly the stork are disproportionately represented because of their greater susceptibility to a disease such as botulism. Within the Anatidae, *Branta woolfendeni* and the dabbling ducks are overrepresented, but the abundances of those four species relative to one another are probably as in the living population.

One final peculiarity of this avifauna must be considered, namely the poor representation of hindlimb elements (Table 10). This is particularly pronounced in the ducks, geese, and swans. An explanation for this might be found in disarticulation patterns of bird skeletons. Little information is available on the subject, but Bickart (1984) reported patterns for six carcasses of Rock Doves (*Columba livia*) observed on a stream floodplain in Baltimore, Maryland. He noted (1) early disarticulation of hind limb joints, and (2) completion of leg disarticulation before completion of wing disarticulation. As noted above, the Big Sandy Formation deposits probably represent birds transported from their place of death to accumulate in one area. It seems probable that most of the carcasses arrived at their place of final burial without their legs, those having dropped off to be buried in some other unsampled part of the lake during the journey of the bloated bodies to the southern shore, carried by wind-blown waves.

The greater differential preservation of leg bones among non-anatid taxa cannot be explained with confidence, because the total number of specimens is so small; it might be real or simply a sampling effect.

In light of the potential biases, only a few brief, qualitative comments should be made on how the Wikieup avifauna compares with the other significant pre-Pleistocene avifaunas. The Wikieup avifauna shares several families with all or most of the other four. These include Podicipedidae, Anatidae, Accipitridae, Rallidae, Phoenicopteridae, and Scolopacidae. Notably absent from the Wikieup fauna are herons (Ardeidae), which occur in the faunas of Love Bone Bed, Bone Valley, and Rexroad, although not in the highly marine Lee Creek. One would expect these large birds, strongly associated with water, to be preserved if they were present, and so perhaps they did not occur in the area at that time. The Florida and North Carolina faunas all include a number of marine taxa not found in the inland Wikieup fauna. In this feature, Wikieup and Rexroad are similar, although the latter also includes several taxa not found at Wikieup, for example, ibises (Plataleidae), New World Vultures (Cathartidae), falcons (Falconidae), gallinaceous birds (Phasianidae), owls (Strigidae), parrots (Psittacidae), and woodpeckers (Picidae).

The different kinds of birds in the Wikieup fauna give clues to the variety of habitats found in the area of the ancient lake. An important question to ask, however, is whether this lake was a breeding ground for all these species, or whether it was just a migration stop for many of them. Birds can often be found on migration in places quite unlike those in which they breed. The dabbling ducks, the flamingo, the stork, and the crane all indicate a predominantly shallow lake, preferred by them for feeding, although the several specimens that might belong to an eider (*Somateria*) suggest some deeper water. The geese and swans suggest nearby grasslands, today a common kind of feeding area for those birds. The rails and grebes perhaps indicate an abundance of marshy vegetation around the edges of the lake, and the various shorebirds suggest the presence of exposed mudflats. The stork and the various hawks, eagles, and vultures indicate the presence of trees nearby, in which they would have nested or perched.

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SUMMARY

The fossil avifauna of the late Hemphillian (late Miocene-early Pliocene) Big Sandy Formation, Mohave County, Arizona, includes 38 species, in 13 families, of which six are described as new. These include a stilt, *Himantopus*; a swan, *Cygnus*; three geese, two species in *Anser* and one in *Branta*; and a crow, *Corvus*. Most of the taxa are forms associated with water, including species in the families Podicipedidae, Ciconiidae, Anatidae, Gruidae, Rallidae, Recurvirostridae, Phoenicopteridae, Charadriidae, Scolopacidae, and Laridae. Also represented are more terrestrial families such as Accipitridae, Columbidae, and Corvidae. Notable are a probable "pygmy goose," *Anabernicula*; a species of the vulture *Neophrontops*; the first extinct harrier, *Circus* from North America; additional material for *Grus haydeni* Marsh and *Rallus phillipsi* Wetmore; the earliest *Coturnicops* rail; the first pre-Pleistocene record of the stilts, *Himantopus*; the first definite pre-Pleistocene record of the plovers, *Charadrius*; and the oldest satisfactory record of the crows, *Corvus*.

The Anatidae dominate the fauna, making up about 80% of the specimens. It is suggested that the relative frequencies of the various families and species in the fauna do not represent the original composition of the fauna, but have been biased primarily by differential mortality caused by the greater susceptibility of some species, particularly ducks, to the disease of botulism. The specimens collected from the main quarry, Bird Bone Quarry, probably represent catastrophic death by disease, whereas the specimens from the secondary Clay Bank Quarry probably represent an attritional death assemblage and gradual accumulation of fossils.

The peculiar lack of hind limb elements in the collection is attributed to their having become disarticulated and lost from skeletons prior to or during transport, and prior to burial.

The taxa in the fauna suggest a warm, shallow lake environment with surrounding marshes and trees.

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APPENDIX I

Explanations of Measurements (Adapted from Becker 1985)

Scapula

1. W-NECK. Least width of the neck of the scapula.
2. W-PROX. Proximal width from the external tip of the glenoid facet to the dorsal margin of the scapular head.
3. ACR-GLN. Length from tip of acromion through external tip of glenoid facet.

Coracoid

1. HEAD-IDA. Length from head through internal distal angle.
2. HEAD-SF. Length from head through scapular facet.
3. D-HEAD. Least depth of head.
4. W-SHAFT. Least width of shaft.

Humerus

1. LENGTH. Greatest length from the head of the humerus through the midpoint of the lateral condyle.
2. W-SHAFT. Least width of shaft.
3. D-SHAFT. Least depth of shaft.
4. W-PROX. Transverse width of proximal end from the external tuberosity to the most ventral face of the bicipital crest.
5. D-PROX. Depth of proximal end, from the bicipital surface to the internal tuberosity, measured at right angles to the long axis of the shaft.
6. W-DIST. Transverse width of distal end from the entepicondylar prominence to the ectepicondylar prominence.
7. D-DIST. Depth of distal end from cranial face of external condyle through ridge slightly mediad from external tricipital groove, measured at right angles to the long axis of the shaft.

ULNA

1. LENGTH. Greatest length from olecranon through tip of internal condyle.
2. W-SHAFT. Transverse width of midshaft.
3. D-SHAFT. Depth of midshaft.
4. W-PROX. Greatest transverse width of proximal articular surface.
5. D-PROX. Depth of proximal end from cranial tip of internal cotyla to caudal margin of shaft of ulna.
6. ECON. Length from external condyle through ventral face of distal end.
7. CPTB. Length from carpal tuberosity through lateral face of distal end.

RADIUS

1. LENGTH. Greatest length from the radial head through distal end of the radius.
2. W-SHAFT. Least width of shaft.
3. D-SHAFT Least depth of shaft.
4. W-PROX. Greatest transverse width of proximal end.
5. D-PROX. Greatest depth of proximal end.
6. W-DIST. Greatest transverse width of distal end.
7. D-DIST. Greatest depth of distal end.

CARPOMETACARPUS

1. LENGTH. Greatest length from most proximal portion of the carpal trochlea through facet for digit III.
2. W-CARPAL. Transverse width of carpal trochlea measured at the proximal edge of the articular facet.
3. D-PROX. Depth of proximal end from tip of process of metacarpal I through caudal part of carpal trochlea, measured at right angles to the long axis of the shaft.
4. W-SHAFT. Transverse width of midshaft of metacarpal II.
5. D-SHAFT. Depth of midshaft of metacarpal II.
6. W-DIST. Transverse width of distal end from edge of facet for digit II through facet for digit III.
7. D-DIST. Greatest depth of distal end, measured across dorsal edge of facet for digit II.

FURCULA

1. LENGTH. Greatest length, measured from symphysis to end of clavicle.
2. D-PROX. Greatest depth of symphysis.

FEMUR

1. LENGTH. Greatest length from trochanter through lateral condyle.
2. W-SHAFT. Least width of shaft.
3. D-SHAFT. Least depth of shaft.
4. W-PROX. Transverse width of proximal end, measured from the head of femur through lateral aspect of trochanter, taken at right angles to the long axis of the shaft.
5. W-DIST. Greatest transverse width of distal end.
6. D-MCON. Greatest depth of medial condyle.

TIBIOTARSUS

1. LENGTH. Greatest length from interarticular area on proximal articular surface through lateral condyle.
2. W-SHAFT. Least width of shaft.
3. D-SHAFT. Least depth of shaft.
4. W-PROX-M. Transverse width of proximal articular surface from articular facet for fibular head to medial border of proximal articular surface.
5. D-PROX. Depth of proximal end from most caudal edge of medial articular face to the most cranial point of the cranial cnemial crest.
6. W-DIST-CR. Transverse width of distal end, measured across cranial portion of condyles.
7. D-ICON. Depth of area intercondylaris.

TARSOMETATARSUS

1. LENGTH. Greatest length from intercondylar eminence through trochlea for digit III.

2. W-SHAFT. Least width of shaft.
3. D-SHAFT. Least depth of shaft.
4. W-PROX. Greatest transverse width of proximal articular surface, measured across dorsal surface.
5. D-PROX. Depth from dorsal edge of proximal articular surface to closest hypotarsal canal.
6. W-D-SHAFT. Width of shaft at cranial edge of distal canal.
7. TRII-TRIV. Greatest transverse width between plantar portion of trochlea II and plantar portion of trochlea IV.
8. TRIII-TRIV. Greatest transverse width from trochlea III through trochlea IV.

CRANIUM

1. LENGTH. Length from nasal-frontal suture to posterior-most part of supraoccipital.
2. INT-ORB. Shortest length between dorsal margins of orbits.

ROSTRUM

1. LENGTH. Greatest length.
2. ANT-LENGTH. Length from anterior end of premaxillary to anterior end of nares.
3. W-NARES. Maximum width of nares.
4. L-NARES. Maximum length of nares.
5. WIDTH. Width of mandible at nares.
6. DEPTH. Depth of mandible from nasal-frontal suture to edge of tomium.

MANDIBLE

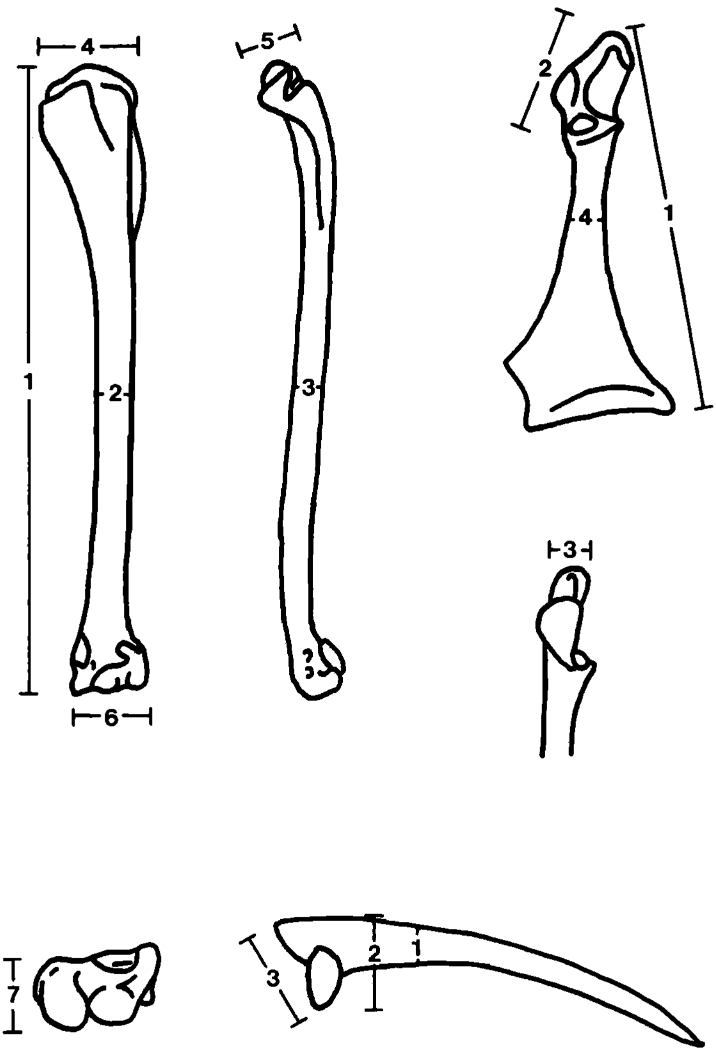
1. LENGTH. Greatest length.
2. L-SYMPH. Length of symphysis.
3. W-SYMPH. Width of symphysis.
4. D-SUR. Depth from dorsal edge of surangular.

STERNUM

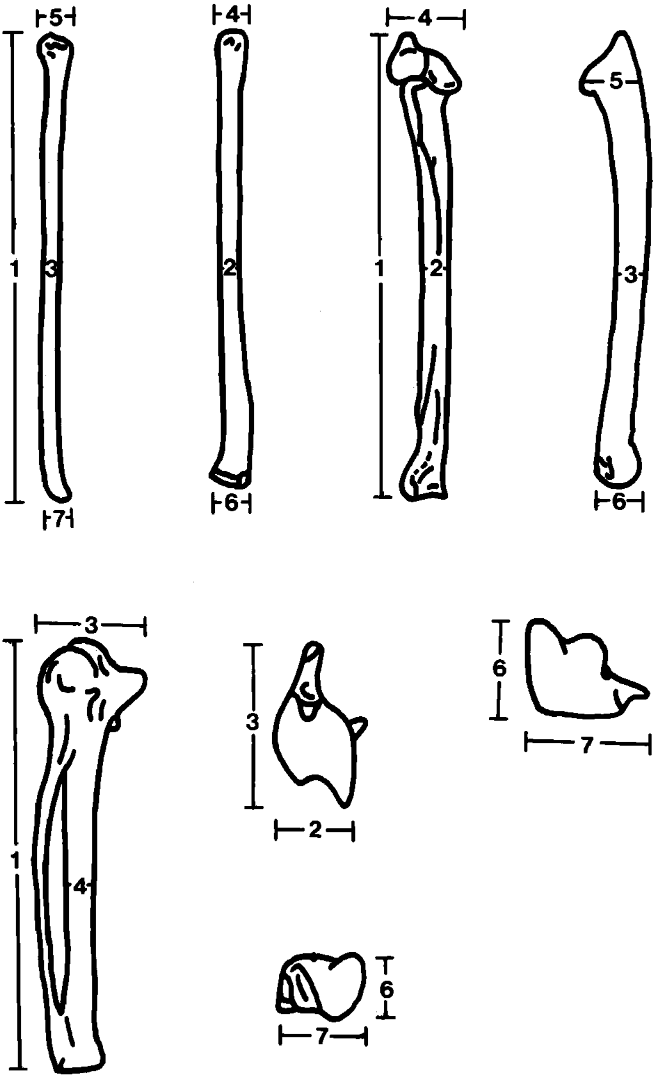
1. D-CARINA. Depth of carina from the tip of the ventral manubrial spine to the anterior ventral tip of the carina.
2. VMS-COST. Length from tip of ventral manubrial spine to anterior edge of the first costal facet.

PELVIS

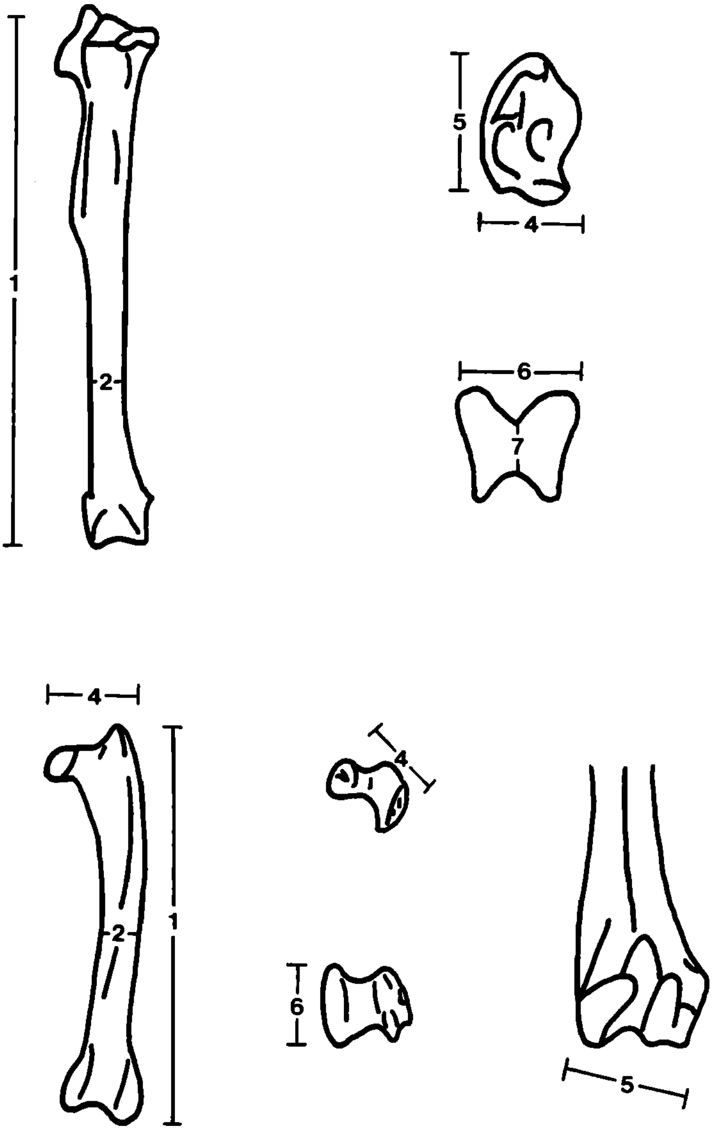
1. L-SYNSAC. Greatest length of synsacrum.
2. L-ANT. Length from anterior end of the synsacrum to the anterior end of the acetabula.
3. W-TROCH. Width between antitrochanters.



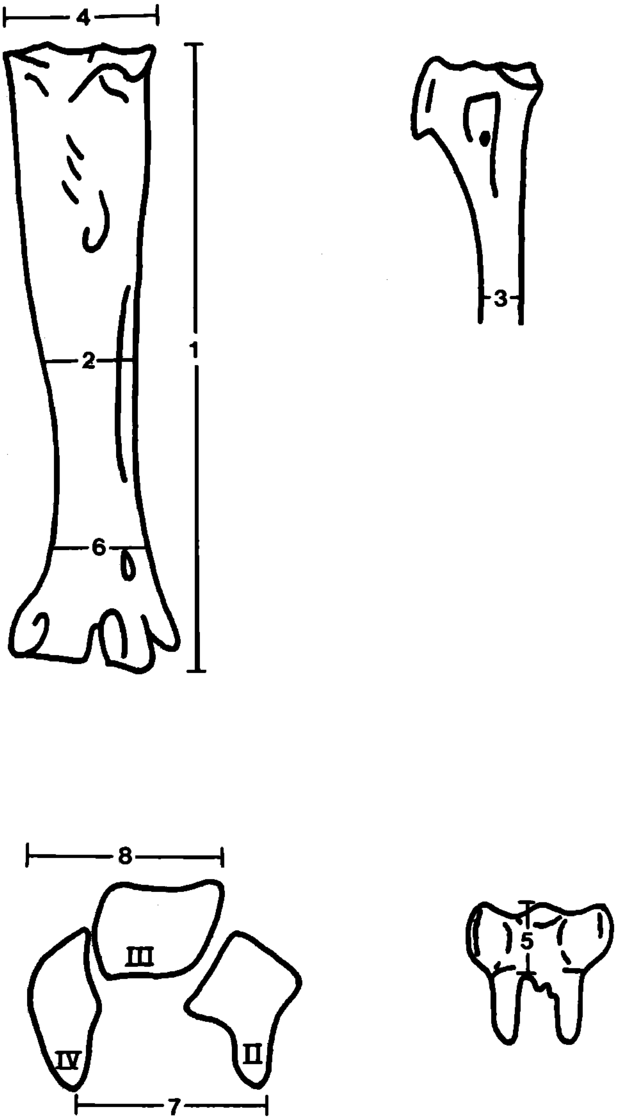
Appendix Fig. 1.1. Measurements taken of the scapula, coracoid, and humerus.



Appendix Fig. 1.2. Measurements taken of the ulna, radius, and carpometacarpus.



APPENDIX FIG. 1.3. Measurements taken of the femur and tibiotarsus.



APPENDIX FIG. 1.4. Measurements taken of the tarsometatarsus.

PART II

FOSSIL BIRDS OF THE SAN DIEGO FORMATION, LATE PLIOCENE, BLANCAN, SAN DIEGO COUNTY, CALIFORNIA

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DEDICATION
TO HILDEGARDE HOWARD

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INTRODUCTION

Late Pliocene (approximately 1.8 to 3.0 mybp) marine sedimentary rocks occur widely in southwestern San Diego County, California. These sandstones lie unconformably on Eocene deposits and are capped by a layer of Pleistocene sediments. The marine sediments were deposited in a large embayment extending from Mission Valley in the north into northern Baja California, Mexico, in the south and from the Pacific Ocean east to approximately the eastern limits of the cities of San Diego and Bonita.

The fossil birds recovered from the San Diego Formation are all marine species except for a single songbird. Those identified previous to this study include a loon, a shearwater, two boobies, a cormorant, a murrelet, an auklet, and three flightless auks. In studying the fossil bird material in the collection of the Paleontology Section, Department of Geology, San Diego Natural History Museum, I identified 39 taxa of birds, 22 to the species level. The San Diego Formation now has the largest and most diverse avifauna of any known deposit of the same general time.

The fossil bird record for the San Diego Formation began with the referral of a humerus to the extinct flightless auk *Mancalla californiensis* Lucas by Loye Miller (1933:34). In 1937, Miller named a supposed new genus and species of puffin, *Pliolunda diegense,* from San Diego. A second and more complete humerus of *Mancalla* was described by Miller (1946) and he established the Mancallidae, a family very close to the Alcidae.

Howard (1949) made the first comprehensive report on the fossil birds from the San Diego Formation, listing 5 orders, 8 families, 8 genera, and 8 species. Previously named species identified by Howard included *Gavia*? *concinna* Wetmore, *Podiceps parvus* (Shufeldt), *Mancalla californiensis* Lucas, and *Pliolunda diegense* Miller. Howard named 4 new species: *Puffinus kanakoffi, Phalacrocorax kennelli, Miosula recentior,* and *Brachyramphus pliocenus.*

Miller and Howard (1949) studied all the known skeletal remains of *Mancalla* and concluded, as previously suggested by Miller (1946:35), that a second species, smaller than *Mancalla californiensis,* was represented in the formation. The fossil "puffin" *Pliolunda* was also reevaluated and synonymized with *Mancalla,* making the name *Mancalla diegensis* available for the smaller species.

Brodkorb (1953:212) reviewed the Pliocene loons of North America and Europe and named *Gavia howardae* as a new species from the San Diego Formation, a loon smaller than *G. concinna,* which was tentatively identified by Howard (1949: 185) from the San Diego fauna.

In 1956, Miller named a new genus and species of owl, *Lechusa stirtoni,* supposedly from the San Diego Formation and presumed to be related to the Barn Owl, *Tyto alba.* Reexamination of the holotypical coracoid, UCMP 45331, showed it was not a fossil but a bone from the extant owl, *Tyto alba* (Chandler 1982).

Miller and Bowman named 3 more species from the San Diego Formation in 1958. These included a small grebe, *Podiceps subparvus,* a booby, *Sula humeralis,* and a fourth species of alcid, *Ptychoramphus tenuis.*

Howard (1970) reviewed the extinct genus *Mancalla,* then in the subfamily Mancallinae (Brodkorb 1967:217), and named a second species in the fauna as *M. milleri,* the smallest and most abundant species in the fauna. As previously suggested (Miller and Howard 1949:225), *M. californiensis* was deleted from the San Diego fauna.

Most recently Olson (1981) described a third species of *Mancalla, M. emlongi,* from the San Diego Formation, bringing the number of species in the fauna to 11.

MATERIALS AND METHODS

I determined character polarities by outgroup comparisons (Wiley 1981:139; Watrous and Wheeler 1981:5–9; Madison et al. 1984:84–89) using what are thought to be the most closely related families based on classifications by Mayr and Amadon (1951), Wetmore (1960), Storer (1971), Cracraft (1981), and Olson (1985b). Monophyly of each family was assumed, although as yet few of these families have been rigorously examined, osteologically, in phylogenetic analyses to the generic level. Exceptions are Livezey's (1986) analysis of anseriform genera and Siegel-Causey's study of phalacrocoracids (1988). All new taxa are diagnosed on the basis of autapomorphic (unique) characters. In the generic diagnoses, synapomorphic (shared derived) characters are given to justify generic assignments of species. I also provide differential diagnoses and discussions of shared derived characters (based on outgroup comparisons) in the "Comparisons" sections, in the hope that these will facilitate future phylogenetic analyses of bird groups by identifying phylogenetically useful characters. At the beginning of each comparative section for each group of birds, I have given the outgroup(s) used to determine these polarities.

Recently collected fossils were prepared, identified, and catalogued, and identifications were made by comparing the fossils with modern skeletons and previously identified fossils in collections at the San Diego Natural History Museum and the Natural History Museum of Los Angeles County. I have attempted to make a comprehensive listing of all referable specimens from this fauna and not a partial listing of only recently collected fossils. More than 2,000 specimens were examined. Descriptive osteological terminology used is from Howard (1929:314–324), Owre (1967), and Bock and McEvey (1969:213–218). The taxonomic sequence follows that of the American Ornithologists' Union Check-list of North American Birds (1983) and for fossils, Brodkorb's Catalogue of Fossil Birds, Parts 1–3, 5 (1963a, 1964, 1967, 1978).

All measurements are in millimeters and were taken with dial calipers. Brackets [ ] around measurements indicates an approximation because of the preserved condition of the fossil. Magnification of all figures is ×1.

Museum acronyms used in the text are as follows:

KU	Charles Dean Bunker Memorial Skeleton Collection, Museum of Natural History, The University of Kansas, Lawrence, Kansas
LACM	Natural History Museum of Los Angeles County
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley, California
SDSNH	San Diego Society of Natural History
UCLA	University of California, Los Angeles, California
UCMP	University of California Museum of Paleontology, Berkeley, California
UKVP	University of Kansas, Vertebrate Paleontology, Lawrence, Kansas
UMMP	University of Michigan, Museum of Paleontology, Ann Arbor, Michigan

USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.

GEOLOGY

The San Diego Formation is a rock unit of late Pliocene age with numerous exposures throughout the southwest corner of San Diego County, California, and northwestern Baja California, Mexico. It is the major depositional unit in the San Diego basin (Deméré 1983). It lies unconformably on the marine Eocene Mount Soledad Formation, and is covered by the nonmarine Pleistocene Linda Vista Formation. The formation in the San Diego area is delimited by the San Diego River in the north, by Rosarito Beach, Baja California, Mexico, about 26 miles to the south, and by the foothills of La Mesa to the east. Additional northern exposures (e.g., at Mission and Pacific beaches and Mount Soledad) are displaced occurrences caused by tectonic movement along the Rose Canyon fault zone (Kennedy et al. 1975). Interpretation of the stratigraphy of the San Diego Formation is complicated by the effects of activity along several fault zones present today and during the time of deposition (Thomas Deméré and Brad Riney, pers. comm.).

The San Diego Formation is divided into "lower" and "upper" units (Arnold 1903; Deméré 1982:128–130, 1983:189). The "lower" unit is a fine-grained, bluish-gray to yellowish-brown sandstone, and the "upper" unit is a more coarse-grained, yellowish-brown to red sandstone (Hertlein and Grant 1939, 1944). In general, the sandstone is friable with occasional gravel and cobble horizons interspersed throughout both units.

The molluscan fossils (Arnold 1903; Grant and Gale 1931; Woodring et al. 1940; Deméré 1982:132) and planktonic foraminifera (Mandel 1973) indicate an age no older than the late Pliocene (approximately 3.0 mybp), to at least as young as early Pleistocene (approximately 1.5 mybp). Barnes (1976:332–334) correlated the San Diego Formation with the Blancan North American provincial mammal age based upon his studies of the fossil vertebrates (mainly marine mammals) from the formation. Barnes also considered the San Diego, Niguel (Orange County, California), the upper part of the Capistrano (Orange County, California), and Merced (San Mateo County, California) formations as temporal equivalents.

SYSTEMATIC PALEONTOLOGY

Order GAVIIFORMES
Family GAVIIDAE
Subfamily GAVIINAE
Genus *Gavia* Forster
Gavia howardae Brodkorb 1953
Figs. 1–6

Holotype.—LACM 2111/1071, distal end of left humerus.

Paratypes.—LACM 2175/1080, distal end left humerus; LACM 2133/1080, distal end right humerus.

Referred material.—Ulnae—SDSNH 21084/2946, left; LACM 119375/4442, left distal end; SDSNH 27229/3265, left carpometacarpus; tarsometatarsi—LACM 117778/4442, right; SDSNH 35251/3418, right proximal end; SDSNH 23751/2971-A, proximal end of right digit III, pedal phalanx 1; SDSNH 25207/2947, fifth thoracic vertebra.

Description.—The distal end of the humerus has already been described by Brodkorb (1953:212–213).

A left ulna (SDSNH 21084) is gracile with an expanded, blade-like carpal tuberosity. The prominence for the anterior articular ligament is long, narrow, and low on the shaft; the lateral border is formed by a shallow groove. The internal cotyla is more oval than round, and the external cotyla has an unnotched external margin.

A left carpometacarpus (SDSNH 27229) is complete except for the metacarpal III. The bone is slender and has an elongate metacarpal I.

An almost complete right tarsometatarsus (LACM 117778) is gracile, laterally compressed, and short. The hypotarsus has three tendinal grooves in an anterior row, and these are enclosed in a single canal between the broken lateral calcaneal ridges. The trochlea for digit II is rotated posteriorly and is proximal to the trochlea for digit III. The relatively broad intercotylar area has the intercotylar prominence placed more towards the lateral side.

Only the proximal end of a right digit III, pedal phalanx 1 (SDSNH 23751) is preserved; this is laterally compressed and slender with a dorsolateral ledge on the proximo-external surface.

A broken fifth thoracic vertebra (SDSNH 25207) is missing both diapophyses, the hypapophysis, and the right neurapophysis. The centrum is short and narrow, and the anterior articulating surface has a broad "V" shaped ventral margin.

Comparisons.—Podicipediform and procellariiform birds were used as the outgroups to determine character polarities.

Gavia howardae was described from the San Diego Formation by Brodkorb (1953:211–214) on the basis of 3 humeri. The other two "Pliocene" species discussed by Brodkorb are now understood to be late Miocene: *G. concinna* Wetmore, 1940 is from the late Miocene (Hemphillian) Monterey County, California, and *G. palaeodytes* Wetmore, 1943 is from the late Miocene (Hemphillian) of Polk County, Florida. *Gavia brodkorbi* Howard, 1978 is late Miocene (Clarendonian) at Laguna Niguel, Orange County, California. European fossil loons include *G. egeriana* Svec, 1982 Lower Miocene (Ottnangian), Dolnice, Cheb basin, Czechoslovakia; and *G. portisi* (Regalia, 1902), middle Pliocene, Orciano Pisano, Italy.

FIGS. 1–12. *Gavia howardae*—1, 2 ulna; 3, 4 tarsometatarsus; 5, 6 carpometacarpus. *Aechmophorus elasson*—7, 8 femur; 9, 10 tarsometatarsus; 11, 12 ulna.

Recently, Howard (1982:3) assigned a tarsometatarsus to *Gavia* sp., from the late Miocene (Hemphillian) marine deposit in Oceanside, San Diego County, California.

Extant loons can be separated osteologically into two distinct groups: *Gavia stellata* (Red-throated Loon) is more gracile whereas *G. immer* (Common Loon), *G. adamsii* (Yellow-billed Loon), and *G. arctica* (Arctic Loon) are more robust. *Gavia howardae* and *G. egeriana* have slender bones as in *G. stellata. Gavia howardae* is smaller than *G. stellata,* and *G. egeriana* is smallest of the three. The blade-like carpal tuberosity is an autapomorphy for *G. howardae,* being even more slender than that of *G. stellata* and much more slender than in *G. concinna, G. brodkorbi,* or the other living loons (the ulnae of *G. palaeodytes* and *G. egeriana* are as yet unknown). The enlarged carpal tuberosity is a synapomorphy for *Gavia,* differing from the smaller, roughly triangular (plesiomorphic) condition seen in the fossil loon *Colymboides* (see Storer 1956:418–419) or in podicipediform birds. *Gavia howardae* differs from all other loons by having a shallow groove below the anterior articular ligamental prominence that is low on the ulnar shaft, whereas other loons have a deeper groove because the ligamental prominence is raised above the shaft. The anterior articular ligamental attachment on the ulna is long and narrow in the ulna of *G. howardae,* and that of its type (LACM 2111) corresponds well with the same attachment in *G. egeriana* and *G. stellata. Gavia concinna, G. brodkorbi,* and other living loons all have a shorter and broader ligamental attachment. [Howard (1978:6) also noted the similarity of the anterior articular ligamental attachments on the humeri of *G. howardae* and *G. stellata.*] The internal cotyla of *G. howardae* is more ovoid (the derived condition as compared with grebes) than round and, therefore, approaches that of *G. concinna* and differs from that of *G. brodkorbi, G. stellata, Colymboides,* and the other extant loons and podicipediform birds. The referred tarsometatarsus (LACM 117778) is not directly comparable to other fossil species because tarsometatarsi of fossil loons are otherwise unknown. However, a late Miocene tarsometatarsus (UCMP 88656) from Oceanside, California, has been assigned to *Gavia* sp. by Howard (1982:3). It is longer and more robust than *G. howardae* and *G. stellata,* as in extant loons. The more proximal placement of the distal foramen on UCMP 88656 is an autapomorphy that distinguishes it from all other fossil (including LACM 117778) or living loons, which all have a more distally placed distal foramen, a symplesiomorphy shared with grebes.

The small size and slenderness of SDSNH 23751 are the only reasons I have for referring this phalanx to *G. howardae.* Size is also the only criterion for assigning a cervical vertebra, SDSNH 25207, to *G. howardae.* The holotype of *G. portisi,* a cervical vertebra, is the size of *G. immer.*

The gracile skeleton of *Gavia howardae* resembles those of *G. stellata* and *G. egeriana* rather than the more robust skeleton of other fossil and living loons. *Gavia howardae* was larger than *G. egeriana* and *G. brodkorbi* (Table 1) but smaller than all other known fossil and living species.

Remarks.—Howard (1978:5) gave a measurement of 91.5 mm for the smallest referred humerus of *Gavia howardae* (LACM 2133) = length from distal end to distal tip of deltoid crest. This measurement is to the distal tip of the bicipital crest rather than the deltoid crest (Howard pers. comm.).

Measurements.—Carpometacarpus: length—61.4; proximal breadth—5.6; length metacarpal I—19.1.

Gavia sp. indet.

Referred material.—LACM 2110/1071, incomplete premaxillary; UCMP 45870/5520, left tibiotarsus missing cnemial crests and distal condyles; tarsometatarsi—SDSNH 35259/3418, right; SDSNH 22916/2978, right.

TABLE 1

MEASUREMENTS OF ULNAE FOR SPECIES OF *Gavia*

	G. brodkorbi		*G. howardae*		
	LACM 311731	LACM 119375	SDSNH 21084	*G. concinna*	*G. stellata* (N = 7)
Length	81.0	–	93.9	–	104.8–118.3
Proximal breadth	9.4	–	9.4	11.6[2]	9.6–10.7
Shaft[1]	4.9 × –	–	4.5 × 5.5	5.3 × 7.6[3]	4.5–5.1 × 5.3–6.0
Distal breadth of condyles	–	4.8	5.3	8.0	6.3–6.4
Distal depth through carpal tuberosity	11.3	11.6	11.7	16.6	11.3–12.3

[1] Breadth × depth at midpoint of shaft.
[2] See Howard 1978.
[3] See Brodkorb 1953.

Description.—The partial bill (LACM 2110) consists of the tip and the dorsal nasal bar. It is robust but short with a ventral groove the entire length of the bill tip.

A tibiotarsus (UCMP 45870) has a low, centrally located medial shaft ridge on the anterior surface, which gradually slopes to the external side and has a slight depression on the internal half of the shaft.

A worn yet distinctive tarsometatarsus (SDSNH 22916) is robust with a laterally compressed shaft and a shallow outer extensor groove on the anterior surface. The proximal foramina are separated by a partition of bone; the distal foramen is located close to the trochlear end. The outer calcaneal ridge of the hypotarsus is broken.

Comparisons.—Not gracile as in *Gavia howardae* and *G. stellata.* The tarsometatarsus (SDSNH 22916) is instead that of a small but robust individual (Table 2) resembling *G. arctica* and, most likely, *G. concinna* and *G. brodkorbi* as well (tarsi are unknown). *Gavia concinna* is larger than *G. arctica,* whereas SDSNH 22916 is slightly smaller than these bones in *G. howardae* (LACM 117778). The tarsometatarsus is unknown for *G. brodkorbi,* but the ulna of *G. brodkorbi* (LACM 31173) is 13.6 percent smaller than *G. howardae* (SDSNH 21084). The difference in length between that of *G. howardae* (LACM 117778) and SDSNH 22916 is 2 mm, or less than 1 percent. Unless *G. brodkorbi* had a very long foot, this tarsometatarsus does not seem properly assigned to it. Also, it is not assigned to *G. howardae* because: (1) of its overall robustness; (2) of the shallow outer extensor groove on the anterior surface, where *G. howardae* and *G. stellata* each have sharp lateral borders with a deeper groove; (3) the distal foramen is nearer the trochlear end whereas *G. howardae* and *G. stellata* have a more proximally placed distal foramen; and (4) the proximal foramina are more broadly separated by bone whereas *G. howardae* and *G. stellata* have them set closer together, almost uniting the proximal foramina. In these features SDSNH 22916 agrees more with *G. arctica* and *G. immer.*

Discussion.—The bill fragment (LACM 2110) was originally assigned (Howard 1949:185) to the late Miocene species *Gavia concinna* because of its breadth. However, it is not from a particularly long-billed individual, and the measurements given by Howard (1949:186) are close to those for *G. arctica* and equal to that species in depth of nares.

TABLE 2

MEASUREMENTS OF TARSOMETATARSI FOR SPECIES OF *Gavia*

	Gavia sp. SDSNH 22916	*G. howardae* LACM 117778	*G. stellata* (N = 7)
Length	60.8	62.8	66.1–77.5
Proximal breadth	—	10.9	11.3–12.5
Shaft[1]	3.7 × 5.4	3.4 × 5.8	3.1–3.7 × 6.0–6.6
Distal breadth	7.3	7.5	7.5–8.3

[1] Breadth × depth at midpoint of shaft.

The tibiotarsus (UCMP 45870) was referred to *Gavia howardae* by Miller (1956: 617) and described as "stockier" and slightly shorter than in *G. stellata.* The tibiotarsus of *G. stellata* is distinguishable from UCMP 45870 and that of other living loons by a centrally located medial shaft ridge bordered on both sides by deep depressions that set the ridge off as a raised rib of bone (a derived condition), as opposed to a single depression on the internal side of the shaft. Also, in *G. stellata* the tendinal groove on the anterodistal end of the tibiotarsus is more to the external side with a thin lateral border of bone (derived), whereas UCMP 45870 and the other living loons have a more centrally located groove and a thick bony lateral border. Although the tibiotarsus of *G. howardae* is unknown, the greater resemblance of that species to *G. stellata* among living loons as noted above suggests that UCMP 45870 should not be referred to *G. howardae.*

Remarks.—Based on the material preserved in the current collections, I think that *Gavia concinna* is not represented in the San Diego Formation collections. Some of the material previously referred to *G. concinna* has been reassigned to *G. howardae* (Brodkorb 1953:213; Miller 1956; Miller and Bowman 1958). An additional humerus (UCMP 45872) identified by Miller (1956:617) as *G. concinna* belongs to a cormorant (see Phalacrocoracidae gen. et spp. indet.). In addition to *G. howardae,* a robust species of loon much smaller than *G. concinna* is present in this fauna, but the material now available is insufficient to name it.

Measurements.—Premaxillary: length from bill tip to distal tip of nasal opening—22.0.

Order PODICIPEDIFORMES
Family PODICIPEDIDAE
Genus *Podiceps* Latham

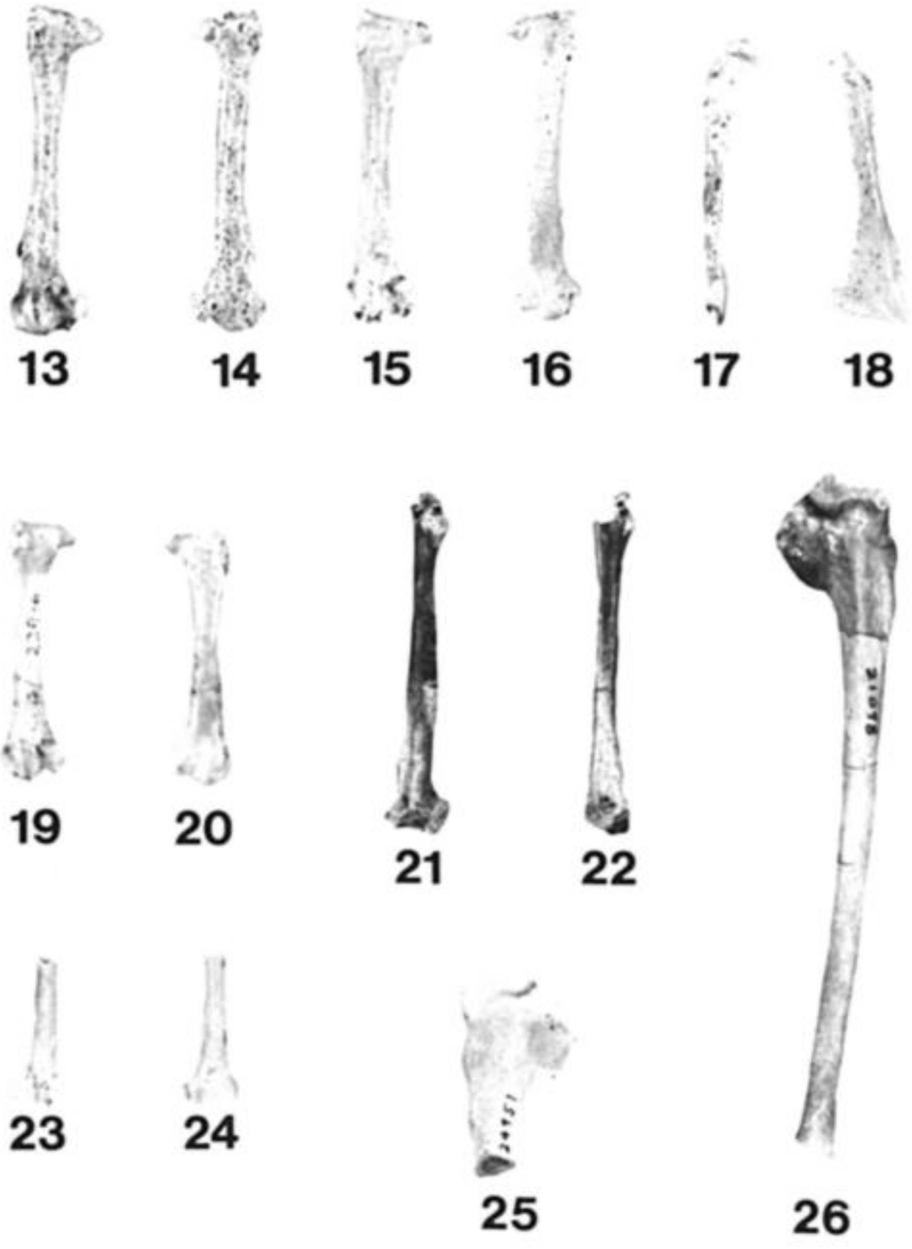
Diagnosis.—Femur of *Podiceps* with broad anterior surface of external condyle, whereas *Aechmophorus* has a narrow external condyle.

Podiceps arndti n. sp.

Figs. 27–39

Holotype.—LACM 2189/1070, right femur.

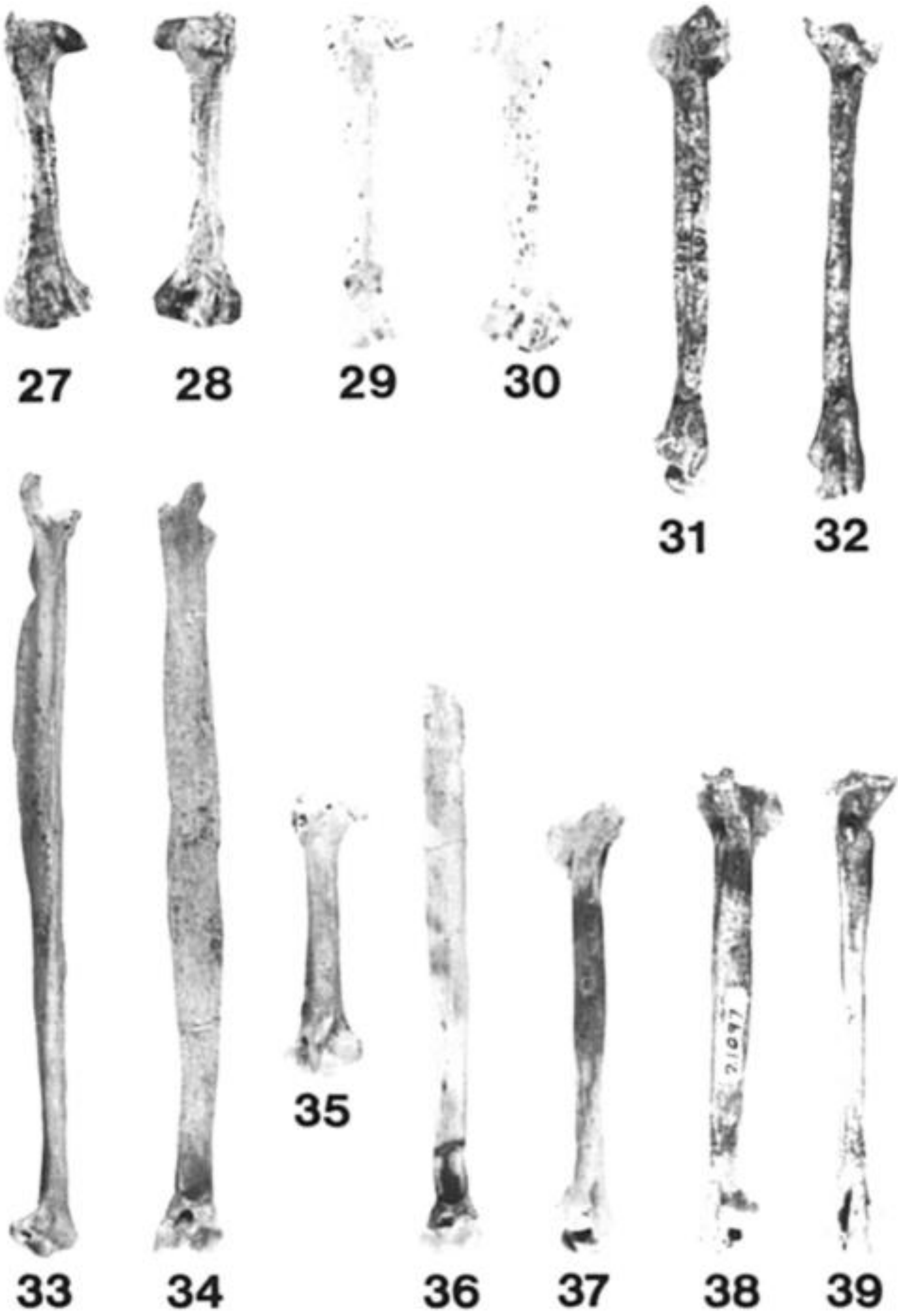
Paratypes.—Femora—LACM 2838/1095, right; UCMP 45881/V5518, left distal end; SDSNH 24961/3175, left; SDSNH 21228/2977, external half of distal end; LACM 115170/4271, associated left femur, tibiotarsus missing proximal end, and tarsometatarsus; tibiotarsi—LACM 2265/1075-B, left missing cnemial crests; UCMP 45876/V5519, left missing distal end; tarsometatarsi—SDSNH 21097/3031, right; SDSNH 27145/3265, right; SDSNH 28614/3305-A, left; LACM



FIGS. 13–26. *Podiceps subparvus*—13–16 femora; 17, 18 coracoid; 21, 22 tarsometatarsus. *P. discors*—19, 20 femur; *Podiceps* sp.—23, 24 femur; *Podiceps* indet.—25, 26 humeri.

2809/1080, right; LACM 2187/1071, left; LACM 2266/1075-B, left missing internal cotyla; SDSNH 248964/2971-A, right proximal end; UCMP 109395/V73130, right proximal end.

Etymology.—This grebe is named in honor of Joseph Arndt in recognition of



FIGS. 27–39. *Podiceps arndti*—27–30 femora; 31, 32, 38, 39 tarsometatarsi; 33, 34 tibiotarsus; 35–37 associated femur, tibiotarsus, and tarsometatarsus.

TABLE 3

MEASUREMENTS OF FEMORA FOR SPECIES OF *Podiceps*

	Length	Proximal breadth	Shaft[1]	Distal breadth	Depth external condyle
Podiceps sp.					
LACM 2605	–	–	–	8.0	–
P. discors					
SDSNH 23836	34.9	9.1	3.6 × 4.0	9.2	–
UMMP 52423	35.1	9.3	3.6 × 4.0	9.0	6.8
P. subparvus					
LACM 2568	–	–	4.2 × –	11.0	4.9
LACM 2118	–	–	4.1 × –	[10.2][2]	5.0
SDSNH 21056	43.1	10.5	4.1 × 5.0	11.1	4.9
SDSNH 24863	41.5	10.9	4.1 × 5.2	10.9	4.8
P. arndti n. sp.					
UCMP 45881	–	–	–	12.0	8.7
LACM 2189	42.1	12.0	4.7 × –	12.6	5.5
LACM 2838	44.5	12.9	5.2 × 6.4	[13.0]	–

[1] Breadth × depth of shaft at midpoint.
[2] [ ] = approximate measurements.

his fossil collecting in the San Diego Formation for the Los Angeles County Museum of Natural History.

Diagnosis.—Differs from other species of *Podiceps* in having the trochanteric ridge of the femur separated from the trochanter, and the depression inside of the trochanteric ridge more distal to the iliac surface than beside the ridge.

Description.—The holotype has a slightly laterally compressed shaft and a narrow proximal end. The trochanter is raised proximad above the level of the head of the femur, and the iliac surface slopes from the head to the trochanter. The trochanter is separated from the trochanteric ridge, which is a wedge of bone pointed out from the proximal end. The rotular groove is shallow, and the external condyle on the anterior surface is broad. The walls of the fibular groove are approximately equal in height.

The robust tibiotarsus has the cnemial crest converging at the proximal end. The supratendinal bridge is centrally located on the distal end of the shaft.

The tarsometatarsus is laterally flattened, and the lateral edges of the shaft are well defined. The intercotylar depression has a distinct drop into the single foramen in the anterior row of the hypotarsus. A canal for the tendon of M. flexor perforatus digit II is present.

Comparisons.—Gaviiformes, Procellariiformes, and other genera of podicipediform birds were used as outgroups to determine character polarities.

Podiceps arndti is slightly smaller than the living species *P. grisegena* (Red-necked Grebe) but is larger than any other grebe known from the San Diego Formation (Tables 3–5). *Podiceps parvus* Shufeldt, 1915 was previously recorded from the San Diego Formation by Howard (1949:183). *Podiceps parvus* is an early Pleistocene species equal in size to *P. arndti,* but separable osteologically by differences in the femur noted in the diagnosis.

Storer (1963:563) considered the absence of the canal for the tendon of the M.

TABLE 4
MEASUREMENTS OF TARSOMETATARSI FOR SPECIES OF *Podiceps*

	Length	Proximal breadth	Shaft	Distal breadth
P. discors				
UMMP 29079	42.3	6.9	2.3 × –	5.5
P. cf. *P. subparvus*				
SDSNH 21124	[45.9]	–	3.1 × 4.1	–
P. arndti n. sp.				
SDSNH 21097	65.4	10.5	3.3 × 5.1	7.5
SDSNH 24864	–	1.1	–	–
LACM 2187	63.1	–	3.4 × 5.6	7.2
LACM 2266	63.2	–	3.4 × 5.9	–
LACM 115170	59.3	–	2.9 × 5.0	6.8
UCMP 109395	–	9.9	–	–
SDSNH 28614	65.5	10.6	3.1 × 4.9	8.5
SDSNH 27145	64.2	10.3	3.1 × 5.2	8.3

flexor perforatus digit II in the tarsometatarsus to be diagnostic for *Podiceps.* However, I found this primitive character in skeletons of *P. major* (Great Grebe SDSNH 38347, 38348, KU 78267, 78269, 79482, 79483, 82234) and *P. rolland* (White-tufted Grebe KU 83649, 83650) as well as the present species. This canal is a symplesiomorphy for podicipediform and procellariiform birds. Because of synapomorphies shared by *P. arndti* and other extant species of *Podiceps,* I place the new species in *Podiceps.*

Podiceps subparvus Miller and Bowman 1958
Figs. 13–18, 21, 22

Holotype.—LACM 2568/1080, right femur missing proximal end.

Paratype.—LACM 2118/1071, left femur missing proximal end.

Referred material.—LACM 2354/1079, left coracoid; femora—SDSNH 21056/2977, left; SDSNH 24863/3088, left; tibiotarsi—LACM 2113/1071, left missing cnemial crests; LACM 2129/1080, left proximal end; SDSNH 21124/3006, left tarsometatarsus.

Description.—The femur has been described by Miller and Bowman (1958:6).

TABLE 5
MEASUREMENTS OF ULNAE FOR SPECIES OF *Aechmophorus*

	A. elasson			
	UMMP 48914	UMMP 45316	UCMP 109389	*A. occidentalis* (N = 4)
Length	91.3	93.9	–	97.2–109.8
Proximal breadth	–	[7.8][2]	7.1	8.2–8.7
Proximal depth	–	[6.4]	6.3	7.0–7.2
Length brachial depression	–	[16.9]	16.0	14.3–15.0
Shaft[1]	–	[3.7 × 4.4]	3.4 × 3.6	3.6–3.9 × 4.3–4.4

[1] Breadth × depth at midpoint of shaft.

[2] Measurements from UKVP 24764.

The tibiotarsus (LACM 2113) is slender and the supratendinal bridge is on the internal side of the shaft.

Comparisons.—Gaviiform and procellariiform birds were the outgroups used to determine character polarities.

Both referred femora have long, narrow shafts with flattened external sides and agree with the holotype in these features. They agree with the holotype and paratype (LACM 2118) in having an anteriorly placed external intermuscular line and a deep fibular condyle. These characters differ from those of *Podiceps arndti,* which has a robust femur, a shallower fibular condyle, and a more posteriorly placed external intermuscular line. A deep fibular condyle and more posteriorly placed external intermuscular line are primitive characters seen in *Gavia.* The tibiotarsus (LACM 2113) has a gracile shaft and the supratendinal bridge is on the internal side of the distal end, whereas *P. arndti* has a more robust shaft and the tendinal bridge is in the middle of the distal end.

Podiceps cf. *P. discors* Murray 1967
Figs. 19, 20

Holotype.—UMMP 29079/UM-K1-47, a left tarsometatarsus from the Rexroad Formation (Lower Pliocene, Blancan) in Meade County, Kansas.

Referred material.—SDSNH 23836/3168, left femur.

Description.—The femur has previously been described by Murray (1967:281).

Comparisons.—The referred femur, SDSNH 23836, agrees with a paratype femur, UMMP 52423, of *Podiceps discors* from the Hagerman Local Fauna, Glenns Ferry Formation, Twin Falls County, Idaho, in size (Table 3) as well as being narrow, as described by Murray (1967:281), with a broad obturator ridge and a narrow trochanteric ridge. The trochanter is low, whereas on *Podiceps arndti* it is raised higher above the iliac facet. Also, *P. arndti* has a deeper depression proximal to the rotular groove, thus differing from *P. discors* and the holotype of *P. subparvus* (LACM 2568). *P. discors* has a much shorter internal condyle than the external condyle, whereas *Podiceps subparvus* and *P. arndti* have the distal condyles extending distad more equally, the external condyle slightly longer. *Podiceps discors* agrees with *P. subparvus* in having steeper lateral walls of the rotular groove and differs from *P. arndti,* which has a shallower rotular groove. *Podiceps discors* also differs from *P. subparvus* and *P. arndti* by having on the anterior surface the external condyle narrow, as opposed to the broad surface that is primitive in grebes.

UMMP 52423 differs from SDSNH 23836 in having a more deeply depressed proximoposterior surface below the iliac facet. This condition is highly variable, however, in Recent species of grebes.

Discussion.—*Podiceps discors* has now been reported from three late Pliocene localities in western North America: the Rexroad, Glenns Ferry, and San Diego formations. The possibility of the same species of grebe occurring in these formations was first proposed by Murray (1967:286). *Podiceps discors* may well have had a distribution similar to the Recent species *P. nigricollis* (Eared Grebe), which occurs widely through western North America.

Additional fossil grebes in the collections (Figs. 25, 26) could not be identified to species because of the similar size of *Podiceps subparvus* and *P. arndti.*

Podiceps sp. Miller and Bowman 1958
Figs. 23, 24

Referred material.—LACM 2605/1095, left femur distal half.

Comparisons.—The femur is from a species the size of *Podiceps nigricollis* and is smaller than *Podiceps discors.*

Genus *Aechmophorus* Coues
Aechmophorus elasson Murray 1967
Figs. 7–12

Holotype.—UMMP 45316/19217, left humerus and associated left ulna from the Glenns Ferry Formation (Upper Pliocene, Blancan) in Twin Falls County, Idaho.

Referred material.—UCMP 109389/V73130, right ulna missing distal one quarter; SDSNH 24903/3176, right femur; LACM 2113/1071, left tibiotarsus missing cnemial crests; tarsometatarsi—SDSNH 24904/3176, right missing distal end; SDSNH 24905/3176, left.

Description.—The proximal end of the ulna (UCMP 109389) has a slightly ovoid internal cotyla, and the lateral margin is angular below the cotyla. A transverse ridge below the external cotyla also has a very angular margin. The anterior articular ligamental attachment and the brachial depression are both close to the proximal end. The brachial depression is shallow and pointed distally where the lateral border of the depression and the intermuscular line meet.

The shaft of the femur (SDSNH 24903) is short and laterally compressed. Both the trochanteric and obturator ridges are robust and very short. Distally, the muscle scar above the popliteal area is low on the shaft, not raised. On the anterior side a rotular groove is present but lacks steeply sloped lateral walls.

On the tibiotarsus (LACM 2113) both anterior and posterior sides of the shaft have medial shaft ridges that are constricted and raised. The posterior side of the internal condyle is flared laterally and is long. There is a notch between the anterior and posterior portions of the internal condyle, and the anterior portion extends farther distad.

The shaft of the tarsometatarsus (SDSNH 24905) is laterally compressed with a raised external side. The single canal in the anterior row of the hypotarsus is gradually sloping to the intercotylar depression, and there is no canal for the tendon of M. flexor perforatus digit II. The articulating surface of trochlea II is offset to the medial side of the shaft of the trochlea, and there is a ridge on the lateral surface of the trochlea at the level of the offset.

Comparisons.—Gaviiformes and Procellariiformes were used as outgroups for determinations of character polarities.

Aechmophorus elasson Murray 1967, from the Pliocene Glenns Ferry Formation, Twin Falls County, Idaho, and a subspecies of the Western Grebe, *A. "occidentalis" lucasi* (Miller, 1911), from the Pleistocene of Fossil Lake, Oregon, are the only named fossil forms of the genus. Murray (1967:282) did not give a detailed osteological diagnosis or description of the humerus holotype and associated left ulna (UMMP 45316) of *A. elasson.* I have compared the ulna (UCMP 109389) with a good cast of *A. elasson* (UKVP 24764) and find them identical except that UCMP 109389 has a slightly smaller shaft (Table 5).

Aechmophorus "*occidentalis*" *lucasi* from the Pleistocene of Oregon was larger than its Recent relatives and, therefore, much larger than *Aechmophorus elasson.* The slightly ovoid shape and angular lateral margin of the internal cotyla of the ulna in *Aechmophorus* are primitive characters for grebes and loons. The transverse ridge below the external cotyla in *Aechmophorus* is derived; its absence in grebes, loons, and tubenoses I consider primitive. The proximal position of the anterior articular ligamental attachment and brachial depression is primitive and exhibited in *Aechmophorus* and the outgroups. However, the distally converging intermuscular line and lateral border of the brachial depression is an apomorphic condition in UCMP 109389 and primitive in *A. occidentalis/clarki,* in which the brachial depression is rounded distally.

The short trochanteric and obturator ridges of the femur in *Aechmophorus* I think are primitive and are shared with loons, whereas *Podiceps* has a narrow proximal end and these ridges are elongated. A muscle scar above the popliteal area is raised and considered primitive in *Aechmophorus* and the outgroup.

The raised medial shaft ridge of the tibiotarsus is a symplesiomorphy in *Aechmophorus, Podiceps, Podilymbus,* and *Gavia,* except *G. stellata,* in which an autapomorphic condition is exhibited. The posterior side of the internal condyle is flared outward and is long in *Aechmophorus, Gavia,* and Procellariiformes, and is considered primitive. In *Podiceps* the condyle is derived in being directed distad and being shorter. A notched internal condyle between the anterior and posterior portions with both portions level in distal extent is primitive for Procellariiformes. In *Aechmophorus,* the anterior portion extends slightly farther distad, whereas in *P. grisegena* the posterior portion extends farther distad, and in *Gavia* the anterior portion extends considerably farther distad.

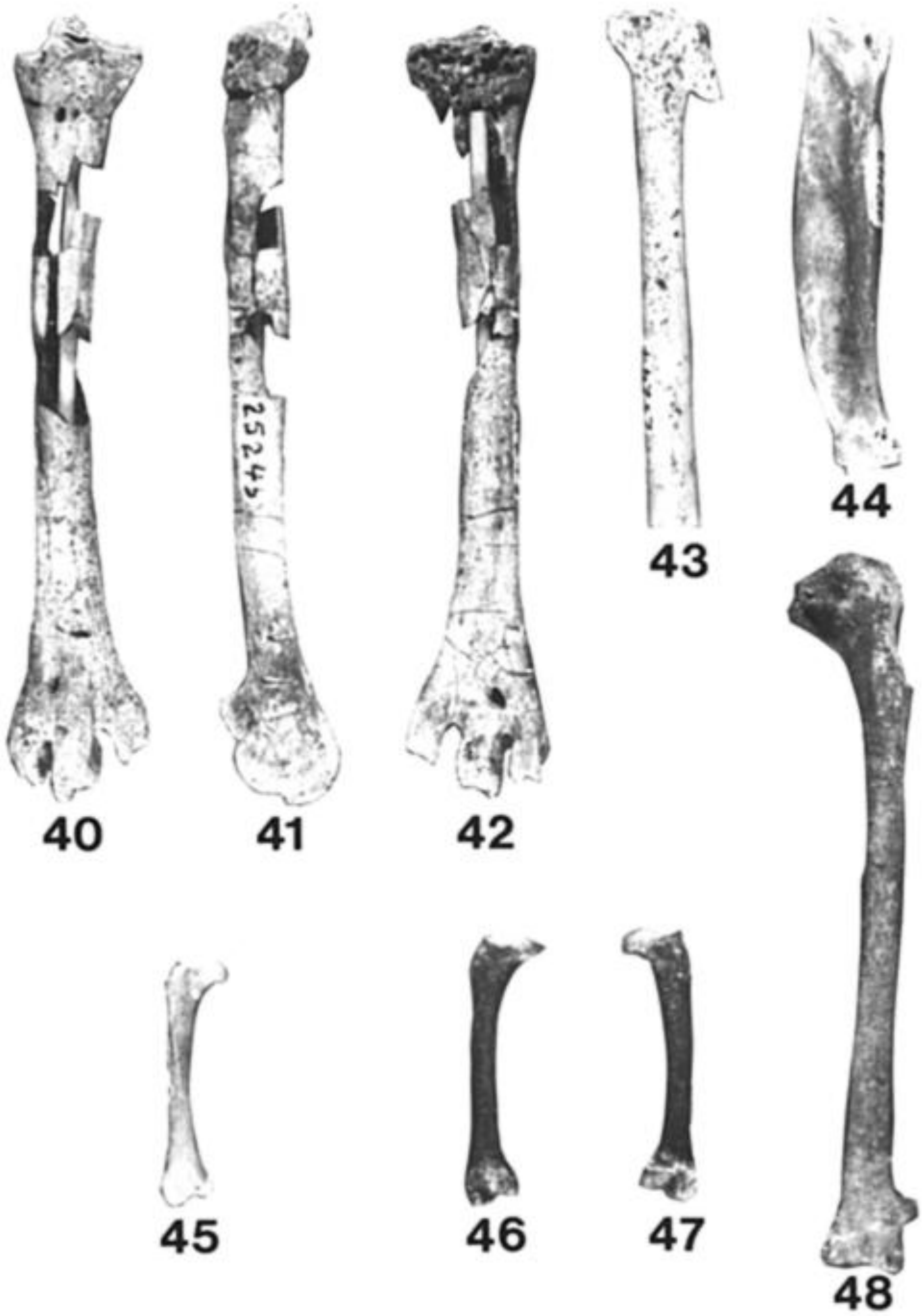
The lateral ridge and the medially offset trochlea II of the tarsometatarsus in *Aechmophorus* is derived, whereas grebes, loons, and Procellariiformes have an in-line trochlea II and no lateral ridge, the primitive condition. The gradual sloping for the intercotylar depression to the single canal in an anterior row of the hypotarsus is primitive in *Aechmophorus* and the outgroups, whereas in *Podiceps grisegena* a stepped, more angular separation is found between the intercotylar depression and the hypotarsus.

Discussion.—*Aechmophorus elasson* is now known from two late Pliocene faunas: the San Diego fauna and the contemporary Hagerman Local Fauna in Idaho. This and *Podiceps discors* are common to both faunas.

Order PROCELLARIIFORMES
Family DIOMEDEIDAE
Genus *Diomedea* Linnaeus
Diomedea howardae n. sp.
Figs. 40–44

Holotype.—SDSNH 25245/3158-C, a right tarsometatarsus.

Paratypes.—Humeri—SDSNH 35234/3418, left; SDSNH 21849/3076, shaft; SDSNH 25823/3181-A, left ulna, proximal end; SDSNH 25244/3181-C, metacarpal II of left carpometacarpus; SDSNH 25243/413, phalanx 1 of digit II; SDSNH 25834/3181-C, phalanx 2 of digit II; SDSNH 26199/3206, fragment of head of coracoid; SDSNH 25258/3179, right quadratojugal; SDSNH 25279/3006, pedal phalanx.



FIGS. 40–48. *Diomedea howardae*—40–42 tarsometatarsus; 43 carpometacarpus; 44 phalanx 1 of digit II. Procellariidae gen. et sp. indet.—45 femur. *Puffinus gilmorei*—46, 47 femur; 48 humerus.

Etymology.—This albatross is named in honor of Hildegarde Howard in gratitude for her enthusiasm, guidance, and inspiration during this project.

Diagnosis.—The tarsometatarsus differs from that in all other species of *Diomedea* by having the distal foramen with a more rounded margin and a more oblique orientation; posterior exit of the distal foramen more rounded than in other albatross species, in which the metatarsal II either cuts across the proximal margin of the opening (e.g., *Diomedea immutabilis, D. cauta, D. melanophris,* and *D. californica*) or the opening is ovoid (e.g., *D. exulans, D. nigripes,* and *Phoebetria palpebrata*); shaft relatively narrow.

Description.—Anterior articular ligamental attachment on the ulna (SDSNH 25823) swollen distally; brachialis anticus impression deeply excavated proximally.

On the carpometacarpus (SDSNH 25244) the lateral margin of the facet for phalanx 1 of digit II is a broad arch, with the tuberosity of metacarpal II raised and rounded. The distal metacarpal symphysis is narrow.

The proximal articulating surface of phalanx 1 of digit II (SDSNH 25243) is triangular with rounded apices, and the depth is about equal to the breadth. The anconal margin is blade-like and a long, broad arch in profile.

A round prominence lies within the triosseal canal below the medial margin of the glenoid facet of the coracoid (SDSNH 26199). The coracohumeral surface is sloped laterally and the medial border has a blade-like edge. The neck is narrow.

The tarsometatarsus (SDSNH 25245) is long and narrow with shallow anterior and posterior metatarsal grooves. The distal foramen penetrates the shaft obliquely. In profile, trochlea III is raised above the shaft whereas the other trochleae are in line with it. On the posterior surface the medial shaft ridge extends from the center of the distal end proximad to the external side short of midpoint in length but does not merge with the external side ridge.

Comparisons.—I determined character polarities for *Diomedea* by using other procellariiform birds and Pelecaniformes as outgroups.

Four fossil species of albatross have been named in the genus *Diomedea. Diomedea californica* Miller 1962 and *D. milleri* Howard 1966 are both from the middle Miocene Round Mountain Silt, Sharktooth Hill Bonebed, Kern County, California, and have tentatively been reported also from the late Miocene, Laguna Niguel, Orange County, California (Howard 1978:6). Howard (1978:6) compared MCZ 2328 with LACM 37629 from the late Miocene Laguna Niguel and tentatively referred it to *D. californica. Diomedea thyridata* Wilkinson (1969) is from the late Miocene Black Rock Sandstone, Beaumaris, Victoria, Australia. Finally, *D. anglica* Lyddeker (1891), based on a tarsometatarsus, is an early Pleistocene species from Red Crag, Suffolk, Foxhall, England. Brodkorb (1963a:242) noted that Wetmore's referral (1943:66–67) of a tibiotarsus from the late Miocene Bone Valley Formation in Florida to *D. anglica* was uncertain because the element (MCZ 2328) is not directly comparable to the holotype of *D. anglica.*

Various elements of albatrosses undetermined to species come from several late Tertiary California localities and represent birds of different sizes. Examined in this study were SDSNH 26218 and LACM 3184, 4612, and 6625 (see also Miller 1935:75 and Howard 1978:7, 1982:3–4). Indeterminate Tertiary albatrosses were also reported by Olson from South America (1984:741) and South Africa (1985a: 124).

TABLE 6
MEASUREMENTS OF TARSOMETATARSI FOR SPECIES OF *Diomedea*

	Length	Proximal breadth	Shaft	Distal breadth
D. angelica				
Cast Brit. Mus. #A.87	114.8	20.7	7.9 × –	21.5
Diomedea sp.				
SDSNH 27872	112.8	–	8.5 × 7.2	20.8
D. californica				
UCMP 61392	–	–	9.4 × 8.3	20.6
Diomedea sp.				
SDSNH 26218	–	–	10.3 × 7.6	[20.4]
D. howardae				
SDSNH 25245	101.7	[17.4]	7.1 × 7.2	17.9
D. cauta				
SDSNH 39608	98.1	20.0	7.0 × 7.7	19.5

Comparisons of tarsometatarsi (Table 6) and other elements of the fossil and living albatrosses indicate that *Diomedea howardae* is of medium size, about the size of *D. cauta* (White-capped Albatross).

On the anterior surface, the distal foramen is most like that of *D. cauta* and *D. californica* by having a rounded distal margin, all other species having a "tear-drop" shaped opening with the apex distad; in *D. exulans* (Wandering Albatross), *Diomedea* sp. (SDSNH 26218) from Oceanside, and *Phoebetria palpebrata* (Light-mantled Sooty Albatross) the intertrochlear tendinal opening is visible.

On the posterior surface of the holotype (SDSNH 25245) the medial shaft ridge extends proximad to the external side at approximately mid-length of the shaft, but then merges with the external side and resembles *Diomedea exulans, D. immutabilis* (Laysan Albatross), and *D. cauta,* and possibly *D. californica* and *Diomedea* sp. (SDSNH 26218) from Oceanside in this feature. *Diomedea nigripes* (Black-footed Albatross) has a centrally positioned posterior medial ridge, and *D. melanophris* (Black-browed Albatross) and *Phoebetria palpebrata* have a posterior medial shaft ridge merging with the external side. The condition in *D. nigripes* is that seen in the outgroups and is here considered primitive, the other conditions being derived.

The swollen distal end of the anterior articular ligamental attachment on a paratypical ulna (SDSNH 25823) is larger than that of any Recent albatross compared with it. Medial to the ligamental attachment, the proximal end of the brachialis anticus impression is deeper than in any Recent albatross. Also, the medial border of the brachialis anticus impression is formed by a central area of elevated bone resembling that of *Diomedea nigripes,* but higher than in other Recent species. The swollen anterior articular ligamental attachment is an autapomorphy for *D. howardae*; the raised medial border of the brachial impression that extends distad as the intermuscular line is present in the outgroups and is considered primitive for procellariiform birds, whereas *D. howardae* has a broader, raised surface on which the line extends.

The rounded margin of the facet for digit II, which is continuous with the tuberosity of metacarpal II of the paratypical carpometacarpus (SDSNH 25244) is derived for *Diomedea howardae* and differs from that of other albatrosses and other procellariiform birds, which have a more angular contour. The narrow distal metacarpal symphysis of *D. howardae* is plesiomorphic in procellariiform birds.

The paratypical phalanx of digit II (SDSNH 25243) has a triangular proximal articulating surface with rounded apices, and the depth is about equal to the breadth. This condition differs from other recent albatrosses, which generally have a more angular internal margin with breadth greater than depth. The angular internal margin is plesiomorphic in procellariiform birds.

A round prominence in the triosseal canal of the paratypical coracoid (SDSNH 26199) of *Diomedea howardae* and also in *D. immutabilis* is a derived character for Diomedeidae. The plesiomorphic condition is a deep medial groove (long axis) that is present in the outgroups and in certain albatrosses (*Diomedea nigripes, D. exulans, D. melanophris,* and *Phoebetria palpebrata*).

Diomedea sp. A
Figs. 61–63

Referred material.—SDSNH 27872/3283, a right tarsometatarsus.

Description.—A right tarsometatarsus is from a large albatross. The external cotylae and the internal half of trochlea II are missing, and in general the bone is worn. The intertrochlear notches are broad, spreading the toes. The distal foramen is round and close to the intertrochlear notch. The trochleae are narrow, and the shaft is slender. The hypotarsus has one deep groove (internal side) and two shallow grooves.

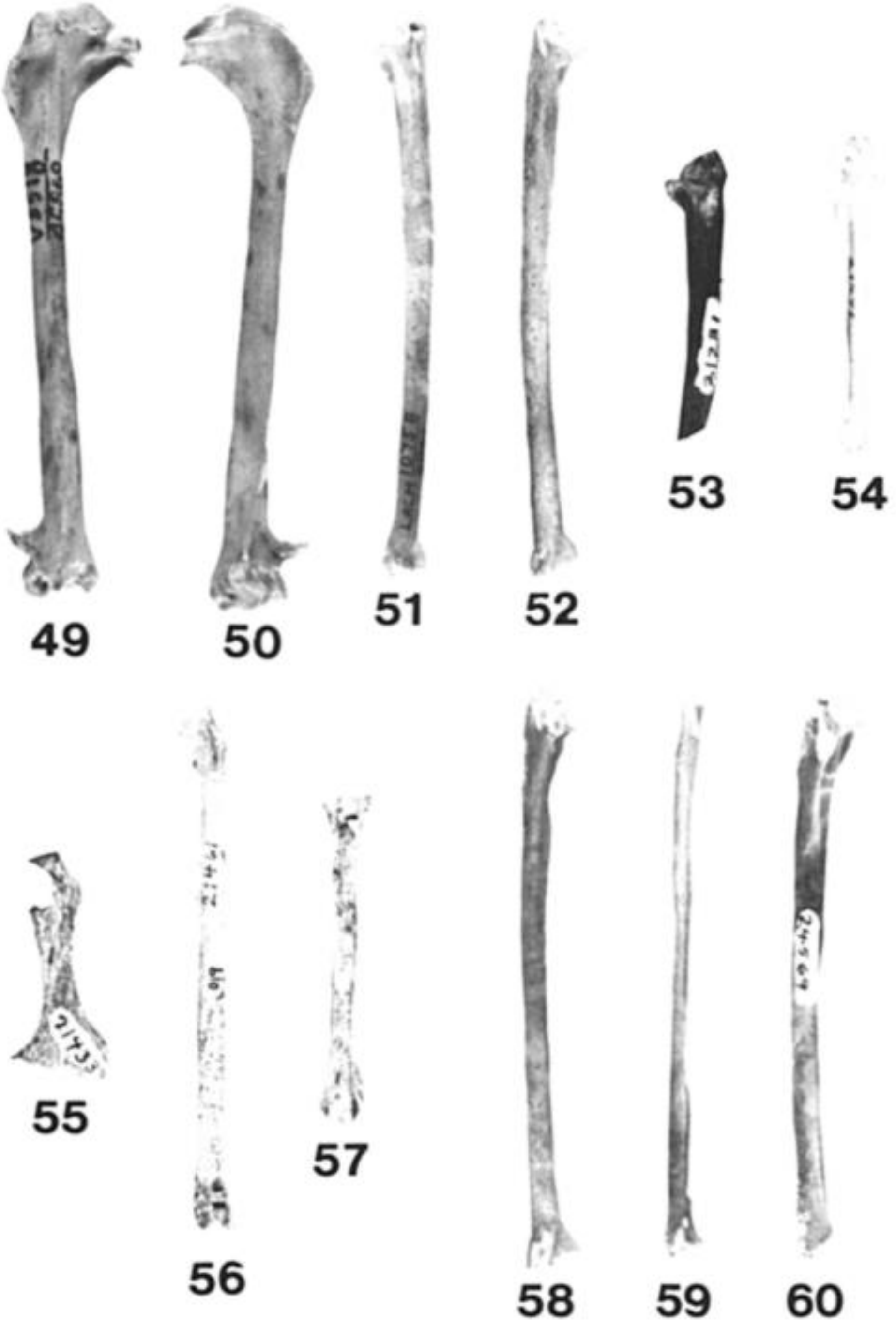
Comparisons.—A tarsometatarsus (SDSNH 27872) is from a large individual only 2 mm shorter and <1 mm in distal width than *Diomedea anglica. Diomedea californica* has a slightly more robust shaft, but the distal width is essentially the same as in SDSNH 27872. *Diomedea howardae* (SDSNH 25245) is much smaller and qualitatively different (see comparisons for *D. howardae*), whereas SDSNH 27872 is more like *D. anglica* and *D. californica.* SDSNH 27872 is like *D. californica,* having a rounded distal foramen and trochlea II diverging at a greater angle from the shaft, but SDSNH 27872 appears to have more slender trochleae and the intertrochlear notches are broader than in *D. californica. Diomedea californica* is known from older, middle Miocene, rock units. *Diomedea anglica* is known from late Pliocene to early Pleistocene rock units in the Atlantic and differs from SDSNH 27872 in having robust trochleae and narrower intertrochlear notches. A tarsometatarsus (SDSNH 26218) from the early Pliocene, San Mateo Formation (Lawrence Canyon Local Fauna), Oceanside, California, is larger than SDSNH 27872, and the distal foramen is tear-drop shaped.

Although specimens for comparison are few, it seems that SDSNH 27872 might have affinities with *Diomedea californica,* e.g., the diverging trochlea II might be a shared derived character.

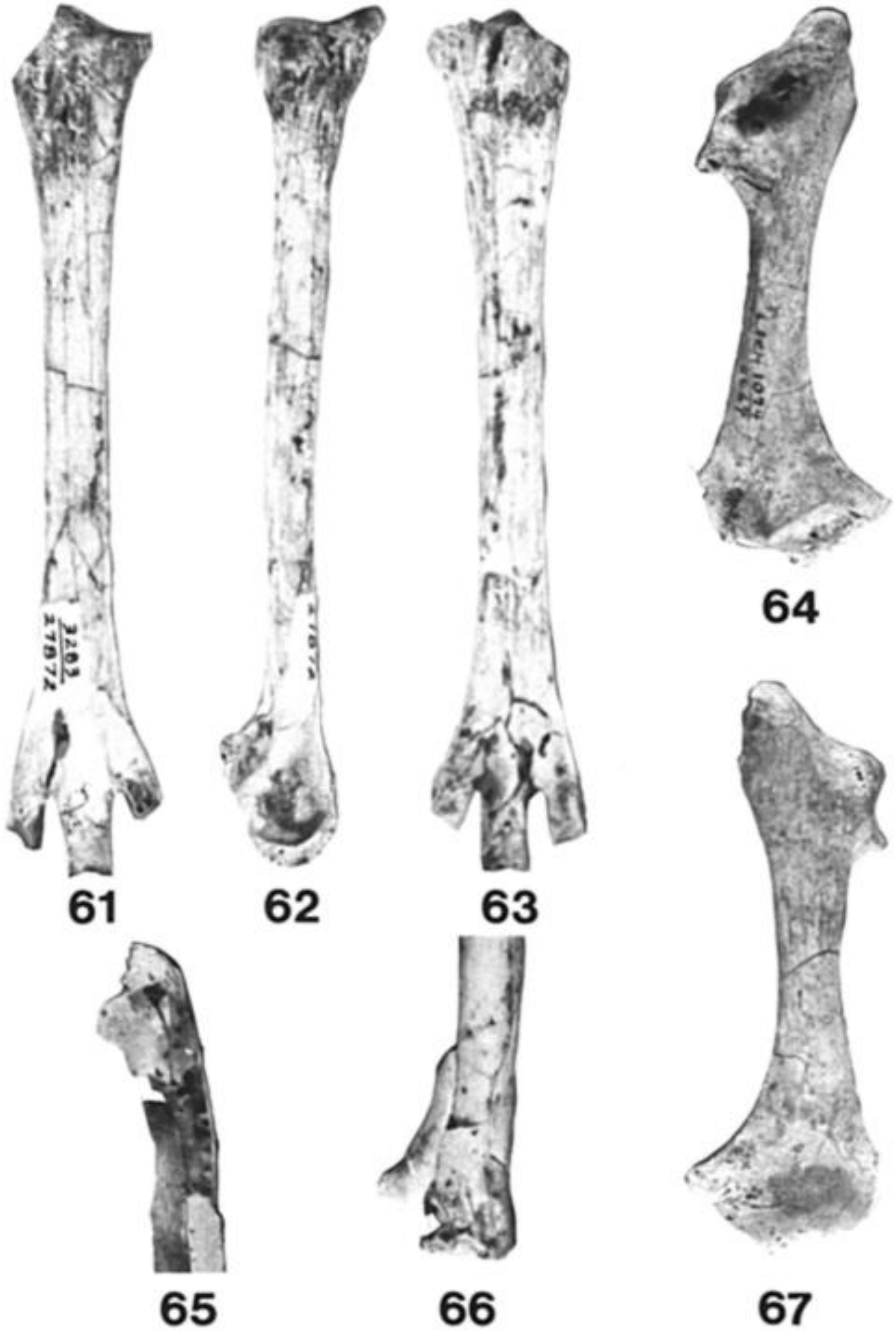
Diomedea sp. B

Referred material.—SDSNH 23790/3006, left tibiotarsus distal end.

Description.—A small individual with narrow distal condyles and a deep, roughly square anterior intercondylar fossa.



FIGS. 49–60. *Puffinus kanakoffi*—49, 50 humerus; 51–53 ulnae; 54 carpometacarpus; 55 coracoid; 56 tibiotarsus; 57 tarsometatarsus. 58–60 associated ulnae and radius.



FIGS. 61–67. *Diomedea* sp. A—61–63 tarsometatarsus. *Morus recentior*—64, 67 coracoid; 65, 66 ulna.

Comparisons.—A tibiotarsus (SDSNH 23790) is from a very small albatross, possibly as small as middle Miocene *Diomedea milleri* Howard 1966. *Diomedea milleri* is known only from the holotypical ulna (LACM 7319). Howard (1966:4) compared the holotype of *D. milleri* with the Recent species *D. nigripes* and found that *D. milleri* was 82 percent of that of *D. nigripes* in proximal breadth. SDSNH 23790 is 86 percent that of *D. nigripes* in distal breadth.

Family PROCELLARIIDAE
Genus *Puffinus* Brisson

Diagnosis.—*Puffinus* differs from all other procellariiform birds in having a long, roughly pointed ectepicondylar process nearer the distal end; bicipital margin short; bicipital area raised but not on the dorsal margin, more centrally located and extending transversely across the bicipital area.

Puffinus gilmorei n. sp.
Figs. 46–48

Holotype.—SDSNH 25298/2971-A, almost complete right humerus.

Paratype.—UCMP 83325/68153, right femur.

Etymology.—Named in honor of the late Raymond M. Gilmore, formerly the Curator of Marine Mammals at the San Diego Natural History Museum, in recognition of his interest in all marine vertebrates.

Diagnosis.—The holotypical humerus is more like *Puffinus* (*Thyellodroma*) *pacificus, P.* (*T.*) *bulleri,* and *P.* (*Ardenna*) *creatopus* (and differs from *P. opisthomelas, P. tenuirostris, P. griseus, P. puffinus,* and *P. kanakoffi*) in having the shaft less laterally compressed; *P. gilmorei* differs from *P.* (*Thyellodroma*) *pacificus, P.* (*T.*) *bulleri,* and *P.* (*A.*) *creatopus* in having the anconal surface below the head more broadly excavated.

Description.—The overall configuration of the humerus of *Puffinus gilmorei* is an open S-shaped shaft compressed laterally. The bicipital crest is short and continuous with the internal contour of the shaft. The capital shaft ridge is angular and centrally located on the shaft, medial to the external tuberosity, and it extends to the head. The head is not deeply excavated but the lateral extent of the excavation, which accommodates the external triceps, is broad almost to the lateral edge of the capital groove. Distally, the internal condyle is narrow and laterally flattened. The long and roughly pointed ectepicondylar process is close to the distal end. The impression of the brachialis anticus attachment is deep and diagonal in orientation from the proximointernal side to the distoexternal side.

The narrow shaft, only slightly curved anteriorly, of the paratypical femur of *Puffinus gilmorei* is its most overt characteristic. The head is narrow anteroposteriorly but broad proximally. Distally, the internal condyle is broad, almost flat on its posterior surface, shallow, and has almost no rotular sulcus. The external condyle is hooked proximally and is deeper than the fibular condyle.

Comparisons.—The capital shaft ridge of the holotype humerus (SDSNH 25298) is centrally placed; the femur of the paratype (UCMP 83325) has a shallow but broad internal condyle, a shallow rotular sulcus, and an almost flat posterior surface of the internal condyle without a distinct groove between internal and

TABLE 7

MEASUREMENTS OF HUMERI FOR SPECIES OF *Puffinus*

	Length	Proximal breadth	Shaft	Distal breadth	Ectepicondyle height
P. kanakoffi					
LACM 2120	—	—	3.5 × 5.3	7.3	—
LACM 2114	79.9	[13.8]	3.5 × 5.4	7.2	10.0
LACM 2516	85.1	14.6	3.6 × 5.6	—	10.3
UCMP 45869	81.1	14.8	3.3 × 5.7	7.6	9.3
UCMP 45884	—	—	3.5 × 5.5	7.4	10.0
SDSNH 25300	80.7	14.3	3.6 × 5.4	7.3	9.7
SDSNH 22995	—	—	3.7 × 5.7	7.4	10.0
P. felthami					
LACM 2037	—	—	3.8 × 6.9	6.9	11.0
P. diatomicus					
UCMP 26451	80.0	—	—	—	11.6
P. barnesi					
LACM 42652	[80.0]	—	3.9 × 5.9	7.7	9.5
P. calhouni					
LACM 17508	—	—	3.0 × 6.0	7.1	9.3
P. gilmorei n. sp.					
SDSNH 25298	96.7	—	3.8 × 5.6	8.1	10.1

external condyles. *Puffinus gilmorei* is referred to the subgenus *Thyellodroma* because it has a rounded humerus shaft and slightly anteriorly curved, slender femur shaft, as in *P. pacificus* (Wedge-tailed Shearwater) and *P. bulleri* (Buller's Shearwater). The short, straight bicipital crest of the humerus, which is continuous with the internal contour of the shaft, is most like that of *P. pacificus.*

The distally placed, long, and roughly pointed ectepicondylar process is a synapomorphy for *Puffinus,* whereas the primitive condition is probably a distally located but short and blunt process as exhibited by *Fulmarus* (Table 7). Other procellariiform birds also show other derived conditions of the ectepicondylar process: e.g., distal location; long, but very much squared in profile, as in the albatrosses (*Diomedea* and *Phoebetria*); or more proximally located, short and blunt as in petrels (*Pterodroma* and *Pagodroma*).

A plesiomorphic condition in procellariiform birds is a capital shaft ridge that does not extend proximad to the head (anconal surface below the head is relatively flat) and is centrally placed. This condition is exhibited in the albatrosses and the large shearwater *Procellaria.* Derived conditions are: capital shaft ridge centrally located but extending to the head, with the ridge being more angular, as in *Puffinus* and *Fulmarus*; ridge more laterally located, extending proximad to the external tuberosity and angular, as in Hydrobatidae (storm petrels); or ridge laterally located but not angular as in *Pterodroma.*

The femur of *Puffinus gilmorei* (UCMP 83325) is like that of *Puffinus* and differs from all other procellariiform birds by having an anteroposteriorly shallow internal condyle, a shallow rotular sulcus, and no intercondylar groove between the medial side of the internal condyle and the medial side of the external condyle; *P. gilmorei* is more like *P. pacificus, P. bulleri,* and *P. creatopus* (Pink-footed

TABLE 8

MEASUREMENTS OF ULNAE FOR SPECIES OF *Puffinus*

	Length	Proximal breadth	Proximal depth	Shaft	Distal depth
P. kanakoffi					
LACM 2821	75.7	7.1	8.2	3.5 × 4.5	6.0
LACM 30810	—	6.4	7.6	3.6 × 4.2	—
UCMP 109409	—	—	—	3.4 × 3.6	5.6
Puffinus sp.					
SDSNH 24569					
(right)	79.4	7.5	8.9	3.8 × 4.7	6.4
(left)	79.1	7.5	8.8	3.8 × 4.8	6.3
Puffinus sp.					
LACM 15403	86.7	7.8	9.2	4.1 × 4.8	6.9
P. calhouni					
LACM 17530	—	6.6	7.7	—	—
P. barnesi					
LACM 42654	—	6.5	—	3.5 × 5.3	5.3
P. diatomicus					
UCMP 26541	75.0	—	—	—	—

Shearwater) and differs from *P. opisthomelas* (Black-vented Shearwater), *P. tenuirostris* (Short-tailed Shearwater), *P. griseus* (Sooty Shearwater), and *P. kanakoffi* in having a straighter and narrower shaft (Table 10).

For the femur the plesiomorphic condition is a deep but narrow internal condyle with a distinct intercondylar groove, and a deep rotular sulcus as in all the procellariid genera other than *Puffinus,* which is as described for *P. gilmorei.* The straighter shaft of *P. gilmorei, P. pacificus,* and *P. bulleri* (the subgenus *Thyellodroma*) is derived from the plesiomorphic condition of a completely straight shaft, but is not as curved, shortened, and robust as those species in the subgenus *Puffinus.* The straighter shaft is characteristic of gliding species such as albatrosses and some petrels, rather than like diving shearwaters such as *P. griseus* and *P. tenuirostris.*

Discussion.—Including *Puffinus gilmorei,* 15 fossil species of shearwaters (*Puffinus*: see discussion of *P. kanakoffi*) are known, 13 of which can be referred to the subgenus *Puffinus,* and one, *P. inceptor* Wetmore (1930), which could be put in a subgenus of its own because of derived characters of the distal end of the humerus as suggested by Miller (1961:400). *Puffinus gilmorei,* therefore, might be distinguished from all other fossil species by referring it to the subgenus *Thyellodroma.*

Puffinus kanakoffi Howard, 1949
Figs. 49–57

Holotype.—LACM 2122/1080, a left tarsometatarsus.

Paratypes.—Humeri—LACM 2120/1078; LACM 2114/1071; LACM 2116/1071; LACM 2146/1080; LACM 2160/1075; Miller 2270/1075B; LACM 2124/1080, femur; LACM 2123/1080, tibiotarsus, proximal end; LACM 2126/1080, tarsometatarsus.

TABLE 9

MEASUREMENTS OF *Puffinus kanakoffi*

Carpometacarpi:	Length	Proximal breadth	Proximal depth	Length MC I	Distal breadth
SDSNH 21471	42.9	3.5	9.3	4.7	3.4
LACM 2827	39.9	3.7	7.9	5.8	3.6
Coracoid:	Length	Neck breadth	Head to scapular facet		Shaft at level of fenestration
SDSNH 21433	29.1	4.3	11.5		5.0 × 2.8
Tibiotarsi:	Length	Proximal breadth	External condyle depth	Internal condyle depth	Shaft below fibular crest
SDSNH 21461	64.4	—	5.8	6.3	3.2 × 4.0
SDSNH 21466	—	—	5.8	6.3	3.2 × 4.3
SDSNH 26200	65.7	5.9	—	—	3.6 × 3.0
Tarsometatarsi:	Length	Proximal breadth	Shaft	Distal breadth	
LACM 2122	45.2	6.7	2.9 × 3.7	—	
LACM 2126	47.0	7.1	2.8 × 3.6	—	
LACM 2572	45.5	—	—	6.3	
SDSNH 21430	44.5	6.8	2.8 × 3.8	6.8	
SDSNH 24581	44.0	6.5	2.5 × 3.4	6.0	
SDSNH 27148	47.1	[6.4]	2.8 × 3.6	6.2	

Referred material.—SDSNH 21235/2977, premaxillary; humeri—SDSNH 25300/3175; SDSNH 22995/3031; LACM 2516/1080; UCMP 45869/5518; UCMP 45884/V5565; ulnae—LACM 2821/1075B, right; LACM 30810/1072, right; UCMP 109409/6783, right; SDSNH 21231/2977, right proximal end; SDSNH 22883/2977, radius distal end; carpometacarpi—LACM 2827/1075, left; SDSNH 21471/3067; coracoids—SDSNH 21433/2979; SDSNH 28608/2971, head end of coracoid; SDSNH 25829/3181-C, right scapula; SDSNH 21425/2977, ventral fragment of synsacrum; femora—SDSNH 22889/2977, distal end; SDSNH 22878/2977, proximal end; tibiotarsi—SDSNH 21461/2977; SDSNH 21466/2979; SDSNH 26200/2971-A; tarsometatarsi—LACM 2572/4231; LACM 117780/4442, right; SDSNH 21430/2977 right; SDSNH 24581/2971 right; SDSNH 27148/3265 left.

Description.—The tarsometatarsus has been described by Howard (1949:187). A beak (SDSNH 21235) and the right ramus of a mandible (SDSNH 23081) are decurved.

A complete right ulna (LACM 2821) has a slender shaft with a shallow brachialis anticus impression. The anterior articular ligamental attachment is low in relief and ends distally at the proximal lateral end of the brachialis anticus impression. The olecranon protrudes proximad and is pointed. The internal and external cotylae are elongated in a palmar direction.

The distal portion of a radius (SDSNH 22883) has a deep and narrow tendinal groove, which is almost enclosed in a canal.

A right scapula (SDSNH 25829) has a robust neck, distally restricted blade, and an acromion that is not hooked dorsally.

The ventral surface of a synsacrum (SDSNH 21425) has a depression extending down the long axis; the caudal vertebrae are greatly elongated and narrow.

TABLE 10

MEASUREMENTS OF FEMORA FOR SPECIES OF *Puffinus*

	Length	Proximal breadth	Shaft	Distal breadth
P. gilmorei n. sp.				
UCMP 83325	35.1	7.5	3.3 × 3.3	7.2
P. kanakoffi				
LACM 2124	—	—	—	7.1
SDSNH 22889	—	—	—	6.6
SDSNH 22878	—	6.8	—	—
P. diatomicus				
UCMP 26541	30.0	—	—	—

A tibiotarsus (SDSNH 21461) has a slender shaft with the anteroproximal surface flattened. Anterodistally, a narrow tendinal groove is crossed by a bony supratendinal bridge.

Comparisons.—Puffinus kanakoffi (Howard 1949) is a small shearwater, with measurements overlapping those of the slightly larger living species *P. opisthomelas*. Smaller size also distinguishes *P. kanakoffi* from a second and unnamed shearwater (SDSNH 24569) represented by three associated wing elements, two ulnae and a radius (Table 8) in the avifauna, which is larger than *P. opisthomelas* and, therefore, than *P. kanakoffi*, from which it differs in other ways also (see *Puffinus* sp., comparisons).

The tibiotarsus of *Puffinus kanakoffi* differs from that of *P. opisthomelas* by its flattened anteroproximal surface, and the short and narrow anterodistal tendinal groove. *Puffinus opisthomelas* has a more rounded shaft and a longer and broader tendinal groove (Table 9).

Small size is the criterion for referring the scapula (SDSNH 25829), beak (SDSNH 21235), mandible (SDSNH 23081), synsacrum (SDSNH 21425), and radius (SDSNH 22883) to *Puffinus kanakoffi*. These bones are not known for the other fossil shearwaters, and thus are not directly comparable with them. The scapula is narrower proximally than that of *P. opisthomelas* because the acromion does not hook dorsally. Also, the slightly dorsal curvature of the beak and mandibular ramus appears greater than in *P. opisthomelas*. The synsacrum and radius are like those of *P. opisthomelas* except in size.

Puffinus kanakoffi is referred to the subgenus *Puffinus* based on certain shared probably derived characters, e.g., lateral compression of wing element shafts; the brachialis anticus depression within the brachialis anticus impression of the ulna extending proximally to the level of the anterior articular ligamental attachment; proximally protruding and pointed olecranon; and palmarly elongated cotylae. Plesiomorphic conditions of the above characters in the outgroup are: more rounded shafts of wing bones (e.g., *Diomedea, Procellaria, Fulmarus*); brachialis anticus depression distally placed within impression (e.g., *Diomedea, Procellaria, Pterodroma*); olecranon short proximally and blunt (e.g., *Procellaria, Pterodroma*); cotylae with a short, oval, almost rounded margin (e.g., *Procellaria, Diomedea*).

Autapomorphies for *Puffinus kanakoffi* are low relief of the anterior articular ligamental attachment on the ulna, and anteroproximal flattened tibiotarsus shaft.

A total of 15 fossil species of shearwaters (genus *Puffinus*) are recorded from Tertiary rock units in Europe and North America (Brodkorb 1963:242–244; Howard 1968:6, 1971:2–4, 1978:7; *P. gilmorei* n. sp. described herein); two are from Europe: *P. aquitanicus* and *P. antiquus* Milne-Edwards 1874, from the middle Miocene of France. *Puffinus micraulax* Brodkorb 1963, from the Hawthorne Formation, early Miocene, Florida, is the oldest North American fossil species followed by the only other west Atlantic species, *P. conradi* Marsh 1870, Calvert Formation, middle Miocene, Maryland. The remaining 10 fossil shearwater species all come from West Coast deposits. *Puffinus inceptor* Wetmore 1930, *P. priscus* Miller 1961, and *P. mitchelli* Miller 1961 are from the Sharktooth Hill Bonebed, Round Mountain Silt, middle Miocene, Kern County, California. Three late Miocene fossil species are known: *P. diatomicus* Miller 1925, from the Sisquoc Formation, Lompoc, Santa Barbara County, California; *P. calhouni* Howard 1968, from the Monterey Formation, Laguna Hills, Orange County, California; and *P. barnesi* Howard 1978, Monterey Formation, Laguna Niguel, Orange County, California. Two species are known from the early Pliocene: *P. tedfordi* Howard 1971, Almejas Formation, Cedros Island, Baja California, Mexico and *P. felthami* Howard 1949, from the Capistrano Formation, Corona del Mar, Orange County, California. The last two fossil species known from the late Pliocene of San Diego are *P. kanakoffi* Howard 1949 and *P. gilmorei* n. sp. (described herein). Besides the species named above *Puffinus* spp. records of note come also from the middle Miocene Rosarito Beach Formation, La Mision Local Fauna, Baja California, Mexico (Chandler *in* Deméré et al. 1984); middle Miocene Calvert Formation, Maryland (Wetmore 1938); late Miocene Monterey Formation, Laguna Hills, Orange County, California (Howard 1968); early Pliocene Almejas Formation, Baja California, Mexico (Howard 1971); late Miocene San Luis Ray and early Pliocene Lawrence Canyon Local Faunas, San Mateo Formation, San Diego County, California (specimens in the SDSNH collection, Chandler MS); and late Pliocene San Diego Formation, San Diego County, California (this paper). These additional records of *Puffinus* sp. are important because in most cases the referred material represents a distinct species but is insufficiently represented to permit naming it.

Puffinus kanakoffi is larger than *P. micraulax* Brodkorb (1963b:161), about the size of *P. priscus, P. barnesi* and *P. diatomicus,* and smaller than all other species. *Puffinus kanakoffi* differs from *P. diatomicus* in having the ectepicondylar process of the humerus closer to the distal end, and a longer tarsometatarsus; from *P. barnesi* by having a longer brachial impression, more compressed humeral shaft, less inflated anconal tip of the internal condyle, and more palmad-facing attachment for the anterior articular ligament (see Howard 1978:9). *Puffinus kanakoffi* differs from *P. priscus* by having a narrower anterior articular ligament.

Puffinus sp. from Rosarito Beach Formation, middle Miocene, Baja California (Chandler *in* Deméré et al. 1984:53), has a shallow brachial impression like *P. kanakoffi,* but differs by having a prominent anterior ligament attachment, and the measurements of the proximal end of SDSNH 21237 are like those of *P. kanakoffi.* Two humeri (SDSNH 25354 and 25355) are slightly larger than in *P. kanakoffi.*

Discussion.—The phylogenetic relationships of the fossil and extant species in *Puffinus* are unknown except that *P. inceptor* seems to be a sister group to all other species of *Puffinus* (see Miller 1961), and *P. gilmorei* is placed here in the subgenus *Thyellodroma.* All other fossil species are best referred to the subgenus *Puffinus* because of the extreme lateral compression of their wing and leg bones. Primarily, the fossil species in *Puffinus* are distinguished by size and their geochronologic occurrence (see Howard 1978:8–9). A more detailed phylogenetic study of *Puffinus* is needed to extend the study by Kuroda (1954).

Puffinus sp. (USNM 15160) from the middle Miocene Calvert Formation of Maryland was described by Wetmore (1938:22) as having "dimensions of living Cory's Shearwater (*Puffinus diomedea borealis*)." Cory's Shearwater was placed in *Calonectris* by Kuroda (1954:102; A.O.U. 1983:21) and *Puffinus* sp. (USNM 15160) should be reexamined to determine if it belongs in *Puffinus* or *Calonectris* and hence establish the antiquity of *Calonectris.*

Certain errors in the literature concern *Puffinus kanakoffi.* A humerus (UCMP 45869) wrongly appears as UCMP 45896 (Miller and Bowman 1958:8). Also, the length given for UCMP 45869 was 91.2 mm but should be 81.2 mm, and the measurement "greatest breadth across distal condyles, 11.4 mm" is in error. The distal breadth of UCMP 45869 is 7.6 mm, confusing with a measurement of the distal breadth (see Table 7). Miller and Bowman's (1958:8) measurement is taken diagonally across the distal end from the external condyle (palmar side) to the entepicondyle (anconal side).

Puffinus sp.

Figs. 58–60

Referred material.—SDSNH 24569/2971, three associated wing bones, right and left ulnae, and a right radius.

Description.—The shafts of the ulnae are laterally compressed with a blade-like edge on the anconal surface. Both ulnae have a deep brachialis anticus impression. The brachialis anticus depression within the impression extends to the distal level of the anterior articular ligamental attachment, which is raised. The brachialis anticus impression extends the anterior articular ligamental attachment by undercutting it distomedially. The proximal cotylae are elongated palmad and are deep. The olecranon is protruding proximad and is pointed. Distally, the carpal tuberosity is robust, and the distal edge protrudes perpendicular from the shaft.

The radius has a very angular shaft that is flattened palmarly. Distally, the edges of the tendinal groove enclose the groove, almost forming a canal.

Comparisons.—This third species of *Puffinus* is referred to the subgenus *Puffinus* because it has laterally compressed wing bones like *P. kanakoffi* and differs from *P. gilmorei,* which has more rounded bones and belongs in the subgenus *Thyellodroma.* The ulnae of SDSNH 24569 differ from those of *P. kanakoffi* by having a prominent anterior articular ligamental attachment and a deep brachialis anticus impression, whereas *P. kanakoffi* has a ligamentary attachment of low relief and a shallow brachialis anticus impression. The proximal protruding olecranons of *Puffinus kanakoffi* and SDSNH 24569 are pointed. Overall, *P. kanakoffi* is smaller, with more gracile bones, than the species of SDSNH 24569 (Table 8).

The ulnae of SDSNH 24569 are like that of *Puffinus barnesi* Howard (1978:9, LACM 42654) in its prominent anterior articular ligamental attachment, but the ulna of *P. barnesi* is smaller than that of SDSNH 24569, closer to *P. kanakoffi* in size. The ulna of *Puffinus barnesi* does not have a palmarly projected external cotyla as does SDSNH 24569, and a distinct ridge from the external cotyla to the shaft is lacking on SDSNH 24569.

An ulna from Cedros Island, Mexico, LACM 15403, is from a larger individual than SDSNH 24569. Both have a deep brachialis anticus impression extending proximad on the distomedial side of the anterior articular ligament attachment as do several other species of *Puffinus.*

The ulnae of most fossil shearwaters are not known and cannot be compared with SDSNH 24569. Because certain species (e.g., *Puffinus felthami*) are approximately the same size as SDSNH 24569, it is impossible to name this species at this time.

Procellariidae gen. et sp. indet.

Fig. 45

Material.—SDSNH 25299/3175, right femur.

Description.—The shaft is curved anteriorly just below mid-shaft and is laterally compressed. The proximal end is narrow. The distal end is narrow with a deep, narrow internal condyle. The rotular groove is deep anteriorly, and posteriorly the internal condyle is narrow and deep. The intercondylar groove is deep. A depression distal to the intercondylar groove is deep, and a bony wall separates the anterior and posterior sides.

Comparisons.—The femur is from a shearwater similar in size to *Puffinus opisthomelas.* The anterior curvature and lateral compression of the shaft resemble that of *Procellaria* or *Puffinus pacificus* in not being greatly curved, compressed, and robust, as in *P. opisthomelas.* This type of shaft, narrow at both ends, deep internal condyle, deep rotular groove, and distinct intercondylar groove is also seen in albatrosses, some petrels, and some storm-petrels, and is probably plesiomorphic. However, the fibular condyle of the fossil is directed approximately 90 degrees laterally, as it is also in *Puffinus.* The referred femora of *P. kanakoffi* and *P. gilmorei* agree with Recent *Puffinus* by having a narrow, flattened internal condyle with the laterally extended fibular condyle.

Family HYDROBATIDAE

Genus *Oceanodroma* Reichenbach

Diagnosis.—The species of *Oceanodroma* differ from all other genera of the Hydrobatidae by having an ulna as long as or longer than the humerus.

Oceanodroma sp.

Referred material.—SDSNH 22621/2978, proximal one half of a left ulna.

Description.—The internal cotyla of the ulna is pointed proximally and extends out over the olecranon. The lateral border of the external cotyla has a long gradual arch from the cotyla to the shaft. The prominence of the anterior articular ligament is short, swollen, and reaches the lateral border of the internal cotyla proximally. The radial depression is very shallow and short, swollen, and reaches the lateral border of the internal cotyla proximally. The radial depression is very shallow.

Comparisons.—Six extant species in *Oceanodroma* occur at some time of year off some part of the California coast. Ulna SDSNH 22621 is slightly smaller (breadth and depth of the proximal end) than ulnae of two of these, *O. leucorhoa*

TABLE 11

MEASUREMENTS OF ULNAE FROM SPECIES OF *Oceanodroma*

	O. microsoma	*O. tethys*	SDSNH 22621	*O. homochura*	*O. leucorhoa*	*O. furcata*
Proximal breadth	2.9	3.2	3.6	3.6–3.7	3.7	4.2
Proximal depth	2.5	2.7	3.0	3.0–3.1	3.0–3.1	3.6

(Leach's Storm-petrel) and *O. homochroa* (Ashy Storm-petrel; see Table 11). It differs from those of all six living species by having a proximally pointed internal cotyla extending over the olecranon, whereas the olecranon protrudes only slightly beyond the proximal point of the internal cotyla. All living species, conversely, have a round proximal border on the internal cotyla, with the olecranon protruding greatly beyond the internal cotyla and truncated (*Oceanodroma leucorhoa* and *O. homochroa*), or greatly protruding and rounded (*O. furcata*, Fork-tailed Storm-petrel, and *O. tethys*, Wedge-rumped Storm-petrel), or protruding and pointed (*O. microsoma*, Least Storm-petrel, and *O. melania*, Black Storm-petrel). Unique to SDSNH 22621 is the lateral border of the external cotyla, which forms a long, gradual arch to the shaft of the ulna from the cotyla; all living species have either a greatly arched lateral border on the external cotyla (*O. microsoma*, *O. homochroa*, and *O. furcata*) or a greatly arched border with distally hooked end (*O. tethys*, *O. melania*, and *O. leucorhoa*).

In common with *Oceanodroma homochroa*, SDSNH 22621 has a short laterally swollen prominence of the anterior articular ligament which reaches the lateral border of the internal cotyla. The other extant species compared have a prominence of the anterior articular ligament which does not extend proximally far enough to incorporate its border with that of the internal cotyla.

The depth of the proximal radial impression is highly variable within *Oceanodroma*. Nevertheless, SDSNH 22621 has the shallowest proximal radial depression of the individuals studied.

A late Miocene (Hemphillian) California fossil, *O. hubbsi* Miller, 1951, is represented by a partially associated skeleton (skull, vertebrae, pelvis, left leg). Miller estimated the size of *O. hubbsi* as similar to *O. homochroa* but more robust. Comparing the measurements of the proximal end of the ulnae, *O. leucorhoa* and *O. homochroa* are very similar and only the length of the ulna separates them, *O. leucorhoa* having the longer. The San Diego fossil ulna is slightly smaller than these extant species. Therefore, *O. hubbsi* and the San Diego fossil species were probably similar in size. The robustness of *O. hubbsi* is questionable because the fossil is poorly preserved (pers. obs.). The ulna of *O. hubbsi* was not preserved and, therefore, direct comparisons are not possible. I think the San Diego Pliocene specimen (SDSNH 22621) represents a species distinct from *O. hubbsi* and living species; however, it is best to await further data before naming this single, incomplete specimen.

Howard (1978:14) assigned a right tarsometatarsus (LACM 42659) from Laguna Niguel (late Miocene, Clarendonian) to *Oceanodroma* sp. The individual, however, was like Recent species *O. melania* in size, and, therefore, much larger than *O. hubbsi* or SDSNH 22621.

Oceanites zaloscarthmus Olson, 1985a is an extinct fossil species from early Pliocene deposits at Langebaanweg, southwestern Cape Province, South Africa.

Order PELECANIFORMES

Family SULIDAE

Genus *Morus* Vieillot

Diagnosis.—*Morus* has forelimbs and hindlimbs more nearly equal in size than does *Miosula,* whose wings are small relative to the legs.

The humerus of *Morus* differs from that of *Sula* by having a capital shaft ridge on the external side extending proximad to just below the external tuberosity, deltoid crest longer than bicipital crest, internal margin of bicipital crest gradually rounded, medial border of olecranon fossa not overhanging fossa, fossa apneumatic, proximal end of external condyle continuous with shaft, and ectepicondyle ridge with straight profile. In *Sula* the capital shaft ridge is centrally located below the head, length of deltoid crest equal to or shorter than bicipital crest, internal bicipital crest margin irregular and more angular, olecranon fossa pneumatic and medial border overhangs fossa, proximal end of external condyle separated from shaft by groove, ectepicondyle ridge rounded palmarly.

Pneumatic opening in radial depression of ulna absent in *Morus,* present in *Sula*; olecranon short and broad with rounded contour in *Morus,* olecranon gracile and longer in *Sula*; carpal tuberosity of ulna expanded and ventrally pneumatic in *Morus* but not in *Sula.*

Carpometacarpus apneumatic in *Morus,* pneumatic in *Sula.*

Femur of *Morus* with a shallow fibular groove forming an obtuse angle, external condyle deeper than internal condyle, a derived condition; in *Sula* fibular groove forms a right angle and external and internal condyles equal in depth.

Tibiotarsus of *Morus* has external condyle broad at base and hence a narrow anterior intercondylar fossa, a long fibular crest and long ankylosis of the fibular attachment; in *Sula* fibular crest and ankylosis of the fibular attachment shorter, external condyle narrow at base, hence with broad anterior intercondylar fossa. Descending muscle scar from external edge of external articular surface lacking in *Morus,* present in *Sula.*

Tarsometatarsus of *Morus* has trochlea III posteriorly elongated beyond proximal margin of distal foramen proximad, in *Sula* the distal foramen extends proximad to proximal end of trochlea III.

Morus recentior (Howard 1949)

Figs. 64–67

Synonyms.—*Miosula recentior* Howard 1949. Carnegie Institution of Washington Publication, no. 584:190.

Holotype.—LACM 2117/1071; a left tibiotarsus.

Referred material.—SDSNH 25596/3179, left ulna; LACM 2669/1074, almost complete left coracoid; SDSNH 24861/3181, seventh cervical vertebra; LACM 2279/10809, cervical vertebra; LACM 2505/1075.

Revised diagnosis.—Tibiotarsus differs from other fossil and extant sulid species by having distal condyles less vertical, and the internal condyle thrust toward the internal side more than in any Recent sulid.

Description. —The reassembled portion of an ulna (SDSNH 25596) is long with a broad distal end and a robust shaft. The carpal tuberosity is large, rounded, and ventrally pneumatic. Proximally the end is fragmented, but the olecranon is intact and is deep, short in its proximal extent, and rounded proximally (lateral view). The preserved radial depression is apneumatic.

The neck of the coracoid (LACM 2669) is broad on the anterior surface, with a furcular facet which is flattened on the posterior side. Several pneumatic openings are present within the triosseal canal. The shaft is very robust. The sternocoracoidal impression has an evenly rounded edge. The sternal facet is simple, with a curved anterior edge.

The holotype, a left tibiotarsus (LACM 2117), has the proximal half badly fragmented. Proximally, the shaft at the level of the fibular crest is very robust. Distally, the condyles are equal in distad extent, and both are slanted toward the internal side, the internal condyle notably so. The external condyle has a broad base, and the intercondylar fossa is narrow. The fibular spine is ankylosed to the tibiotarsus.

A seventh cervical vertebra (SDSNH 24861) is missing the neural spine, both pleurapophyses, and both diapophyses.

SDSNH 24861 is a large cervical vertebra with few pneumatic openings. The ventral side of the centrum between the articular surfaces is smooth, slightly concave toward the anterior end, and is roughly square in outline.

Comparisons. —Procellariiform and other pelecaniform birds were used as the outgroups to determine character polarities.

Known fossil sulids first occur in the Miocene, and diagnostic generic characters for *Sula* and *Morus* are then already present (Harrison *in* Nelson 1978). The earliest species referable to *Morus* is *M. loxostyla* (Cope 1870) from the middle Miocene of Maryland. *Morus atlanticus* (Shufeldt 1915) from the middle Miocene of New Jersey, was synonymized by Wetmore (1926:465) with *loxostyla.* The third middle Miocene (Barstovian) *Morus* species recorded is *M. vagabundus* Wetmore 1930 from California. Additional California material referable to *M. vagabundus* has been reported by Compton (1936), Miller (1961:401), and Howard (1966:5–6). A new middle Miocene locality from Rosarito Beach, Baja California, Mexico, was reported by Chandler (*in* Demëré et al. 1984:53) and also includes a record of *Morus* sp. The next record of *Morus, M. lompocanus* (Miller 1925: 114), is from the late Miocene (Clarendonian) diatomaceous deposits at Lompoc, California. *Morus lompocanus* has also been recorded from the late Miocene (Clarendonian) at Laguna Hills and Laguna Niguel, Orange County, California. *Morus magnus* Howard 1978 is also from Laguna Niguel. *Morus peninsularis* Brodkorb 1955 is from the late Miocene (Hemphillian) of Florida. Other Pliocene sulid fossils remain unpublished. The late Pleistocene *M. reyanus* Howard (1936: 213) is reported from Los Angeles County, California. At present a gap in the west coast Tertiary records of *Morus* extends from the late Miocene to the late Pleistocene. With the reassignment of *M. recentior, M. humeralis* (see herein) and the occurrence of *Morus* sp. from the late Miocene on Cedros Island, Baja California (Howard 1971:5), and late Miocene (Hemphillian) LACM locality 4616, California (Chandler MS), the fossil record indicates continuous occurrence for gannets along the coast of California from the Miocene until very near the Recent.

TABLE 12

MEASUREMENTS OF FEMORA FOR SPECIES OF *Morus*

	M. humeralis LACM 2522	*M. lompocanus*	*M. magnus*	*M. bassanus*
Length external side	58.2	69.0	—	71.2
Depth fibular condyle	10.3	—	—	12.8
Depth external condyle	10.5	—	—	13.9
Least breadth of shaft	5.7	7.0	8.9	7.0–7.5
Depth of shaft	6.3	—	9.6	7.8
Breadth proximal end	13.2	—	—	15.7
Breadth across anterior face of distal end[1]	—	13.9	—	14.2

[1] See Howard 1978.

Howard (1949:190–191) reported on two sulid elements from the San Diego Formation, a relatively long tibiotarsus and a relatively short ulna. She assumed that they represented one species and thus assigned them to the genus *Miosula,* which is characterized by a high leg/wing ratio (Miller 1925:114–115). Howard stated, however, that in the absence of the ulna, she probably would have assigned the tibiotarsus to the genus *Morus.* The two elements were not associated; nevertheless, she designated the tibiotarsus (LACM 2117) as the holotype of *Miosula recentior,* with the ulna (LACM 2112) being included as a paratype.

Miller and Bowman (1958) described a fossil humerus from the San Diego Formation as *Sula humeralis* and concluded that the ulna (LACM 2112) formerly included with *Miosula recentior* should be considered as *Sula humeralis.* The relative sizes of the humerus and ulna were in keeping with the proportions of those two elements in Recent sulids. Also, the articular surfaces of the two elements indicated that they belonged to the same species.

I reexamined the tibiotarsus (LACM 2117) of *Miosula recentior* and concluded (as Howard indirectly suggested) that it properly belongs in the genus *Morus.* Also from the San Diego Formation, and described here for the first time, are a coracoid and ulna representing a species of *Morus.* On the basis of size, I refer them to *Morus recentior.*

Morus recentior is known by a tibiotarsus, a coracoid, an ulna, and several cervical vertebrae. This severely limits comparisons with few remains of the other fossil species. Generally the size of the known elements of *M. recentior* is greater than that of *M. lompocanus* and the living *M. bassanus* (Northern Gannet). How-

TABLE 13

MEASUREMENTS OF TIBIOTARSI FOR SPECIES OF *Morus*

	M. recentior[1] LACM 2117	*M. lompocanus*[2] LACM 52217	*M. bassanus*[2] LACM Bi1764	*M. bassanus*[2] SDSNH 43061
Length	114.0	—	—	—
Breadth, distal end	14.0	13.7	13.0	12.9
Depth, distal end	13.0	12.4	12.0	12.1
Ratio, depth to breadth	92.1%	90.5%	92.0%	93.8%

[1] Measurements from Howard 1949.
[2] Measurements from Howard 1978.

TABLE 14
MEASUREMENTS[1] OF CORACOIDS FOR SPECIES OF *Morus*

	M. recentior LACM 2669	*M. peninsularis*	*M. loxostyla*	*M. reyanus*
Length: head to internal sternal facet	64.7	54.0–55.6	48.2–51.3	56.6
Length of external sternal facet	15.9	14.2–14.5	14.2	—
Length of internal sternal facet	11.2	8.6–10.8	—	—
Least depth of shaft	12.3	7.0–7.4	5.0–5.8	—
Head to procoracoid	26.7	25.0–25.1	—	24.7
Breadth of head	14.1	14.2	—	15.5
Breadth at level of scapular facet	21.4	17.0–17.7	—	17.1

	M. lompocanus	*M. bassanus*	*M. capensis*	*M. serrator*
Length: head to internal sternal facet	62.0	58.6–61.3	55.8	54.7
Length of external sternal facet	—	17.4–20.8	17.2	18.2
Length of internal sternal facet	—	13.8–14.3	14.0	12.0
Least depth of shaft	—	7.4–8.2	7.4	7.8
Head to procoracoid	—	27.9–29.6	27.4	27.6
Breadth of head	—	14.4–15.4	15.4	15.5
Breadth at level of scapular facet	—	17.5–20.4	19.0	18.7

[1] All measurements except those for *Morus recentior* are those from Brodkorb (1955, table 4).

ever, they are closer to these species than is the larger fossil species *M. magnus,* with the possible exception of the estimated length of the ulna (SDSNH 25596). Table 16 compares measurements of *M. recentior* with those of fossil and living gannets.

The tibiotarsus of *Morus recentior* differs from that of *M. lompocanus* and *M. humeralis* (next species account) in the probably derived, less vertical orientation of the distal condyles as compared to the outgroups (see Howard 1978:17). No tibiotarsi are known for other fossils of *Morus.*

The coracoid of *Morus recentior* is longer than that of any fossil sulid listed by Brodkorb (1955, table 4). The Recent gannets are slightly larger than *M. recentior* in certain coracoid measurements (Table 14). The internal sternal articulating surface of *M. recentior* is evenly rounded like that of *M. reyanus* and *M. peninsularis* (Brodkorb 1955, pl. 1, fig. 4) and differs from that of *M. loxostyla* described (Cope 1870:236) as "wider at median end . . . then contracts abruptly, leaving the remaining portion only one-half as wide." This condition equally applies to *M. bassanus.* This area is not visible on the holotype of *M. lompocanus,* and the coracoids for *M. vagabundus* and *M. magnus* are not yet known. The internal edge of the shaft on *M. recentior* has a more gradual curve of its length than in the other fossil or living species of *Morus,* which have a straighter shaft and more abruptly up-turned internal end of the external sternal facet. Brodkorb (1955:8) states, as a difference between *M. peninsularis* and *M. reyanus,* that *M. peninsularis* has a narrower and more pointed head on the coracoid. In this respect *M. recentior* is more like *M. peninsularis* than *M. reyanus.*

Ulnae have been referred to three extinct species of gannets all smaller than *M. recentior* (Table 16): *Morus lompocanus, M. vagabundus,* and *M. humeralis* (see below). The ulna of *M. magnus* is unknown, but indirect comparisons can be made between it and *M. recentior* by comparing each of these with *M. bassanus.* The carpometacarpus of *M. magnus* (LACM 37632) is 20 percent longer than

TABLE 15

MEASUREMENTS OF HUMERI FOR SPECIES OF *Morus*

	Breadth distal end	Anterior articular ligament length	Breadth proximal end
M. magnus	29.2	9.9	—
M. lompocanus	ca. 23.9	—	28.0[3]
M. loxostyla	21.1	8.5	—
M. humeralis	19.7	6.5	28.0
M. vagabundus	17.2–18.3	5.3[2]	—
Morus sp.[1]	20.5	7.5	—

[1] From Cedros Island, see Howard 1971.
[2] Measurements from Wetmore 1930, fig. 4.
[3] Miller's (1925) "transverse diameter of head."

that of a female specimen of *M. bassanus* (Howard 1978:17). The reassembled portion of the shaft and distal end of *M. recentior* (SDSNH 25596) is about as long as an ulna of *M. bassanus* (SDSNH 43061, unsexed). Although the proximal end of SDSNH 25596 cannot be rejoined to its shaft and distal end, there is no overlap in length of the two fragments, and their total length is at least 20 percent greater than *M. bassanus* (SDSNH 43601), a difference equal to that of *M. magnus* for the carpometacarpus. The other elements referred to *M. recentior* are all relatively closer in size to *M. bassanus* than to *M. magnus,* and for that reason and because of the time separating *M. recentior* from *M. magnus* I think they are distinct.

A cervical vertebra known for *Morus peninsularis,* from Brodkorb's description, is not the seventh, and, therefore, not directly comparable with the vertebra of *M. recentior* (SDSNH 24861; see Table 17). The preservation of vertebrae of *M. lompocanus* does not allow for comparisons. Vertebrae of *M. recentior* have been compared with the larger *M. vassanus,* yet it is apparent that both are from the genus *Morus.*

Discussion.—A small fragment of a humeral shaft referred by Howard to *Morus recentior* (LACM 2169) is evidently too small for this species and belongs to one even smaller than *M. bassanus,* perhaps *M. humeralis.*

TABLE 16

MEASUREMENTS OF ULNAE FOR SPECIES OF *Morus*

	M. recentior SDSNH 25596	*M. bassanus* SDSNH 43061	*M. lompocanus*[1] LACM 37636	*M. lompocanus*[2]	*M. vagabundus*[3] USNM 11971	*M. humeralis*[4] LACM 2112
Distal breadth (through carpal tuberosity)	17.9	15.3	—	—	10.2	—
Distal condyle breadth	11.0	10.0	10.5	—	—	—
Depth external condyle	14.1	12.6	—	—	—	—
Length	[248.3]	195.9	—	107.6	—	—
Proximal breadth	[18.2]	16.6	—	—	—	14.7

[1] From Howard 1978.
[2] From Miller 1925.
[3] From Wetmore 1930.
[4] From Howard 1949.

TABLE 17

MEASUREMENTS OF CERVICAL VERTEBRAE FOR SPECIES OF *Morus*

	M. recentior[1]			*M. bassanus*
	LACM 2279	SDSNH 24861	*M. peninsularis*[2]	SDSNH 43061
Length through zygapophyses	—	26.6	25.4	25.3
Least posterior breadth of centrum	—	8.9	6.0	8.5
Length of body of vertebra	14.4	17.0	25.4	16.4
Breadth through prezygapophyses	—	22.4	16.6	20.4

[1] Vertebrae for *Morus recentior* (SDSNH 24861) and *M. bassanus* are both seventh cervicals; *Morus recentior* (LACM 2279) and *M. peninsularis* are not.

[2] From Brodkorb 1955, p. 9.

Morus humeralis (Miller and Bowman 1958)

Figs. 68–77

Synonym.—*Sula humeralis* Miller and Bowman, 1958. Los Angeles County Museum Contributions in Science, no. 20:9.

Holotype.—UCMP 45889/V5566, distal third of a right humerus.

Referred material.—SDSNH 23771/2971-A, proximal end left humerus; LACM 2112/1071, proximal half left ulna; LACM 33663/1080, left carpometacarpus missing proximal end; LACM 2522/1128, a right femur; tibiotarsi—LACM 2356/1094, right distal half; LACM 123552/1094, left; tarsometatarsi—SDSNH 18564/3155, right; SDSNH 24655/2971-A, left missing proximal end; LACM 6458/1075-B, left distal end.

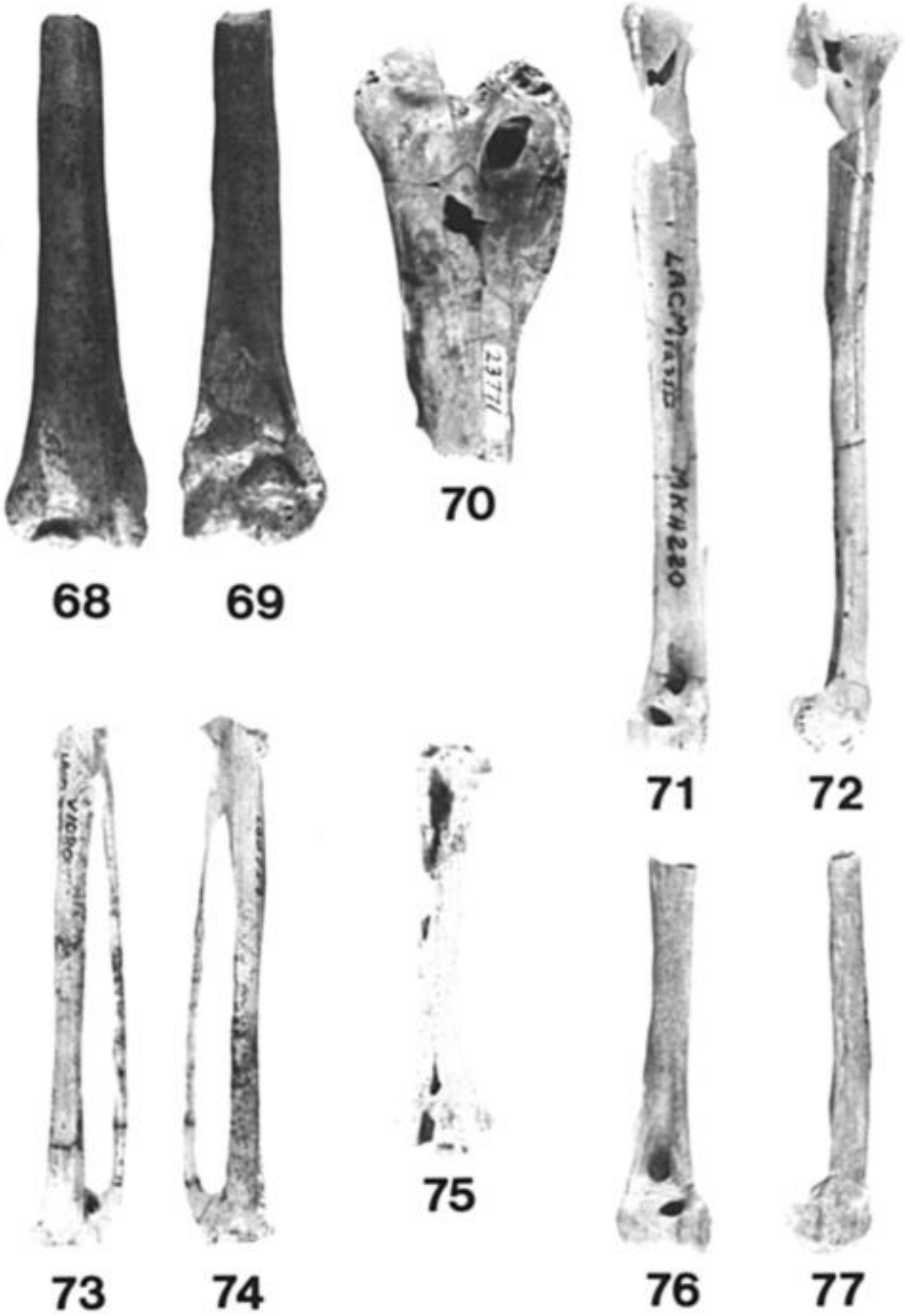
Revised diagnosis.—*Morus humeralis* differs from *Morus bassanus* by having pneumatic opening in humerus larger than that species. *M. humeralis* is smaller than any extant species.

Description.—Brachial depression of the humerus of the holotype extends diagonally across distal end of shaft and is shallow on external half. Brachial impression distally pointed, deep on internal half. Internal tricipital groove shallow. The proximal end has a large pneumatic fossa which extends distad to the distal end of the bicipital crest, and within it is a large pneumatic opening. External side of shaft in the area of deltoid crest flattened. On the palmar surface the bicipital area is restricted. Overall the shaft is flattened.

The facet for digit III of the carpometacarpus extends to the level of the distad extent of the facet for digit II, and a deep groove separates these facets.

Shaft of femur gracile and apneumatic. Rotular groove deep, internal contour of lateral wall of groove rounded. The trochanter is squared off, being unlike the usual condition in *Morus* or in *Sula*. It protrudes laterally from the external side, with a large scar for attachment of the round ligament.

Shaft of tibiotarsus oval in cross-section and slender. Outer cnemial crest almost straight, inner cnemial crest rounded anteriorly. The intermuscular line extends from the inner cnemial crest to the ligamentary attachment on the internal edge of the shaft. Tendinal groove central to shaft, and groove for M. peroneus profundus is between the tendinal groove and the fibular attachment, facing directly anterior. The supratendinal bridge is narrow, robust, and oriented diagonally across the tendinal groove. External condyle externally sloped on anterior surface. Internal condyle thrust inward.



FIGS. 68–77. *Morus humeralis*—68–70 humeri; 71, 72, 76, 77 tibiotarsus; 73, 74 carpometacarpus; 75 tarsometatarsus.

The shaft of the tarsometatarsus is narrow, flattened, and apneumatic. Trochlea II is shorter than trochlea III, and trochlea III and IV are separated by a broad external intertrochlear notch. On the posterior surface, the distal foramen is near the intertrochlear notch. The hypotarsus has two tendinal canals.

Comparisons.—The fossil record for *Morus* is reviewed in the "Comparisons" section for *M. recentior. Morus humeralis* is the second species of *Morus* reported from the Pliocene of San Diego. Thus, *Morus* might have had a more continuous post-Miocene occurrence along the west coast than previously thought.

The humerus of the holotype (UCMP 45889) of *Morus humeralis* can be compared to referred specimens of *M. loxostyla, M. vagabundus, M. lompocanus, M. magnus,* and a *Morus* sp. from Cedros Island, Baja California, Mexico. A humerus tentatively identified and referred to *M. reyanus* (Howard 1949:24) cannot be compared to *M. humeralis* because of its poor preservation. The humerus of *M. peninsularis* is unknown.

The humerus of *Morus loxostyla* is larger than that of *M. humeralis,* with a greater distal breadth and longer attachment of the anterior articular ligament (Wetmore's pronator tubercle, see Table 15). The holotype of *M. vagabundus* and later described humeri (Howard 1966:5) show *M. vagabundus* to have a narrower distal breadth than both *M. humeralis* and *M. loxostyla.* The proximal end of the humerus has been referred and described for *M. vagabundus* by Howard (1966: 5–6). *Morus humeralis* is like *M. vagabundus* by having a more abrupt contour from the shaft to the external tuberosity than in Recent sulids and both have very angular shafts. *Morus humeralis* differs from *M. vagabundus* in lacking a deeply grooved distal end of the bicipital crest, and the deltoid crest extends distad farther down the shaft in relation to the distal extent of the bicipital crest than in *M. vagabundus.* The distal end of the humerus of *M. lompocanus* has not been described, but its size has been estimated as close to that of *M. bassanus* (Miller 1925:114) and, therefore, larger than in *M. loxostyla* and *M. humeralis. Morus magnus* is 20 percent larger than *M. bassanus* in distal breadth (Howard 1978: 17) and, therefore, is much larger than *M. humeralis. Morus magnus* (Howard 1978:18) has a slightly palmad projecting proximal end of the anterior articular ligament; this differs from that of *M. loxostyla,* which has a long, narrow ligamental scar, and *M. humeralis,* which has a short, wide scar. *Morus humeralis* and LACM 15413 from Cedros Island are smaller than *M. lompocanus.* LACM 15413 has a well developed entepicondyle (Howard 1971:5); the entepicondyle is missing on *M. humeralis* (see Discussion). The breadth of the distal end of LACM 15413 is <1 mm larger than that of *M. humeralis.* Because of the poor preservation of the palmar surface of the Cedros Island specimen, positive identification is impossible. However, LACM 15413 does have a narrower and longer anterior articular ligamental scar and a very distinct intercondylar groove different from that of *M. humeralis.*

The humerus of *Morus humeralis* agrees with the other species having synapomorphic characters that separate *Morus* from *Sula* and other pelecaniform birds (see Diagnosis, p. 112).

Ulnae are known for *Morus lompocanus* (see Miller 1925:114 and Howard 1978:16), *M. vagabundus* (see Wetmore 1930:91 and Howard 1966:6), and *M. recentior* (herein). The ulna of *M. vagabundus* is smaller than that of *M. humeralis,* and those of *M. lompocanus* and *M. recentior* are both larger than in *M. humeralis* (Table 16). The ulna of *M. humeralis* is directly comparable to *M. vagabundus* (LACM 16472 and 16473, Howard 1966:6) and *M. recentior* (SDSNH 21596, herein). *Morus lompocanus* (Miller 1925:114) is not comparable because of its flattened preservation in diatomaceous matrix, and the ulna Howard (1978:16) referred is the distal end. The ulna referred to *M. vagabundus* by Wetmore (1930: 91) is also the distal portion. The proximal ends of LACM 16472 and 16473, SDSNH 21596, and LACM 2112 are all very similar in form, differing most noticeably only in size. *Morus* differs from *Sula* as noted in Diagnosis, p. 112.

Carpometacarpi are known for *Morus lompocanus* and *M. magnus* (see Howard 1978:16–17), both of which are larger than in *M. humeralis.* This bone in *M. humeralis* agrees with *Morus* by being less pneumatic and having the facet for digit III extend distad to the level of facet II with a deep groove between its two facets. It differs from that of *Sula* by being more pneumatic and having the facet of digit III shorter, with a shallow groove. I think the greater length of the facet for digit III is derived for *Morus,* being shorter in *Sula,* cormorants, and pelicans.

Femora from two fossil species of gannets, *Morus lompocanus,* and *M. magnus* can be compared with *M. humeralis.* The length of the holotype of *M. lompocanus* exceeds the corresponding measurement (LACM 2522) for *M. humeralis* by 15.7 percent (Table 12). Howard (1978:17) referred a second femur (LACM 37633) to *M. lompocanus,* with two additional measurements (breadth across anterior face of distal end and breadth of shaft) which are equal to the holotype and exceed those of *M. humeralis.* A femur shaft referred to *M. magnus* (Howard 1978:18) has a shaft breadth 18 percent broader than *M. bassanus,* 21.4 percent broader than *M. lompocanus,* and 32.6 percent broader than *M. humeralis.* The femur of *M. humeralis* is, therefore, consistent in size with the preceding elements, being smaller than that of *M. lompocanus* and considerably smaller than that of *M. magnus.*

The form of the femoral trochanter in *M. humeralis,* as mentioned under description (p. 117), is unique, but its rather central position is more like the condition in *Morus* than in *Sula.*

The tibiotarsi of *Morus humeralis* can be compared with *M. lompocanus* (referred specimen Miller 1925:114, Howard 1968:12, and 1978:17) and *M. recentior* (Howard 1949:190). Tibiotarsi of *M. humeralis* are considerably smaller than those of *M. recentior* (Table 13). The internal condyle of *M. humeralis* is thrust inward, resembling those of *M. lompocanus, M. recentior,* and Recent gannets. However, *M. recentior* has the distal condyles angled inward, which is a derived condition, whereas *M. humeralis* and *M. lompocanus* and the Recent gannets have the primitive condition, vertically oriented condyles. Also, the shaft of the tibiotarsus of *M. humeralis* is more oval in transverse section than that of *M. recentior,* or more like that of *M. bassanus. Morus humeralis* differs from *M. bassanus* with a rounded inner cnemial crest; *M. bassanus* has a hooked inner crest, a derived condition among pelecaniform and procellariiform birds.

The relations of the tibiotarsus of *Morus* with the fibula (see Diagnosis), which I think are derived (fibula rather extensively ankylosed with tibiotarsal shaft), are lacking in *Sula, Pelecanus, Phalacrocorax,* and procellariiform birds.

Proximal ends of tarsometatarsi are known from *Morus lompocanus* and *M. reyanus.* Howard (1978:17) referred two tarsometatarsi to *M. lompocanus* and compared them to a cast of the type. The measurements given by Howard for *M. lompocanus* are 18.8 percent broader than the proximal end of SDSNH 18564. A tarsometatarsus (LACM 2052) referred to *M. reyanus* by Howard (1949:24) is described as having the size proportions of *M. bassanus*. Of two specimens of *M. bassanus* available for comparisons, the smaller is still 24.7 percent broader proximally than SDSNH 18564 (referred to *M. humeralis*).

The tarsometatarsi of *Sula* and *Morus* are easily separable. In *Sula*, this bone is broad with an excavated anterior surface, whereas in *Morus* the tarsometatarsus is narrow, tapering from the proximal to the distal end, and is flatter on the anterior surface. In this, *Morus* has the primitive condition shared with *Pelecanus*. *Sula* also has a raised intercotylar prominence, which is derived, as compared to the lower prominence in *Morus*, *Pelecanus*, and *Phalacrocorax*. A derived condition for *Morus* is the elongation of trochlea III proximad on the posterior surface; the primitive condition in *Sula*, *Pelecanus*, and *Phalacrocorax* is a shorter, rounded trochlea III. An autapomorphy for *M. humeralis* is elongation proximad of the articulating face of trochlea III beyond the distal foramen; in other species of *Morus* the trochlea is elongated but ends distal to the distal foramen. The external intertrochlear notch is broader in *Morus* than in *Sula*, and trochlea II is the longest in *Sula*, with trochlea III longest in *Morus*.

Discussion.—Miller and Bowman (1958:9) named the booby *Sula humeralis* from the San Diego Formation; it is the second Pliocene sulid from the west coast of North America. As documented above, close examination of the holotype (humerus) of *S. humeralis* along with the more recently collected and identified sulid material from the San Diego area shows that it should be reassigned to the genus *Morus*.

Miller and Bowman's diagnosis (1958:9) of *Sula humeralis* states that the "internal tricipital groove [is] relatively shallow as compared with *S. leucogaster*." The species of *Sula* have a variable yet distinct internal tricipital groove, whereas the species of *Morus* have a shallow groove (see the revised diagnosis). Also in their diagnosis, Miller and Bowman commented that the "entepicondyle is less prolonged up the shaft . . . both epicondyles broadened." These are misleading statements because the entepicondyle of the type is eroded away.

The "detailed description" section given by Miller and Bowman (1958:9–10) uses characters that are highly variable intraspecifically to describe *Sula humeralis*. These do not permit distinction between *Sula* and *Morus*. For example, (1) the distal border of the impression of M. brachialis anticus is a distinct, transverse ridge in the holotype humerus of *S. humeralis* and in *S. leucogaster* (Brown Booby). However, according to Miller and Bowman, "this ridge is lacking or only faintly indicated in *S. dactylatra*, *S. sula*, and *Morus bassanus*." (2) A three-point description is given for the "brachial depression" distal to this ridge. But the brachial depression is not located here; this is a description of the ulnar fossa (1). Their second point states that the external side of the ulnar fossa is "defined by a ridge extending obliquely inward from the external condyle." This is also true in *M. bassanus*, but the species in *Sula* lack a continuous ridge from the proximal tip of the external condyle, having instead a notch or groove between the condyle and the shaft. (3) Nor is it correct that the ulnar fossa has "its internal side defined by the entepicondylar prominence." The anterior articular ligamental attachment is the lateral border to the ulnar fossa.

Under "Referred material," Miller and Bowman (1958:10) describe a femur (LACM 2522) referred to *Sula humeralis* as "complete except for inner condyle." Also they stated that it "is longer than in *Sula sula websteri,* but the shaft is more slender and the contours are more rugged." There is no figure and upon examination several diagnostic characters show this femur to be better referred to *Morus* than *Sula* (see Comparisons).

Miller and Bowman (1958:12) also recommended that the cotype for *Miosula recentior* Howard 1949 (LACM 2112, a left ulna) be reassigned to *Sula humeralis* (see Comparisons). They compared the relative size of the humerus, ulna, and femur of living sulids and found that the ulna of *M. recentior* compared better to the elements so far referred to *S. humeralis,* but gave no comparative osteological characters. Howard (1949:190) says of the ulna: "The cotype is closer to *Morus* than to *Sula* in general contours, greater flare through the cotylae, shape of olecranon, and absence of pneumatic foramen below the external cotylae on the palmar face." I agree with Miller and Bowman's reassignment of the left ulna to *S. humeralis,* but the characters given by Howard corroborate my reassignment of *S. humeralis* to *Morus humeralis.*

Genus *Sula* Brisson

Diagnosis.—*Sula* has the anterior surface of the neck of the coracoid, between furcular and glenoid facets, narrow with a deep U-shaped contour; an open, flatter neck is found in *Morus*; sternum of *Sula* lacks a ventral manubrial spine, and the sternocoracoidal articulating surfaces are separated; *Morus* has a manubrial spine, and the articulating surfaces meet at midline of sternum.

Sula clarki n. sp.
Fig. 78

Holotype.—SDSNH 26214/3181-C, left coracoid.

Paratypes.—LACM 2438/1080, shaft of right humerus; SDSNH 24942/3168, anterior portion of sternum.

Etymology.—Named for Robert L. "Fritz" Clark, in recognition of his distinguished collecting of vertebrate fossils in southern California, including the San Diego Formation.

Diagnosis.—The holotype differs from all other known species of *Sula* by having the least overhang of the triosseal canal by the brachial tuberosity.

Description.—The shaft of a right humerus (LACM 2438) has the capital shaft ridge centered below the head. Scar for M. latissimus dorsi parallel with capital shaft ridge.

Coracoid of holotype (SDSNH 23080) small, missing procoracoid and sternal end. Head pointed and neck narrow and round. Triosseal canal has a distinct, essentially apneumatic lateral depression, which the glenoid facet overhangs. Brachial tuberosity not enlarged and does not overhang head of triosseal canal. Anterior intermuscular line ends in a broad curve near middle of the external sternal facet. Internal sternal facet short but broad.

An anterior sternal fragment (SDSNH 24942) is small and does not have a ventral manubrial spine. Sternocoracoid articulating surfaces short and broad, coracoidal sulci separated, not meeting at midline of sternum.

Comparisons.—The five previously described fossil species in *Sula* are all from

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FIGS. 78–82. *Sula clarki*—78 coracoid. *Phalacrocorax kennelli*—79 ulna. Phalacrocoracidae gen. et sp. indet.—80, 81 ulna. *Sula* sp.—82 skull.

older deposits than is *S. clarki.* They are: *S. universitatis* Brodkorb (1963b:161) from the early Miocene of Alachua County, Florida; *S. guano* and *S. phosphata* Brodkorb (both 1955:9, 11) from the late Miocene of Polk County, Florida; *S. pohli* Howard (1958:4) Los Angeles County, California; and *S. willetti* Miller (1925:112) Santa Barbara County, California. Another early record for *Sula* sp. (Chandler *in* Demêré et al. 1984:53) is from the middle Miocene, La Misiòn, Baja California, Mexico.

Sula universitatis Brodkorb (1963b:161) is only known from a holotype carpometacarpus about the size of that of *S. leucogaster.* Although similar in size to *S. clarki, S. universitatis* is much older.

Sula willetti and *S. pohli* are from lamellar diatomaceous deposits, an abrasive matrix which has destroyed the details of the bones, leaving size and proportions as principal characters. *Sula willetti* is the smallest known booby, fossil or living (Table 18). *Sula pohli* has a longer coracoid than any other fossil species, and is comparable to living *S. nebouxii* (Blue-footed Booby) and *S. dactylatra* (Masked Booby). *Sula pohli* is similar to *S. clarki* in other measurements. *Sula clarki* has a coracoid about the length of *S. guano* and *S. leucogaster.* However, in other measurements of the coracoid head, *S. guano* and *S. phosphata* are both larger than *S. clarki.* Brodkorb's figure 8 (1955:44) of *S. guano* shows that it is less pneumatic than *S. clarki. Sula guano* also differs from *S.clarki* by having a shallow internal sternal facet, whereas *S. clarki* is more like *S. phosphata* by having a more rounded and deeper facet. *Sula clarki* differs from *S. phosphata* and agrees with *S. guano* by having the medial margin of the head weakly depressed, and the lip of the brachial tuberosity more angular and swept upward to the furcular facet.

The sternum (SDSNH 24942) and humeral shaft (LACM 2438) are both referable to *Sula.* A derived condition, I think, is the lack of a ventral manubrial spine (present and primitive in *Phaethon, Fregata, Pelecanus,* Phalacrocoracidae, and some procellariiforms). The humerus has the capital shaft ridge in the center of the anconal surface of the shaft (= primitive); in *Morus* the ridge is on the external side below the external tuberosity (= derived). The sizes of the sternum and humerus as compared to the coracoid suggest they are all from one species. The deep, rounded, external sternal facet of *Sula clarki* and *S. phosphata* are derived characters in *Sula,* whereas the shallow shelf of the sternal facet in *S. guano* is primitive, also occurring in *Morus, Phalacrocorax,* and *Pelecanus.*

Another primitive character of *Sula, Pelecanus,* and *Phalacrocorax* is the rounded external border of the glenoid facet. A notched external border (*Morus*) is derived.

Sula sp. indet.

Fig. 82

Referred material.—SDSNH 23770/2907, bill and skull cap; coracoids—SDSNH 23080/2971-A, right head end; SDSNH 25825/3181—A, left; LACM 2521/1128, right shaft and glenoid facet; LACM 105149/1074, vertebra; LACM 2264/1075-B.

Description.—Skull (SDSNH 23770) with bill, top of braincase, and right jugular bar present. Rhamphotheca reaches craniofacial hinge and tripartite bill grooves present.

A coracoid (SDSNH 23080) has an apneumatic triosseal canal and the brachial tuberosity overhangs it.

Comparisons.—The skull (SDSNH 23770) agrees with *Sula* in which the rhamphotheca reaches the craniofacial hinge (= primitive); it fails to do so in *Morus* (= derived). The least interorbital breadth of SDSNH 23770 is closest to that of the largest Recent species, *Sula nebouxii,* but the breadth of the craniofacial hinge is less than that of *S. leucogaster* (*S. sula,* Red-footed Booby, unavailable). *S. willetti* Miller (1925:112) is smaller than the species of SDSNH 23770.

Coracoids SDSNH 23080 and 25825, and LACM 2521 are about the size of *Sula clarki,* holotype SDSNH 26214. In fact, SDSNH 25825 and LACM 2521 might belong to *S. clarki* but are too fragmentary for certain identification. SDSNH 23080, however, is different from the holotype of *S. clarki.* It is apneumatic in the triosseal canal, the glenoid facet is shorter, the brachial tuberosity noticeably overhangs the triosseal canal, and the anterior surface of the neck is narrower than in *S. clarki.*

The vertebrae LACM 105149 and 2264 are from a small species, but the possible presence of a second small booby in the San Diego area (SDSNH 23080) precludes specific identification. *Sula clarki* might have coexisted with both larger and smaller boobies as suggested by the skull (SDSNH 23770) and the other coracoid (SDSNH 23080).

Measurements.—Least interorbital breadth of skull, 28.2; craniofacial hinge breadth of skull, 17.9.

Family PHALACROCORACIDAE
Subfamily PHALACROCORACINAE
Genus *Phalacrocorax* Brisson
Phalacrocorax kennelli Howard 1949
Fig. 79

Holotype.—LACM 2127/1080, coracoid.

Paratypes.—LACM 2121/1080, right humerus, proximal end; LACM 2115/1080, furcula fragment.

Referred material.—Ulnae- SDSNH 23754/2971-C, left missing proximal end; SDSNH 22376/3114, left; SDSNH 23772/2907, right; coracoids—SDSNH 21023/2977, left; SDSNH 21085/3006, right missing sternal end; LACM 2566/1080, right tibiotarsus.

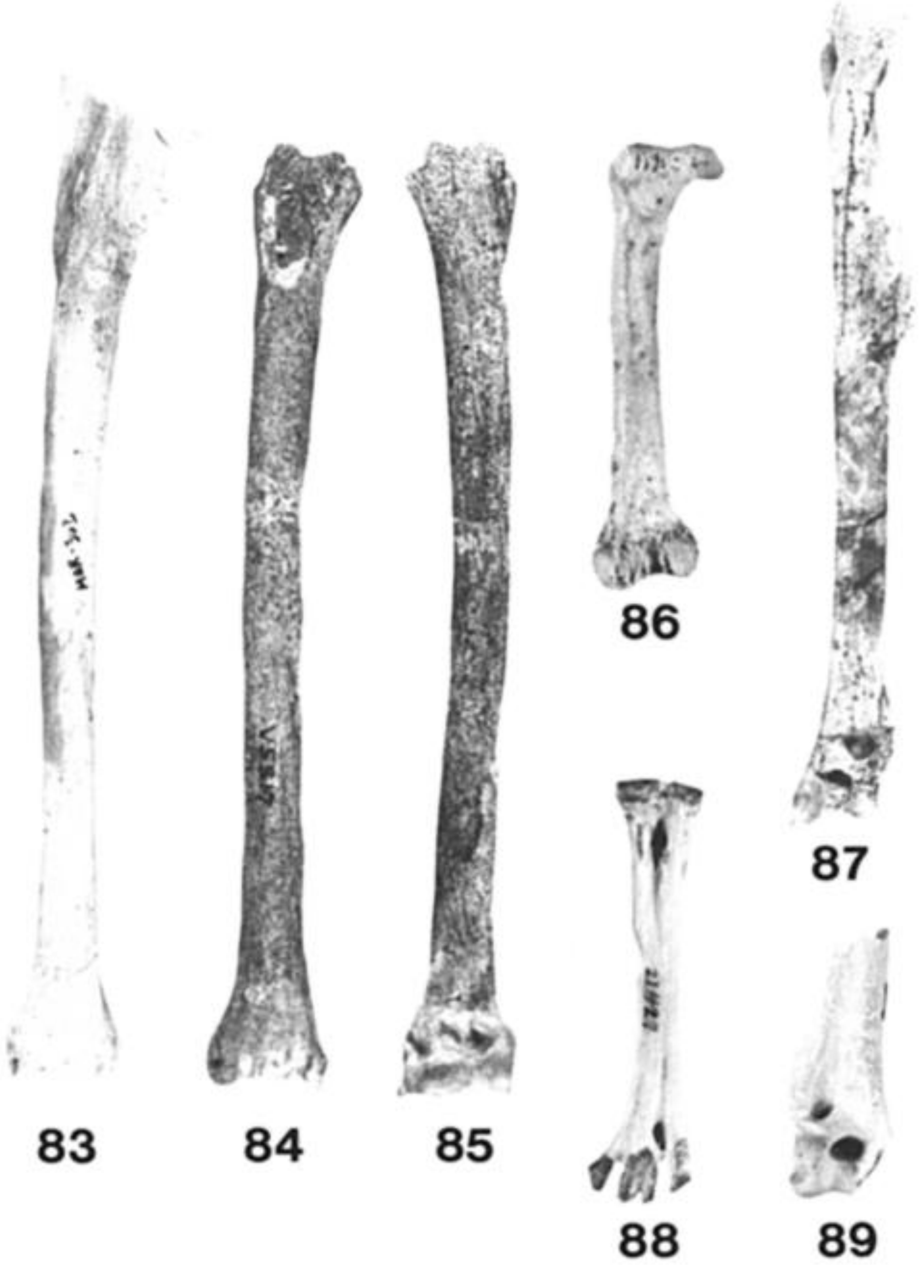
Description.—Ulnae long and slender, shaft tapering toward distal end. Coracoid described by Howard (1949:188).

Comparisons.—See comparisons for *Stictocarbo kumeyaay* n. sp.

Subfamily LEUCOCARBONINAE
Stictocarbo kumeyaay n. sp.
Figs. 86, 87, 90–95

Holotype.—SDSNH 24869/3176, associated left humerus, distal end left ulna, right coracoid, right and left femora, right tibiotarsus, and right tarsometatarsus.

Paratypes.—SDSNH 27296/3265, right femur; SDSNH 22226/2971-A, left tibiotarsus.



FIGS. 83–89. Phalacrocoracidae gen. et sp. indet.—83–85 humeri; 86 femur; 87, 89 tibiotarsi; 88 tarsometatarsus.

Etymology.—The name refers to an aboriginal Indian tribe which once lived in the San Diego County area. Kumeyaay means "those who face the water from the cliffs," an accurate description of how shags rest.

Diagnosis.—*Stictocarbo kumeyaay* is like *S. pelagicus* and *S. urile* by having a

FIGS. 90–96. *Stictocarbo kumeyaay*—90 humerus; 91 coracoid; 92 femur; 93 ulna; 94 tarsometatarsus; 95 tibiotarsus. *Melanitta ceruttii*—96 humerus.

compressed internal contour of the neck below the furcular facet more than *S. magellanicus, S. gaimardi,* and *S. punctatus*; external condyle flattened anconally rather than rounded in *S. magellanicus, S. gaimardi,* and *S. punctatus*; fibular groove deep forming a right angle, whereas *S. magellanicus, S. gaimardi,* and *S. punctatus* have either a shallow, open groove or a deep, more closed groove as in *S. magellanicus, S. gaimardi,* and *S. punctatus*; *S. kumeyaay* has a robust internal cnemial crest which differs from both *S. pelagicus* and *S. urile* which have thin and flared internal cnemial crests.

TABLE 18

Measurements of Coracoids for Species of *Sula*

	Length	Head to procoracoid	Breadth at level of scapular facet
S. guano	50.0	21.0	14.7
S. phosphata[1]	—	21.0	13.8–14.5
S. willetti	45.0	18.2[2]	—
S. clarki n. sp.	50.7	18.8	13.1
S. pohli	55.0	[19.1]	13.7

[1] From Brodkorb 1955, table 4.

[2] Measured from Miller 1925, pl. 3, UCMP 26542.

Description.—The holotype has a robust skeleton for the length of the individual elements. Humerus has internal contour of the pneumatic fossa straight from scar for M. dorsalis scapulae to internal tuberosity. Brachial depression relatively shallow and anterior articular ligamental attachment short, broad, and faces slightly more laterally than palmarly.

Ulna has an internal condyle protruding distad, a long gradually merging external condyle, and carpal tuberosity thick and blunt. Coracoid has a distinct diamond-shaped furcular facet. Femur robust and slightly compressed laterally. Fibular groove approximately at a 90° angle. External condyle deeper than either fibular or internal condyles. Cnemial crests of tibiotarsus close together but not converging. Scar for M. flexor perforatus digiti III on internal edge of shaft. Tarsometatarsus has very rounded trochleae.

Comparisons.—Siegel-Causey's phylogenetic analysis (1988) of the Phalacrocoracidae was used to set character polarities. Prior to his analysis, I had independently allied *kumeyaay* with *pelagicus* (Pelagic Cormorant) and *urile* (Red-faced Cormorant). I am following Siegel-Causey's generic assignment of *pelagicus* and *urile* and place *kumeyaay* in *Stictocarbo.*

Three late Pliocene cormorants are known: *Phalacrocorax idahensis* (Marsh 1870:216) and *P. macer* Brodkorb (1958:237) are from the Glenns Ferry Formation in Idaho; and *P. kennelli* (Howard 1949:188) is from the San Diego Formation. Murray (1970) compared these with the living species *Phalacrocorax*

TABLE 19

Measurements of Humeri for Species of Phalacrocoracids[1]

	S. kumeyaay	*Phalacrocorax* sp.		*P. kennelli*	
	SDSNH 24869	UCMP 45868	UCMP 45872	SDSNH 24862	LACM 2121
Length	132.8	—	—	—	—
Breadth distal end	13.6	—	16.0	—	—
Breadth shaft	7.9	—	8.1	8.4	—
Depth shaft	6.5	—	6.6	7.0	—
Proximal width	—	22.4	—	—	21.6
Head depth	6.9	7.0	—	—	6.5
Length of ligamental furrow	12.2	13.2	—	—	—
Breadth bicipital furrow (Howard 1949)	—	10.3	—	—	9.1

[1] Measurements same as Murray 1970.

TABLE 20
MEASUREMENTS OF ULNAE FOR SPECIES OF PHALACROCORACIDS

	P. kennelli			*S. kumeyaay*	*Phalacrocorax* sp.	
	SDSNH 23754	SDSNH 22376	SDSNH 23772	SDSNH 24869	LACM 2529	UCMP V45866
Length	—	139.7	139.6	—	—	141.2
Proximal breadth	—	11.4	10.3	—	11.0	—
Distal depth through carpal tuberosity	9.4	10.1	9.8	10.6	9.7	9.4
Proximal depth through cotyla and olecranon	—	10.5	9.5	—	9.5	—
Maximum diameter of shaft at distal end of scar [impression] of brachialis anticus (from Murray 1970)	6.1	6.9	6.5	—	6.7	6.1

auritus (Double-crested Cormorant). *Stictocarbo kumeyaay* is better compared with *Stictocarbo urile* than with *Phalacrocorax auritus* because of its short, robust bones (Tables 19–23). Derived for *S. kumeyaay* and *S. urile* is the diamond-shaped furcular facet of the coracoid. Other cormorants (e.g., *P. kennelli,* SDSNH 21023, 21085, and *P. idahensis,* LACM 17819) have a flatter internal contour of the furcular facet. Also, the blunt carpal tuberosity on the ulna of *S. kumeyaay* differs from that of *P. idahensis* (LACM 53902) and *P. kennelli* (SDSNH 23754, 22376, 23772), which have a straighter proximal contour. The oblong external condyle on the ulna of *S. kumeyaay* also differs from that of *P. idahensis* and *P. kennelli,* which have a round condyle, the primitive condition. The tibiotarsi of *S. kumeyaay* and *P. idahensis* are similar, having closely placed cnemial crests. They differ from those of *P. kennelli* (LACM 2566), which has widely set cnemial crests almost to the lateral edge of the shaft. *Stictocarbo kumeyaay* differs from SDSNH 24858, which might be *P. kennelli,* by having M. flexor perforatus digiti III on the internal edge of the shaft, which I consider primitive; SDSNH 24858 has a scar medial to the edge of the shaft as in the Recent species, *P. carbo* (Great Cormorant).

Phalacrocoracidae gen. et spp. indet.
Figs. 80, 81, 83–89

Material.—Humeri- UCMP 45872/V5517, left missing proximal end; SDSNH 25817/3181-A, left missing head; Ulnae- LACM 2529/1080; UCMP 45866/V5517, right; SDSNH 22826/3125, distal end right tibiotarsus; SDSNH 21427/2946, left tarsometatarsus missing hypotarsus.

Remarks.—At least two more species of phalacrocoracids (cormorants and shags) from the San Diego Formation have not been described.

The fragment of tibiotarsus is from an unknown species larger than any fossil, larger than *Phalacrocorax idahensis,* or Recent species, with which I have compared it.

Humeri UCMP 45872 and SDSNH 25817 are from larger, more robust individuals than the ulnae referred to *Phalacrocorax kennelli* and the appropriate articulating ends do not make acceptable joints; the proximal ends of the ulnae

TABLE 21

MEASUREMENTS OF CORACOIDS FOR SPECIES OF PHALACROCORACIDS

	P. kennelli		*S. kumeyaay*	
	SDSNH 21023	SDSNH 21085	SDSNH 24869	SDSNH 24881
Length (head to internal sternal angle)	58.9	—	59.9	[60.0]
Distance from head to scapular facet	20.5	21.4	23.2	22.7
Distance from top of glenoid facet to tip of head	[10.7]	11.6	13.0	11.9
Anteroposterior breadth immediately above procoracoid	9.5	10.0	10.1	10.1
Distance from anterior intermuscular line to internal sternal angle	12.5	—	11.4	—
Dorsoventral head depth	—	8.6	9.7	—

are too small. This species is at least as large as *P. idahensis.* Miller (1956:617) mistakenly assigned UCMP 45872 to *Gavia concinna.*

The tarsometatarsus (SDSNH 21427) is shorter than the holotype of *Stictocarbo kumeyaay* n. sp., but might belong to that species.

Order ANSERIFORMES
Family ANATIDAE
Subfamily ANATINAE
Tribe Mergini
Genus *Melanitta* Bois

Diagnosis.—*Melanitta* differs from all other sea duck genera in having a deep olecranal fossa, high-vaulted proximad, and more distally flared, deltoid crest.

Melanitta ceruttii n. sp.

Fig. 96

Holotype.—SDSNH 23584/3153, right humerus missing the proximal end.

Etymology.—Named in honor of Richard A. Cerutti, who has diligently and unselfishly collected fossil vertebrates in the San Diego area for many years.

Diagnosis.—Holotype differs from all extant species of *Melanitta* in smaller size.

Description.—The humerus of the holotype (SDSNH 23584) is missing the proximal end, entepicondylar process, and part of the proximal end of the internal condyle. Proximally, the deltoid crest is flared at the distal end, and extends distad

TABLE 22

MEASUREMENTS OF FEMORA FOR SPECIES OF PHALACROCORACIDS

	P. idahensis LACM 17819	*S. kumeyaay* SDSNH 24869
Length (external side)	—	57.8
Distal breadth	16.0	16.1
Depth external condyle	10.7	11.0
Depth fibular condyle	8.6	9.3
Depth internal condyle	9.8	8.8

TABLE 23

MEASUREMENTS OF TARSOMETATARSI FOR SPECIES OF PHALACROCORACIDS

	S. kumeyaay		*P. idahensis*
	SDSNH 21427	SDSNH 24869	LAM 17819
Length	56.2	61.5	62.0
Trochlear breadth	14.5	14.7	14.7
Proximal breadth	12.1	12.3	13.9

farther than the bicipital crest. The edge of the deltoid crest is thick, having a bony lip. Distally, the olecranon fossa is deep with the proximal border high vaulted. Also, the anterior articular ligament has an anconal rather than lateral orientation.

Comparisons.—Livezey's (1986) phylogenetic analysis of the Anseriformes was used to set character polarities.

Woolfenden (1961:115) lists eight humeral characters that define the tribe Mergini (sea ducks). Those characters preserved and observable on SDSNH 23584 agree. *Melanitta* is separable from all other sea ducks as follows: "deltoid crest extends farther distad, and its distal portion is more flaring" (Woolfenden 1961: 19). Also, a deep, high-vaulted proximal border of the olecranon fossa is here considered a derived character of *Melanitta.* SDSNH 23584 agrees with these characters.

This is the only extinct species thus far referred to *Melanitta.* The earliest records of the three neospecies are all Pleistocene (Brodkorb 1964:246–247; Howard 1964: 312–313). Smaller size distinguishes *M. ceruttii* from the three living species (see Table 24). *M. ceruttii, M. fusca* (White-winged Scoter), and *M. perspicillata* (Surf Scoter) have the deltoid crest extending farther distad than the distal end of the bicipital crest, possibly a derived condition; in *M. nigra* (Black Scoter) both crests end distad at the same level. *M. ceruttii* and *M. fusca* have a bony lip on the edge of the deltoid crest; *M. nigra* and *M. perspicillata* have a blade-like edge, probably the derived condition. *M. ceruttii* and *M. perspicillata* have an anconally-oriented anterior articular ligamental attachment; *M. nigra* and *M. fusca* have a laterad oriented attachment, probably the derived condition. *Melanitta ceruttii* shares the derived character of the deltoid crest with *M. fusca* and *M. perspicillata* and no derived characters with *M. nigra.* However, *M. nigra* shares a single derived character each with *M. fusca* and *M. perspicillata* making a polytomy from the data for the humerus.

Tribe Mergini gen. et sp. indet.

Material.—LACM 10547/1081, right humerus, partial proximal end.

Description.—A fragment of a proximal right humerus (LACM 10547) has a flared distal end of the deltoid crest and an angular proximal end.

Comparisons.—A distally-flared deltoid crest and an angular proximal end are characters that distinguish the humeri of sea ducks (Woolfenden 1961:115). LACM 10547 agrees. LACM 10547 is near *Mergus merganser* (Common Merganser) in size, much larger than *Melanitta ceruttii.*

TABLE 24

MEASUREMENTS OF HUMERI OF *Melanitta ceruttii* AND ALL EXTANT SPECIES WITHIN THE GENUS

	M. ceruttii Holotype	*M. nigra* N = 1	*M. perspicillata* N = 4	*M. fusca* N = 6
Length	—	79.5	80.6–85.0	98.4–105.5
Length deltoid crest[1] to external condyle	49.4	57.0	57.2–60.0	70.6–73.9
Length bicipital crest[2] to internal condyle	53.5	59.6	62.3–64.8	75.1–79.8
Midshaft width	4.9	5.3	5.0–5.7	6.1–6.5
Midshaft depth	5.3	5.5	5.6–6.0	6.4–7.6
Width distal end	10.0	11.2	10.6–11.9	12.2–14.0
External condyle depth	6.7	7.0	6.7–7.3	8.4–9.7
Internal condyle	4.7	5.2	5.0–5.5	6.2–6.9

[1] Distal end of deltoid crest to farthest extent of external condyle.
[2] Distal end of bicipital crest to farthest extent of internal condyle.

Order CHARADRIIFORMES
Family CHARADRIIDAE
Genus *Charadrius* Linnaeus
Charadrius sp.

Referred material.—SDSNH 28801/3281-U, distal end left tibiotarsus.

Description.—The distal end of a left tibiotarsus (SDSNH 28801) has a narrow shaft, a complete tendinal bridge, and a robust internal condyle.

Comparisons.—The tibiotarsus is essentially identical to that of the Killdeer, *Charadrius vociferus.* The only apparent difference is that the fossil has a more robust internal condyle than the Recent Killdeer.

Discussion.—This is the second shorebird identified from the San Diego Formation (see next species account) and the first Pliocene record of *Charadrius* (Brodkorb 1967:192).

Measurements.—Distal breadth—4.4; external condyle depth—4.2; internal condyle depth—3.6.

Family SCOLOPACIDAE
Shorebird? Howard 1949

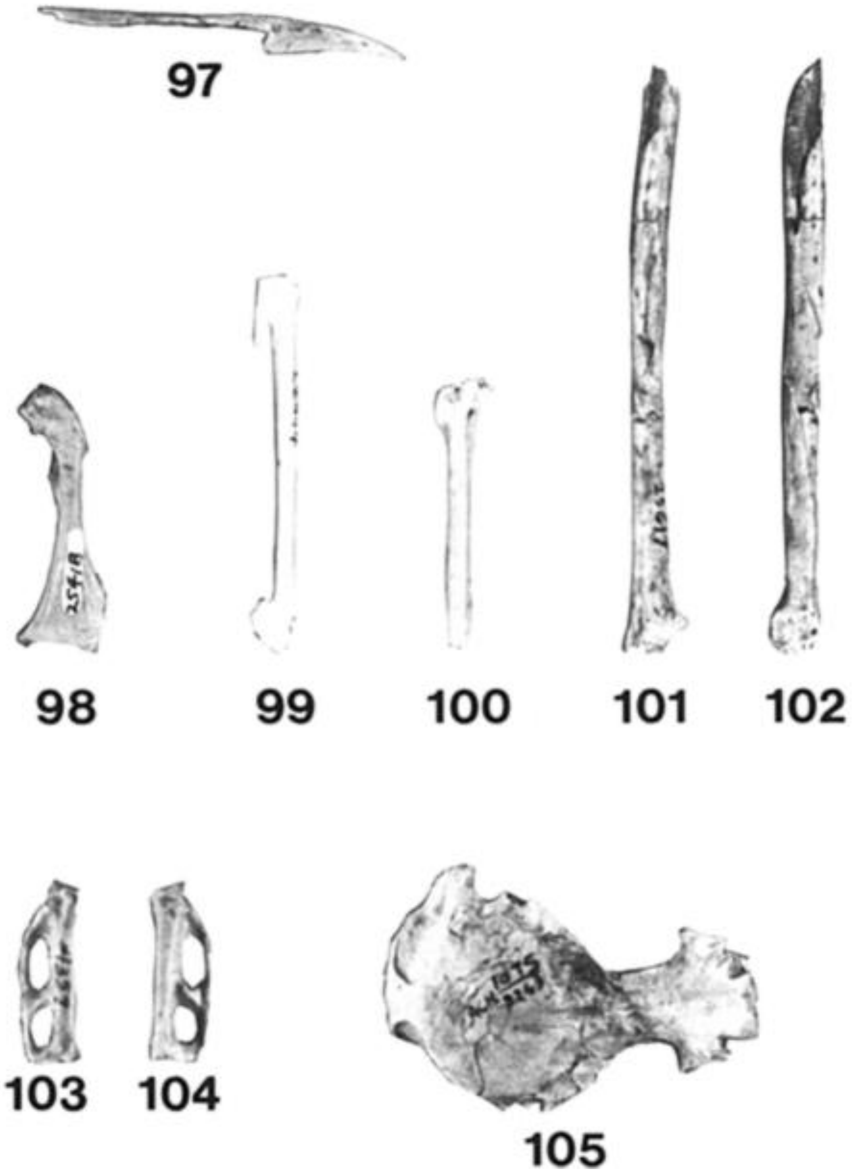
Referred material.—LACM 2128/1080, incomplete left tarsometatarsus.

Discussion.—Howard (1949:193) reported a California Pliocene shorebird near the size of a Western Sandpiper, *Calidris mauri.* There is no material in the present collection.

Family LARIDAE
Subfamily LARINAE
Genus *Rissa* Stephens
Rissa estesi n. sp.
Figs. 97, 98

Holotype.—SDSNH 25418/3181-C, left coracoid, missing internal end of procoracoid and sternocoracoidal process.

Paratypes.—LACM 2107/1080, premaxilla; SDSNH 24920/3176, right scapula.



Figs. 97–105. *Rissa estesi*—97 premaxilla; 98 coracoid. *Larus* sp.—99 carpometacarpus; 100 tarsometatarsus; 103, 104 phalanx 1 of digit II; 105 skull cap. *Sterna* sp.—101, 102 ulna.

Etymology.—Named in honor of Richard Estes for his contributions to vertebrate paleontology, and his years of collecting vertebrate fossils from the San Diego Formation many of which were donated to the San Diego Natural History Museum for the present project.

Diagnosis.—A restricted depression within the pneumatic fossa undercutting the head in the triosseal canal as in *Rissa tridactyla* differs from *R. brevirostris*, which lacks this depression; internal portion of sternal facet straighter than in

TABLE 25

MEASUREMENTS OF SCAPULAE FOR SPECIES OF *Rissa*

	Rissa sp.	*R. estesi*	*R. tridactyla*		*R. brevirostris*	
	SDSNH 25830	SDSNH 24920	SDSNH 36497	RMC 411	SDSNH 40514	SDSNH 40513
Proximal breadth	6.2	8.6	8.2	7.8	8.1	7.8
Proximal depth	1.7	2.5	2.2	2.2	2.0	1.8
Length glenoid facet	3.8	5.9	5.5	5.6	4.7	4.3
Breadth glenoid facet	2.0	3.2	2.1	2.7	3.1	2.7
Neck breadth and depth	2.7 × 1.4	3.9 × 2.2	3.7 × 1.7	—	3.0 × 1.6	3.2 × 1.6

either *R. tridactyla* or *R. brevirostris*; premaxillary symphysis longer and straighter than in either *R. tridactyla* or *R. brevirostris.*

Description.—The holotype (SDSNH 25418) has a slender shaft, which gradually curves medially toward the head of the bone until it forms a slight notch as it meets the lateral side of the furcular facet. Procoracoid broken, but it can be seen that it was flattened and rounded toward the head over the triosseal canal. Shaft fenestrated at base of procoracoid. Brachial tuberosity close to glenoid facet, and furcular facet long, extending from brachial tuberosity to internal margin of proximal end. Pneumatic fossa, below brachial tuberosity and furcular facet, extends across breadth of triosseal canal; it has a distinct, restricted depression within it with a thin wall of bone in common with the neck of the coracoid. This thin wall noticeably allows transmitted light to pass through it. At the sternal end, the internal portion of the sternal facet is only slightly curved internally and is narrow.

The paratypic premaxilla (LACM 2107) consists of the premaxillary symphysis and the dorsal nasal bar; missing are the ventral nasal bars and the dorsal nasal bar is broken through the proximal nasal processes. Bill tip long and decurved. Dorsal nasal bar ventrally flat and uniform in width, except for a slight constriction near base of proximal nasal processes. Maxillae, from their position lateral to proximal nasal processes, wrap beneath dorsal nasal bar onto its ventral surface and fuse with it and each other medially and extend distad along the bar.

The paratypic scapula (SDSNH 24920) is missing the coracoidal articulation and the blade distal to the neck. Proximal end of scapula narrow, relatively flat, and coracoidal articulation central. Acromion laterally flattened and glenoid facet long, narrow, proximal, and meets the neck distally in a gradually curved contour.

Comparisons.—Other charadriiform birds were used to set character polarities. The known elements of *Rissa estesi* are most like those of the Black-legged Kittiwake (*Rissa tridactyla*). They are similar in size (Tables 25–27) and share some osteological characters: the coracoid has a restricted, thin-walled depression, in common with the neck, within the pneumatic fossa; the glenoid facet is proximally positioned, flat, and gradually meets the neck of the coracoid distally; the ventral surface of the dorsal nasal bar of the premaxillary is flat. *Rissa brevirostris* (Red-legged Kittiwake) differs from *R. estesi* and *R. tridactyla* in missing a depression within the pneumatic fossa, the primitive condition found in the outgroups (gulls, terns, and plovers).

Species in *Rissa* have a flat ventral surface on the dorsal nasal bar of the premaxillary, differing from all other gulls and terns, which have a broad V-shaped

TABLE 26

MEASUREMENTS OF CORACOIDS FOR SPECIES OF *Rissa*

	R. estesi Holotype	*R. tridactyla*	*R. brevirostris*
Coracoid length	34.1	34.3–35.2	34.6
Brachial tuberosity to furcular facet	8.3	7.3–8.8	6.7–7.3
Length of sternal facet	10.7	11.5–11.7	10.1–10.6
Least breadth of shaft	3.5	3.7–4.0	3.7–3.8
Least depth of shaft	2.7	2.5–2.8	2.6–2.7

keel on the ventral surface. I think the condition limited to *Rissa* is derived. Likewise, I think the coracoid characters just mentioned for *Rissa* are derived. However, although very similar to the two living kittiwakes, *R. estesi* differs from them by having a straighter and thinner sternal facet of the coracoid, a longer and less decurved bill tip, and an additional ventral crest on the acromion of the scapula, which adds to the greater proximal breadth of *R. estesi.*

Rissa estesi is the first known fossil species of kittiwake, and the first larid recorded from the San Diego Formation.

Discussion.—Only the Black-legged Kittiwake visits California coasts today, as a winter migrant. Perhaps the same was true of *Rissa estesi* if migration in that species had already developed by the Pliocene epoch.

The paratype premaxilla (LACM 2107) was originally described and figured as that of *Mancalla diegensis,* by Miller and Howard (1949:218, pl. 3, fig. 13 a–c). I reassign it to the Laridae because of the laterally placed maxillae which wrap beneath the dorsal nasal bar and fuse to it and each other (in alcids they wrap beneath the dorsal nasal bar and fuse to it, but do not meet or fuse medially). The condition in larids is probably derived.

An additional very small scapula (SDSNH 25830) is assigned to *Rissa* but is specifically indeterminate. Its size appears to be out of the range possible for *R. estesi.* It is almost identical osteologically to the scapula of *R. estesi,* but is best left unnamed until further material is available.

Genus *Larus* Linnaeus

Larus sp.

Figs. 99, 100, 103–105

Referred material.—LACM 2263/1075, skull cap; SDSNH 22994/3088, incomplete left carpometacarpus; SDSNH 31359/3088, left digit II phalanx I; SDSNH 25229/2971, right tarsometatarsus, proximal one half.

TABLE 27

MEASUREMENTS OF PREMAXILLAE FOR SPECIES OF *Rissa*

	R. estesi	*R. tridactyla*		*R. brevirostris*	
	LACM 2107	SDSNH 36497	RMC 411	SDSNH 40514	SDSNH 40513
Length from end of nasal opening to bill tip	18.0	15.1	15.4	11.0	10.6
Breadth of symphysis	4.4	4.6	5.5	4.2	4.1
Least breadth dorsal nasal	3.1	2.8	3.2	3.1	2.9

Description.—LACM 2263 is a skull cap with the proximal end of the premaxillae processes, nasals, and the top of the cranium preserved. The temporal fossae are shallow and separated at their medial margins at the top of the skull. The skull is holorhinal, there are no supraorbital rims, and the salt glands, which probably met medially, extend dorsolaterally onto the prefrontal bones. The nasals are indented medially.

SDSNH 22994 is a metacarpal II with the proximal and distal symphyses of a left carpometacarpus. The metacarpal II is palmoanconally compressed and has a deep external tendinal groove on the distal half of the bone. The intermetacarpal tuberosity is in low relief near the proximal metacarpal symphysis. The preserved proximal and distal ends of metacarpal III are flattened palmoanconally and laterally, respectively. A left phalanx I of digit II (SDSNH 31359) is worn on both ends. The blade of the digit has two fenestrations.

SDSNH 25229 is the proximal half of an elongate, narrow right tarsometatarsus with a shallow anterior tendinal groove. The internal calcaneal ridge is deep and narrow and the hypotarsus has a single deep internal channel and two shallow grooves in an anterior row and a single groove posterior to the internal channel.

Comparisons.—The top of a skull (LACM 2263), a carpometacarpus (SDSNH 22994), a first phalanx of digit II and a tarsometatarsus (SDSNH 25229) are assigned to *Larus.* These represent at least one species of gull between *L. delawarenis* (Ring-billed Gull) and *L. californicus* (California Gull) in size. The palmoanconal compression of the metacarpal II separates the Larinae from the Sterninae, which have a more rounded metacarpal. Also, the narrow, laterally extended prefrontals, onto which the salt glands probably extend dorsally as in *Larus* and LACM 2263, separate the gulls from the terns. Terns have swollen prefrontals and the salt glands do not extend out onto the prefrontals as far and actually extend onto the external surface. The temporal fossae extend farther medially in *Sterna* as well.

Discussion.—This is the first record of gulls of the genus *Larus* in the late Pliocene of North America (see also *Rissa estesi* n. sp. named herein). *Larus elmorei* Brodkorb (1955:25) from the early Pliocene Bone Valley Formation in Florida is the only named species from the Tertiary of North America. Olson (1985b:182) noted the presences of "several unnamed species of *Larus*" in the early Pliocene material from Lee Creek, North Carolina. Because of the limited material described here, species identification is not possible.

Measurements.—Skull: distance from proximal end of proximal premaxillae processes to frontal-parietal suture—45.4; interorbital distance—9.7; distance between lateral extent of prefrontal bones—19.0. Carpometacarpus: metacarpal II mid-shaft—3.5 × 2.5; length intermetacarpal space—36.3. Tarsometatarsus: SDSNH 25229, proximal breadth—[7.2]; proximal depth—[7.1]; shaft—3.0 × 2.9.

Subfamily STERNINAE
Genus *Sterna* Linnaeus
Sterna sp.
Figs. 101, 102

Referred material.—SDSNH 25617/3206, right ulna missing proximal end; LACM 30812/1540, left humerus shaft.

Description.—SDSNH 25617 is a right ulna missing the proximal end. The ulna has a gracile shaft. The carpal tuberosity extends laterad from the internal side of the shaft and is conical with a rounded apex. A deep groove separates the distal condyles, and the internal condyle ends ventrally in a point.

LACM 30812 is a left humeral shaft missing both proximal and distal ends. Although the deltoid crest is broken, the base of the crest extends directly out from the palmar surface. Anconally, the capital ridge extends distad from the proximal end and is a laterally compressed ridge from the middle of the shaft. The remainder of the shaft is palmoanconally flattened.

Comparisons.—The ulna (SDSNH 25617) and humerus (LACM 30812) are in the size range of the Royal Tern, *Sterna maxima.* The isosceles triangle-shaped carpal tuberosity of the ulna indicates it is from a tern rather than a gull (Larinae); gulls have a wedge-shaped tuberosity extended perpendicular from the distal end and then angled proximad straight to the shaft. The derived condition is that shown on the fossil, SDSNH 25617, and in *Sterna.* On the fossil humerus (LACM 30812) the extension directly out from the palmar surface of the deltoid crest is a synapomorphy for *Sterna* and differs from Larinae, which have a more primitive laterally flared deltoid crest.

Suborder ALCAE
Family ALCIDAE
Genus *Brachyramphus* Brandt

Diagnosis.—Ectepicondyle of humerus differs from those of other alcids extending anconodistad from internal margin.

Brachyramphus pliocenum Howard 1949
Figs. 106–108

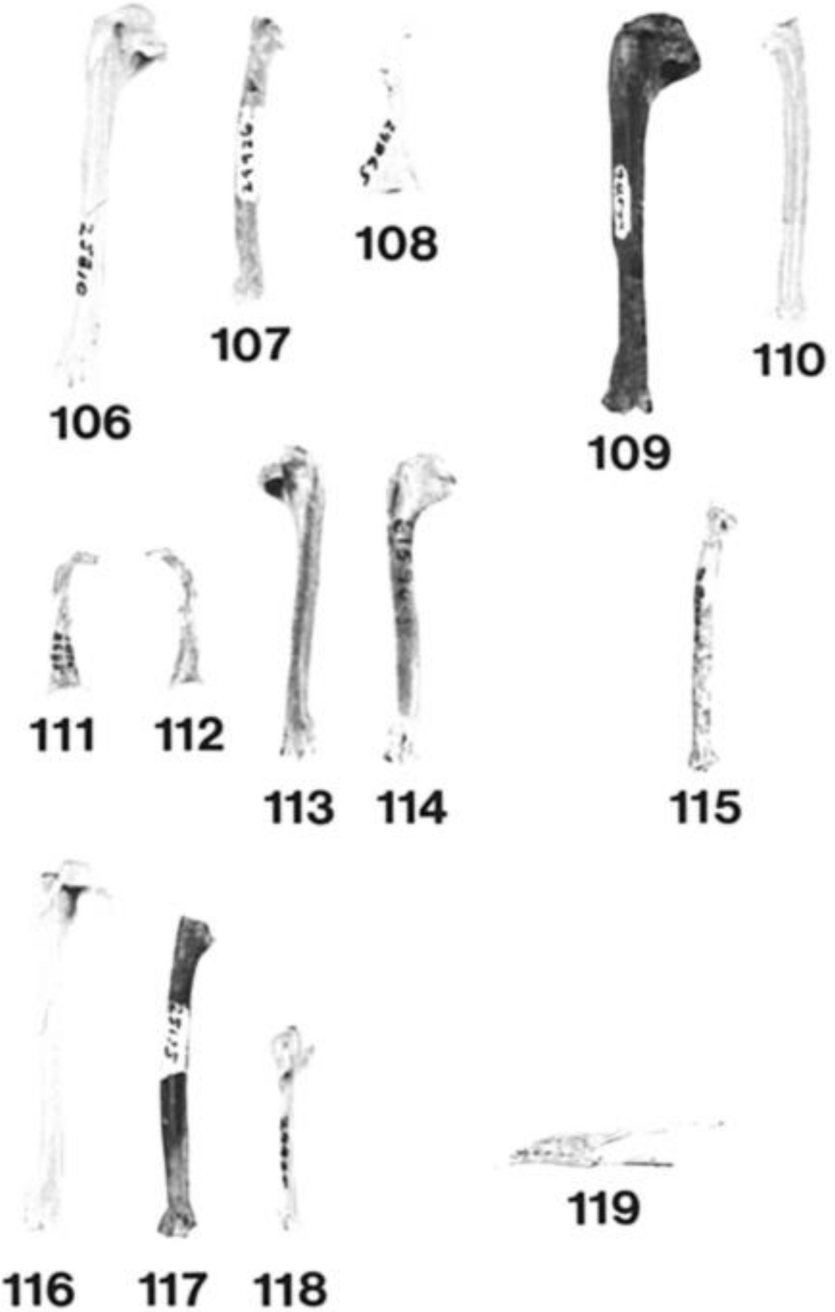
Holotype.—LACM 2119/1080, left humerus missing distal end.

Paratypes.—Humeri—Miller 2218/1075, distal end; LACM 2152/1080, distal end; Miller 2281/1080, ulna; LACM 2172/1071, articular end mandible; LACM 2166/1080, incomplete cranium.

Referred material.—Humeri—SDSNH 25810/3183-A, left; SDSNH 24930/3176, right proximal shaft fragment; SDSNH 22922/3031, right distal end; SDSNH 31358/3088-C, right proximal end; SDSNH 27227/3265, left proximal end; LACM 2830/1075, right distal end; ulnae—SDSNH 24926/3176, right; SDSNH 24931/3176, right proximal half; LACM 2573/1079; SDSNH 24865/3179, left coracoid; scapulae—SDSNH 25293/3006, right; SDSNH 24924/3176, left.

Description.—Proximal margin of humerus (SDSNH 25810) notched lateral to head above ligamental furrow with an obtuse angle. Anconal surface of head undercut for origin of the external triceps. Medial crest short palmad to internal tuberosity and distad crest does not extend to bicipital crest. Capital shaft ridge medial to pectoral attachment. Shaft laterally compressed and deltoid crest extends distad along external edge of shaft. At distal end, internal tricipital groove broader than external groove and medial tricipital crest extends proximad between the two grooves. External condyle extends distad diagonally to ectepicondyle forming a straight distal border which lacks a notch. Ectepicondyle extends slightly distad from this straight margin. Brachial depression proximal to anterior articular ligamental attachment and external condyle.

At proximal end of ulna (SDSNH 24926) on palmar surface, brachialis anticus



FIGS. 106–119. *Brachyramphus pliocenum*—106 humerus; 107 ulna; 108 coracoid. *B. dunkeli*—109 humerus; 110 ulna. *Synthliboramphus rineyi*—111, 112 coracoid; 113, 114 humerus. *Cerorhinca* sp.—115 ulna. *C. reai*—116 humerus; 117 ulna; 118 carpometacarpus; 119 premaxilla.

impression broad and proximal radial depression narrow. In profile palmar contour of internal cotyla has a long, distad sloping ridge from its rounded palmar tip to shaft. A gradual rise extends from distal trochlea to carpal tuberosity, which is truncated. Procoracoid of coracoid (SDSNH 24865) is a short, unfenestrated, inwardly curved bar. Furcular facet extends almost to coracohumeral articulation and is excavated below and short from head to top of the furcular facet. Brachial attachment at lower, lateral edge of furcular facet, and that facet does not extend outward beyond internal margin of long axis of shaft. Sternal facet greatly curved inward at internal end. The two referred scapulae (SDSNH 25293 and 24924) are essentially the same as in Recent species.

Comparisons.—See under *Brachyramphus dunkeli* n. sp.

Brachyramphus dunkeli n. sp.

Figs. 109, 110

Holotype.—SDSNH 24573/2971, left humerus, entepicondyle broken at tip.

Paratypes.—Humeri—LACM 2324/1095, right proximal end; LACM 6185/1075-B, distal end; SDSNH 24927/3176, left ulna; SDSNH 24583/2971, complete right radius.

Etymology.—This extinct murrelet is named for the collector, Scott Dunkel, who donated this and other fossil bird specimens to the San Diego Museum of Natural History.

Diagnosis.—Larger than the fossil species *Brachyramphus pliocenum* and all living species of *Brachyramphus.* Anconal surface of holotype with distinct ridge from the distal apex of head that extends to the internal tuberosity, which is absent in other species; internal margin of bicipital crest between ligamental furrow to attachment of M. dorsalis scapulae broader than in other species; lateral contour of pneumatic fossa stepped from attachment of M. dorsalis scapulae to the internal tuberosity, other species have contour arched to hooked internal tuberosity; bone of internal margin of pneumatic fossa thin and pneumatic fossa large and oblong, whereas bone of margin more robust in other species with a smaller more rounded fossa opening.

Ulna with impression of brachialis anticus narrow (broader in *B. pliocenum*); proximal radial depression broader than in *B. pliocenum*; profile of internal cotyla steep distad (*B. pliocenum* with gradual contour to shaft); carpal tuberosity raised higher than in *B. pliocenum* or living species.

Scapholunar facet of radius broad and internal trochlea narrow, whereas in *B. marmoratus* the trochlea is broader, more equally dividing distal end between the facet and trochlea.

Description.—The deltoid crest of holotype (SDSNH 24573, humerus) is placed distad along external edge of compressed shaft with distal end rotated externally. Viewed from the palmar aspect the proximal margin is round and uninterrupted. Internal margin of bicipital crest between ligamental furrow and scar of M. dorsalis scapulae broad. Internal margin from scar of M. dorsalis scapulae to internal tuberosity stepped. Anconally, the distal margin of the head overhangs the capital groove, which ends medially where a ridge from the distal apex of the head extends distad to the medial edge of the internal tuberosity. Pneumatic fossa has a large, oblong opening and the bone of the lateral margin is thin; medial crest of fossa

TABLE 28

MEASUREMENTS OF THE SKULLS OF *Mancalla emlongi* AND *Pinguinus impennis*

	Length	Frontals breadth
Mancalla emlongi		
SDSNH 25236	118.3	17.8
Pinguinus impennis[1]	150–165	43–50
N = 16	$\bar{X}$ = 156.6	$\bar{X}$ = 46.6

[1] From Lucas 1901.

does not meet the bicipital crest, but extends as far distad as the latter. Pectoral attachment broad and slightly overhangs secondary pneumatic fossa, which undercuts head. Distally, medial ridge of tricipital grooves straight and not indented. Internal tricipital groove broader than external groove. Entepicondyle broad across base in comparison to length.

The paratype, right ulna (SDSNH 24927), is complete with well defined features. Proximally, brachialis anticus impression is narrow, proximal radial depression is broad. Distal tip of internal cotyla pointed, with a steep slope from tip to shaft when viewed from internal side. Distally, carpal tuberosity rises abruptly from internal side diagonally across shaft, and is truncated.

Shaft of paratype, right radius (SDSNH 24583), compressed with internal edge on the anconal surface extending the length of the bone. Margin of humeral cotyla round and a well defined, distal, ulnar depression is round. The scapholunar facet broad distally and rounded with a narrow internal trochlea.

Comparisons.—*Brachyramphus dunkeli* is larger than *B. pliocenum* Howard (1949:192) or the two extant species *B. marmoratus* (Marbled Murrelet) and *B. brevirostris* (Kittlitz's Murrelet; see Tables 29, 30). Besides being larger, *B. dunkeli* is distinguishable from *B. pliocenum, B. marmoratus,* and *B. brevirostris* by having below the head of the humerus a distinct ridge that extends to the internal tuberosity. Proximal margin of humerus lower and more rounded in *B. dunkeli* than the higher more pointed head in other *Brachyramphus* species. Also, *B. dunkeli* has an uninterrupted proximal margin of the humerus, evidently the primitive condition in other alcids and the outgroups. The other species in *Brachyramphus* have the derived condition, a notched proximal margin lateral to the head above the ligamental furrow at the capital groove. These characters are best observed from the palmar side. *Brachyramphus dunkeli* and *B. marmoratus* have the most continuous distad extension of the deltoid crest on the external edge of the shaft, whereas in *B. pliocenum* and *B. brevirostris* the deltoid notch is more apparent.

On the internal contour of the humerus, the amount of bone between the lateral end of the ligamental furrow and the scar for the attachment of M. dorsalis scapulae is broader and the scar has a distad orientation in *B. dunkeli,* which seems to be the primitive condition among alcids and the outgroups. The other species of *Brachyramphus* have the derived condition, which is less bone with the scar facing more laterally. Also, the lateral margin of the pneumatic fossa between the scar for the attachment of M. dorsalis scapulae to the internal tuberosity is stepped (almost a right angle) on *B. dunkeli,* an autapomorphic condition. In the other species of *Brachyramphus* and the outgroups the plesiomorphic con-

TABLE 29

MEASUREMENTS OF HUMERI FOR SPECIES OF *Brachyramphus*

	B. pliocenum	*B. pliocenum*	*B. dunkeli*	
	SDSNH 25810	LACM 2830	SDSNH 24573	LACM 6185
Length	50.4	—	53.2	—
Proximal breadth	10.8	—	12.0	—
Mid-shaft	—	—	3.0 × 5.0	—
Distal breadth	5.4[1]	[2.6][2]	5.5	6.9
Height of ectepicondylar process	7.1	—	7.9	—
Internal depth	5.9	—	—	—
External depth	4.6	—	—	—
Shaft	2.6 × 4.2	2.5 × 3.7	—	—

[1] Not condyles only.
[2] Condyles.

dition is an arch with a distad hooked internal tuberosity. *Brachyramphus dunkeli* has the capital shaft ridge in line with the pectoral attachment, rather than more medial, and extending proximal beyond the distal end of the attachment as in *B. pliocenum.* A medial capital shaft ridge below the head is primitive in the outgroups.

Other autapomorphies for *B. dunkeli* are: a steep sloping profile of the internal cotyla distad to the shaft of the ulna, with the carpal tuberosity raised palmad, whereas the profile of the internal cotyla is more gradual, and the carpal tuberosity flatter in the other species. The radius is unknown for *B. pliocenum* but SDSNH 24583 is referred to *B. dunkeli* on greater length (greater also than in *B. marmoratus*). *Brachyramphus dunkeli* differs from *B. marmoratus* in its broad scapholunar facet and its narrow internal trochlea.

The coracoid SDSNH 24865 is referred to *Brachyramphus pliocenum* solely on size, being approximately the size of *B. marmoratus.* SDSNH 24865 shares the derived condition (with the other species of *Brachyramphus*), a procoracoid that has lost the primitive fenestrated condition characteristic of most alcids and the outgroups.

Discussion.—Howard (1949:192) assigned a distal end of a humerus (Miller no. 2218) as the cotype of *Brachyramphus pliocenum.* After comparing this humerus to the holotype, I think this specimen is better reassigned to *B. dunkeli* than to *B. pliocenum.*

TABLE 30

MEASUREMENTS OF ULNAE FOR SPECIES OF *Brachyramphus*

	B. pliocenum		*B. dunkeli*
	SDSNH 24926	SDSNH 24931	SDSNH 24927
Length	38.7	—	41.0
Proximal breadth	5.0	5.0	5.4
Proximal depth	5.8	—	6.0
Depth external condyle	5.0	—	5.3
Breadth distal end	3.0	—	3.2

Genus *Synthliboramphus* Brandt

Diagnosis.—Humerus with ectepicondyle elongated distoanconally and rounded; internal contour of coracoid an edge on the anterior side that extends toward the head end along the triosseal canal to the bicipital attachment.

Synthliboramphus rineyi n. sp.

Figs. 111–114

Holotype.—UCMP 61590/5566, right humerus.

Paratypes.—Humeri—SDSNH 23760/2971-A, right; SDSNH 25281/3006, left proximal end; SDSNH 21038/2993, right proximal end; LACM 6185/1075-B, proximal fragment; SDSNH 24995/3175, proximal half left ulna; coracoids—LACM 2665/1075, right; SDSNH 24939/3176, right; SDSNH 25282/3006, tarsometatarsus missing distal end.

Etymology.—Named for Brad O. Riney in recognition of his work on fossils from the San Diego Formation.

Diagnosis.—So far as presently known *Synthliboramphus rineyi* differs from other species in this genus only in smaller size.

Description.—Shaft of humerus (UCMP 61590) laterally compressed and deltoid crest continuous with compression of shaft. A proximoanconal excavation below head has its external border medial to external tuberosity and attachment of M. supracoracoideus; internal border extends laterally into the capital groove. Median crest of pneumatic fossa has a broad arched configuration and extends distad to bicipital crest on internal contour. Distally, ectepicondyle is distoanconally elongated and rounded, diagnostic for the genus. External tricipital groove broader than internal groove, and median ridge between grooves extended proximad with only slight indentation along its length. Entepicondyle relatively narrow. On palmar surface, external condyle elongated with a prominence at proximal end of condyle. Brachial impression extends distad between prominence of external condyle and attachment of anterior articular ligament, medially undercutting internal condyle, which is also elongated and laterally flattened.

Distance from head of coracoid (LACM 2665) to furcular facet short, and furcular facet extends internally to brachial attachment. Procoracoid short, broad, and fenestrated. Its internal contour is an edge that extends toward the head end along the triosseal canal to the bicipital attachment, diagnostic for the genus. Bicipital attachment and furcular facet shallowly excavated. Distally, sternal articulation curved and internal end curved inward approximately 45 degrees from width axis.

The extreme compression of the internal side of the shaft of the ulna (SDSNH 24995) results in an internal (medial) orientation of the brachial impression. Olecranon long, protrudes proximad beyond proximal cotylae. Palmar margin of external cotyla higher than the internal cotyla and lateral margin of internal cotyla indented.

The tarsometatarsus (SDSNH 25282) has three distinct grooves in an anterior row.

Comparisons.—A small murrelet has been reported from the late Miocene to early Pliocene (Hemphillian) Almejas Formation of Cedros Island, Baja California and was referred to *Endomychura* sp. by Howard (1971:10). Howard described this small alcid as "commensurate in size with the elements assigned to *c* [*erorhinca*]. *minor*" but insufficiently complete "to permit definite assignment." A proximal fragment of a humerus (LACM 26571) was described by Howard as less excavated below the head than in *Synthliboramphus craveri* (Craveri's Murrelet) or *S. hypoleucus* (Xantus' Murrelet). Howard used *Endomychura* for these species, now included in *Synthliboramphus* (A.O.U. 1983:244). *S. rineyi* is also less excavated below the head, as in LACM 26571; it is much smaller, however, than that unnamed species.

Synthliboramphus (including *Endomychura*) is distinguishable from other genera of alcids by having a distoanconally elongated ectepicondyle. *Synthliboramphus rineyi* also shows this derived condition but not as definitely as the Recent species. The primitive condition is a continuous, flat, distal margin at the external condyle and ectepicondyle as seen in *Brachyramphus, Uria, Cepphus,* and *Pinguinus.*

Synthliboramphus rineyi also differs from Recent species of *Synthliboramphus* in the curvature of the sternal articulation of the coracoid. Recent species have an approximately 90 degree curvature of the sternal articulation of the internal end in relationship to the lateral axis; *S. rineyi* is curved, only about 45 degrees. The primitive condition is a straight sternal articulation as in *Mancalla* and the outgroups. *Synthliboramphus rineyi* is derived compared to *Mancalla* but less than in Recent species of *Synthliboramphus.*

The referred ulna (SDSNH 24995) and tarsometatarsus (SDSNH 25282) are distinguishable from other Recent species in *Synthliboramphus* only by their small size.

Measurements.—Ulna, SDSNH 24995, proximal breadth—4.2, proximal depth—5.1; tarsometatarsus, SDSNH 25282, proximal breadth—4.3, shaft—1.4 × 1.6.

Genus *Ptychoramphus* Brandt

Ptychoramphus tenuis Miller and Bowman 1958

Holotype.—UCMP 45662/V5519, right tarsometatarsus.

Referred material.—SDSNH 24937/3176, left humerus missing proximal end; SDSNH 22884/2977, proximal end left carpometacarpus; SDNH 25276/3006, proximal end left scapula.

Description.—The holotype tarsometatarsus (UCMP 45662) was described by Miller and Bowman (1958:14).

A small humerus (SDSNH 24937) is missing the proximal end including the head and most of the deltoid and bicipital crests. Two medial intertricipital ridges are on the distal end.

A left carpometacarpus (SDSNH 22884) is missing the distal metacarpal symphysis and most of metacarpal III.

The proximal end of a small left scapula (SDSNH 25276) is gracile.

Comparisons.—The humerus, carpometacarpus, and scapula all agree with the characters of the holotype tarsometatarsus (UCMP 45662) by being shorter and more slender than corresopnding elements of *Ptychoramphus aleuticus* (Cassin's Auklet). Except for smaller size and more slender build, these referred elements differ little from those of living species. The humerus is different from that of *P.*

aleuticus by having the primitive condition, seen in the outgroup, of two medial intertricipital ridges; the derived condition is a single ridge, as in *P. aleuticus.*

Genus *Cerorhinca* Bonaparte

Diagnosis.—Humerus with extensive anconomedial excavation of the head, whereas other alcids except for *Fratercula* species have minimal excavation of the dorsal margin of the head.

Cerorhinca reai n. sp.

Figs. 116–119

Holotype.—SDSNH 25319/3176, left humerus.

Paratypes.—SDSNH 24572/2969, distal end right humerus; SDSNH 25175/2971-A, right ulna; SDSNH 24925/3176, left carpometacarpus; LACM 117775/4442, beak.

Etymology.—This species is named for Amadeo Rea, Curator of Birds and Mammals at the San Diego Natural History Museum, in recognition of his paleontological and archaeological studies of birds, and for introducing me to paleornithology.

Diagnosis.—Holotype humerus (25319) agrees with *Cerorhinca* by having medial ridge of pneumatic fossa extending distad to the bicipital crest, whereas *Fratercula* has a distinct separation; resembles species of *Fratercula* by having a depression beneath the internal tuberosity, except deeper in fossil and differs from *Cerorhinca monocerata,* which lacks a depression.

The ulna of the paratype (SDSNH 25175) agrees with the Fraterculini in having a shallow depth of the olecranon and a raised carpal tuberosity; other alcids have a deeper olecranon, and a flattened palmar surface of the carpal tuberosity.

The carpometacarpus of the paratype (SDSNH 24925) agrees with the Fraterculini by having a relatively long metacarpal I which is rounded proximally (lateral view) and raised higher than the pollical facet (other alcids have a long, flat or short and rounded metacarpal I); metacarpal II anconally flattened like *Fratercula,* differing from *Cerorhinca,* which has a more rounded metacarpal II; anconally, the internal carpal trochlea pointed in lateral view, in contrast to *Fratercula* and *Cerorhinca,* which have a more rounded trochlea.

Description.—The holotype is a humerus complete except for a few chips of bone missing from the shaft, the head proximal to the pectoral attachment, and a distal wedge from the bicipital crest. The shaft is laterally compressed and the distal end is rotated externally. The deltoid crest is distinct from a secondary crest which extends distad down the external side of shaft, and has no angular points on the crest. A deep anconomedial excavation undercutting the head is also the medial border for the capital groove and the pneumatic fossa, and laterally undercuts the medial margin of the pectoral attachment. The internal tuberosity has a deep depression below it and is separate from the pneumatic fossa. Distally, an indented medial ridge separates the internal and external tricipital grooves, the internal groove being broader. External condyle separated from lateral ridge of ectepicondylar process by a groove. Distal end of a humerus (SDSNH 24572) agrees with description of holotype except that it is from a larger bird.

The ulna of the paratype (SDSNH 25175) is complete except for an eroded internal cotyla, which might slightly reduce the proximal breadth measurement.

TABLE 31
MEASUREMENTS OF HUMERI FOR SPECIES OF *Cerorhinca*

	C. reai		*C. minor*[1]	*C. monocerata*	
	SDSNH 25319	SDSNH 24572	LACM 15408	SDSNH 39199	SDSNH 38459
Length	48.9	—	—	67.9	65.5
Proximal breadth	11.2	—	10.5	15.4	15.3
Mid-shaft dimensions	4.1 × 3.2	[4.5 × 2.9][2]	3.0 × 4.2	6.2 × 3.7	5.5 × 3.5
Distal breadth	—	6.3	—	7.1	7.0
Ectepicondyle process above distal end	—	7.1	—	8.0	7.9

[1] From Howard 1971.
[2] Shaft above ectepicondyle process.

Shaft laterally compressed and crowned palmad in lateral view. Olecranon truncated and does not extend proximad beyond proximal end of cotylae. Anterior articular ligamental scar relatively long, narrow, and connects proximally by a ridge to lateral margin of internal cotyla at base of cotyla. A groove is formed below this ridge and the olecranon. Distal margin of internal cotyla robust, with a deep radial depression proximally. Shaft tapers toward distal end where external condyle is rounded (lateral view), and internal condyle is approximately one-half depth of external condyle. Articulating blade of internal condyle extends below carpal tuberosity and condyle ends there without rounding back to shaft. At distal end carpal tuberosity is raised palmad above the shaft laterally, and a deep distal radial depression is seen distad to the tuberosity.

The paratype carpometacarpus (SDSNH 24925) is complete except for a missing metacarpal III. Metacarpal II is flattened on its anconal surface; it appears to twist externally from proximal to distal end and a deep tendinal groove is on its external side. Metacarpal I is longer than high proximally, and the proximal end slopes distad to the pollical facet. An intermetacarpal tuberosity is present at the proximal end of the intermetacarpal space. The external trochlea is narrow along its length, and the internal trochlea is anconally pointed. A broad, truncated pisiform process is seen near the mid-point of metacarpal I at the level of the palmar surface of metacarpal II.

A beak (LACM 117775) resembling that of *Cerorhinca monocerata* (Rhinoceros Auklet) is about three-quarters the length of the living species, as are other elements of *C. reai.*

Comparisons.—The genera *Cerorhinca* and *Fratercula* (including *Lunda*) comprise the tribe Fraterculini of the A.O.U. (1983:248) and contain all fossil and Recent species referable to it. As noted by Howard (1971:8), these genera "so closely resemble each other in skeletal characters that the term 'puffin' might properly be applied to all three."

The two fossil species in *Cerorhinca* are: *C. dubia* Miller 1925, from the late Miocene (Clarendonian) of Santa Barbara County, California; and *C. minor* Howard 1971, from the late Miocene-early Pliocene (Hemphillian) of Cedros Island, Baja California, Mexico. Another account of a Fraterculine refers to the late Miocene (Clarendonian) Orange County, California (Howard 1978:22).

Cerorhinca dubia is known only from associated leg elements, and is, therefore, not directly comparable with *C. reai. Cerorhinca reai* and *C. minor* are similar

TABLE 32

MEASUREMENTS OF ULNAE FOR SPECIES OF *Cerorhinca*

	Cerorhinca sp.	*C. reai*	*C. minor*		*C. monocerata*	
	SDSNH 23079	SDSNH 25175	LACM 15406	LACM 26572	SDSNH 38459	SDSNH 39199
Length	36.0	42.6	—	—	54.1	55.9
Proximal breadth	4.4	5.1	5.0	—	—	—
Mid-shaft measurements	2.2 × 8.2	2.5 × 3.8	2.3 × 3.3	2.8 × 3.8	—	—
Distal breadth (through condyles)	2.2	2.6	—	—	—	—
Proximal depth	5.1	5.7	5.5	—	—	—
Distal depth (through external trochlea)	4.2	4.9	—	5.4	—	—

in size (Tables 31–33), 25 to 30 percent smaller than the Recent species *C. monocerata* and *C. dubia* (*dubia* is approximately 2 percent smaller than *monocerata* (Miller 1925:115–116). *Cerorhinca reai* differs from *C. minor* (LACM 15420, holotype humerus) because the opening of the pneumatic fossa in *minor* is round instead of oblong. A depression below the internal tuberosity in *C. reai. C. minor,* and the Recent species of *Fratercula* is absent in *C. monocerata.* Finally, the olecranon in *minor* (LACM 15406, paratype ulna) protrudes proximad from the base of the cotylae, whereas in *reai* it is truncated and ends at the base of the cotylae.

The carpometacarpus of *Cerorhinca minor* is unknown.

Cerorhinca sp.
Fig. 115

Referred material.—SDSNH 23079/2971-A, a right ulna.

Description.—SDSNH 23079 is from a small individual with the olecranon protruding proximad.

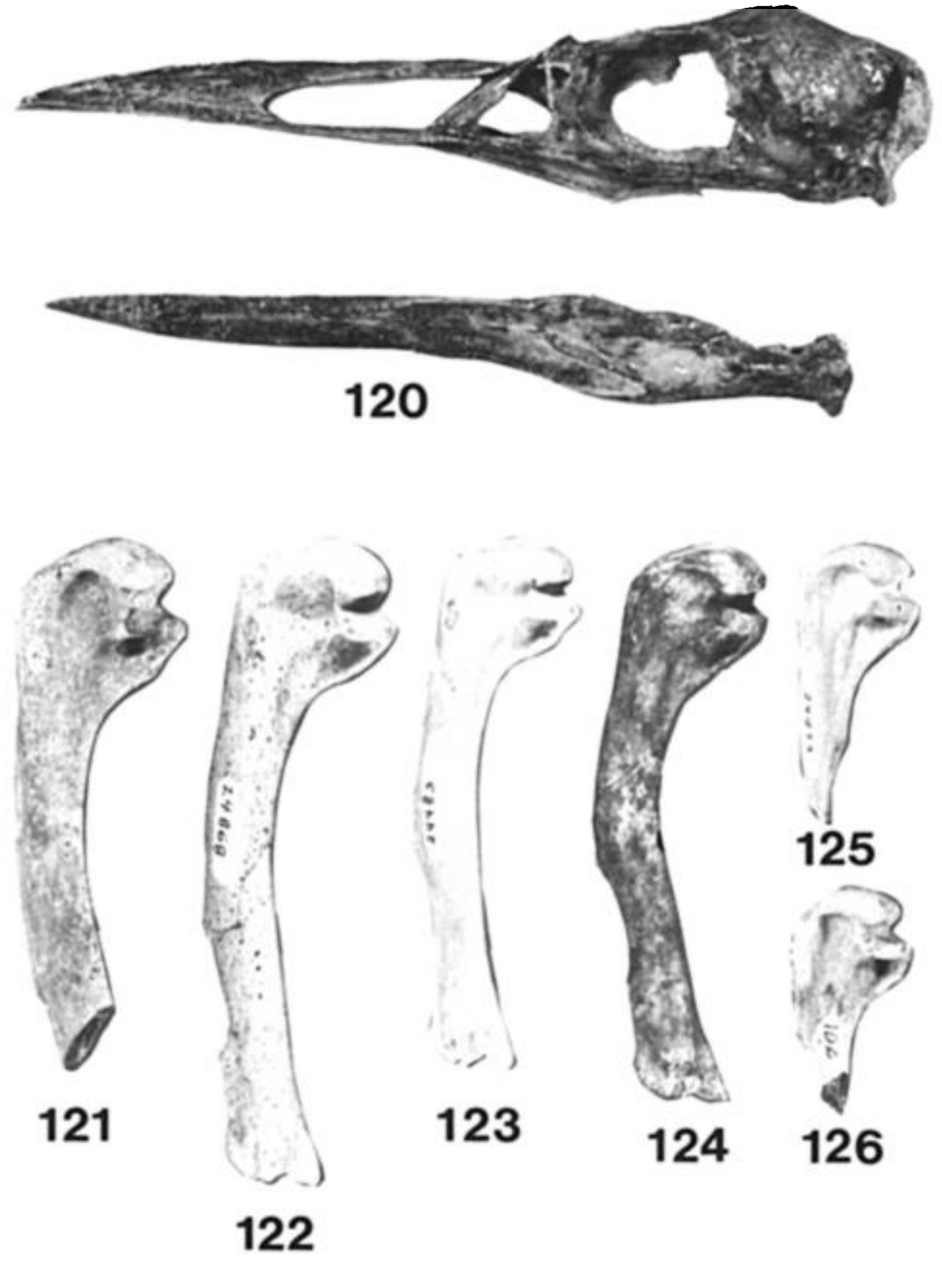
Comparisons.—SDSNH 23079 agrees with *C. minor* and *monocerata* by having the olecranon protruding proximad, whereas *C. reai* has a truncated olecranon ending in line with the proximal cotylae. It also differs from *C. reai* by being 15.5 percent shorter.

Measurements.—Length—36.0; proximal breadth—4.4; proximal depth—5.1; distal breadth—2.2; distal depth external side—4.2.

TABLE 33

MEASUREMENTS OF CARPOMETACARPI FOR SPECIES OF *Cerorhinca*

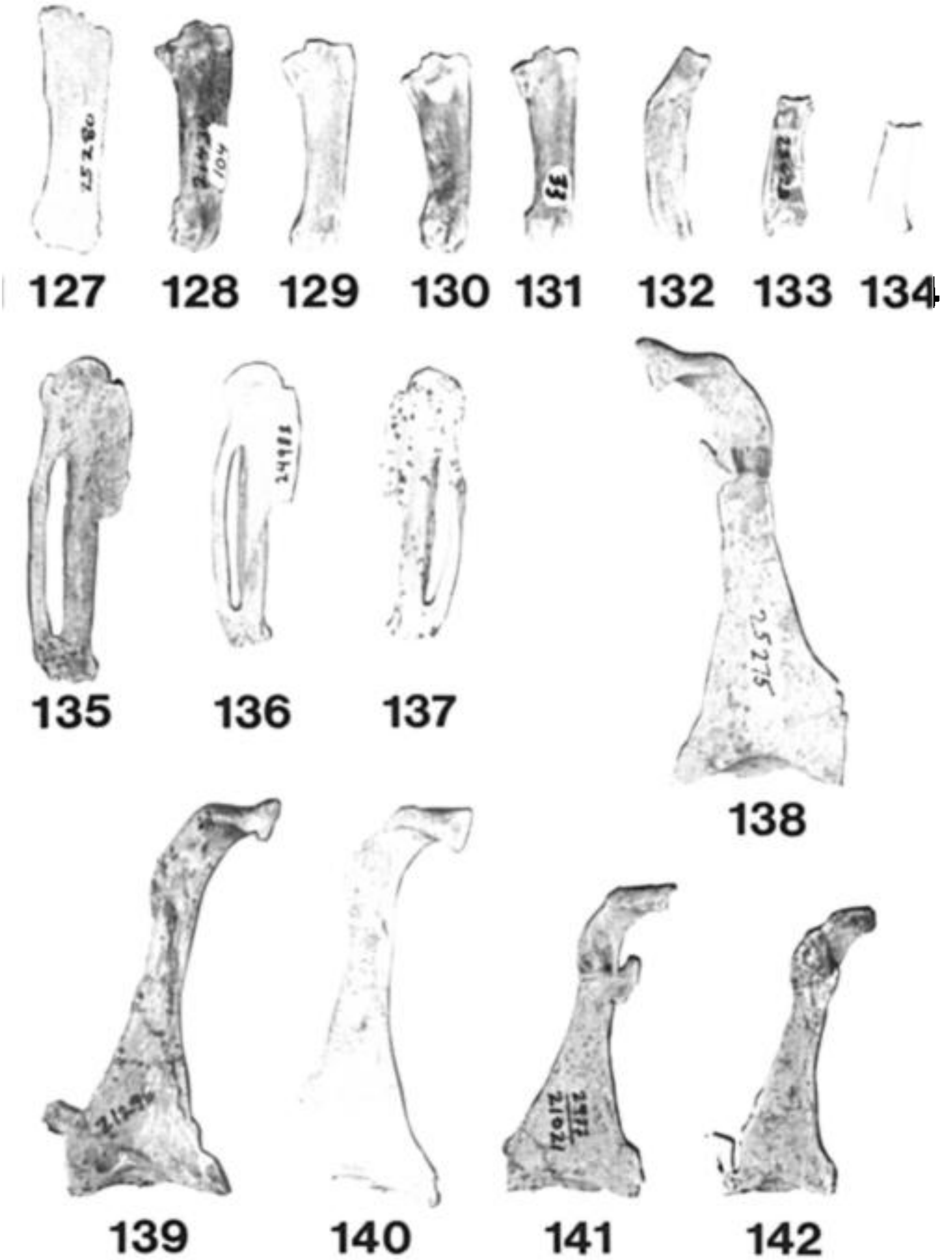
	C. reai SDSNH 24925	*C. moncerata* SDSNH 39199
Length	27.8	37.6
Length MC I	4.6	5.8
MC II dimensions	2.3 × 1.9	2.8 × 2.5
Proximal breadth	3.4	4.7



FIGS. 120–126. *Mancalla emlongi*—120 skull and mandible. *Mancalla* spp.—121–126 humeri.

Genus *Mancalla* Lucas 1901
Figs. 120–126, 128–134, 136, 137, 139–142, 144, 145

San Diego is the type locality for three species of the flightless auk genus *Mancalla*: *M. diegensis* (Miller 1937:376), *M. milleri* (Howard 1970:7), and *M. emlongi*



FIGS. 127–142. *Mancalla emlongi*—127 ulna; 135 carpometacarpus; 138 coracoid. Figs. 128–134, 136, 137, 139–142. *Mancalla* spp.—128–131 ulnae; 132 radius; 133, 134 phalanges 1 of digit II; 136, 137 carpometacarpi; 139–142 coracoids.

143

144

145

FIGS. 143–145. *Mancalla emlongi*—143 sternum. *Mancalla* sp.—144, 145 pelvic bones and synsacrum.

(Olson 1981:97). Howard (1970:4–5) separated a small species (*milleri*) from a larger one (*diegensis*) partly on the basis of quantitative characters (series of mixed elements exhibited bimodal curves and large coefficients of variation) and presented statistics that seemed to indicate no overlap in their size ranges. Olson (1981:98) based *emlongi* mainly on the very large size of its holotype's ulna.

Since Howard's study, a large increase in the number of specimens and consequent length of series has led to somewhat different interpretations, most importantly that *M. milleri* and *M. diegensis* might in fact overlap extensively in size with a much larger *emlongi* somewhat overlapping at least *diegensis* to some extent. Numerous problems await clarification by more extensive statistical analysis and (especially) the discovery of additional specimens for which two or more elements from the same individual are found in association.

At present, while much variation (often falling into two or more types) can be seen and tabulated for many elements, lack of associated elements prohibits specific identification of a large majority of specimens and elements.

The three species, and such material as could be referred to them in the face of the drawbacks just discussed, are listed, compared, and discussed beyond. Description of much more material, not presently assignable to species, would be premature here.

Mancalla diegensis (Miller 1937)
Figs. 146, 147, 151, 156, 157

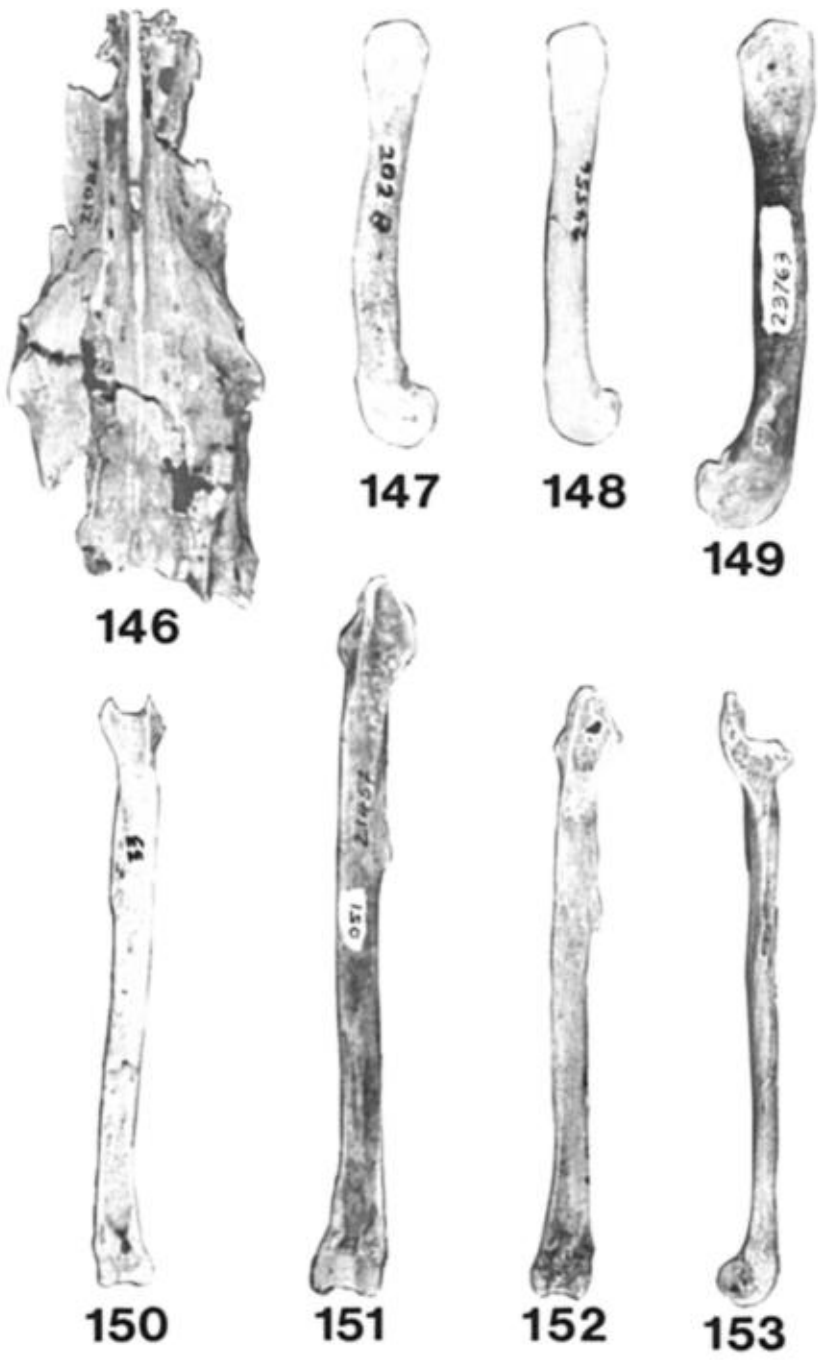
Holotype.—UCMP 33409/V3717, a right femur.

Referred material.—SDSNH 21086/3006, associated pelvic bones, synsacrum, and left femur; tibiotarsi—SDSNH 21457/2977, left; SDSNH 23064/2971-A, right; SDSNH 21401/2993, right proximal end; SDSNH 23764/2971-A, left; SDSNH 21458/2977, right missing cnemial crests; SDSNH 25328/2996, left missing distal end; SDSNH 23066/2971-A, left missing proximal end; SDSNH 25249/3179, right proximal end; UCMP 61589/V5566, left proximal end; tarsometatarsi—SDSNH 21428/2977, right; SDSNH 25811/3181-C, left; SDSNH 25172/2971, right; LACM 2178/1071, left; UCMP 109408/V6783, right; SDSNH 21040/2993, right missing distal end.

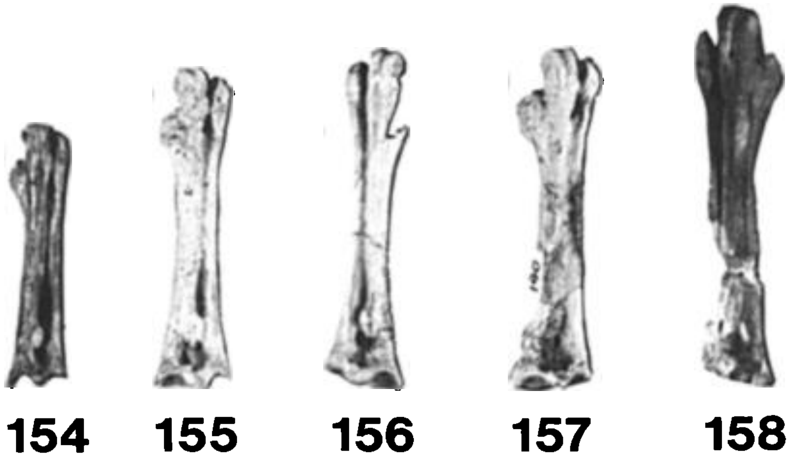
Mancalla milleri Howard 1970
Figs. 148, 150, 152–155

Holotype.—LACM 2185/1070, a left femur.

Referred material.—LACM 2681/1080, associated right femur, right tibiotarsus missing proximal end, and distal end left tibiotarsus; femora—UCMP 83303/V6783, right; UCMP 125646/V73113, right missing distal end; UCMP 125653/V73113, right; SDSNH 21289/2977, right; SDSNH 21287/2946, left; SDSNH 24556/2971, left; SDSNH 21290/2977, left; SDSNH 21288/2977, right; SDSNH 23774/2971-A, right; SDSNH 21459/2977, associated right tibiotarsus and fibula; tibiotarsi—SDSNH 25232/2971, left; LACM 2628/1080, left; SDSNH 24923/3176, right missing cnemial crests; SDSNH 21462/2977, proximal end right; SDSNH 23073/2971-A, left missing cnemial crests; SDSNH 25246/2907, left; SDSNH 24999/3175, right; 22993/3031, right missing distal end; SDSNH 21464/



Figs. 146–153. *Mancalla diegensis*—146, 147 associated pelvic bones, synsacrum, and femur; 151 tibiotarsus. *M. milleri*—148 femur; 150, 152, 153 tibiotarsi.



Figs. 154–158. *Mancalla milleri*—154, 155 tarsometatarsi. *M. diegensis*—156, 157 tarsometatarsi. *M. emlongi*—158 tarsometatarsus.

2977, right missing proximal end; SDSNH 24856/2971-B, left; LACM 2177/1071, associated right tibiotarsus and tarsometatarsus; tarsometatarsi—UCMP 110479/V6783, right; SDSNH 21176/3015, right; SDSNH 22380/3016, right missing trochlea IV; SDSNH 25262/3179, right; SDSNH 21429/2977, right; SDSNH 18576/2907, left; SDSNH 24553/2971, left; SDSNH 23803/2970-A, left missing proximal end; SDSNH 18578/2907, right missing proximal end; SDSNH 21431/2977, left missing proximal end; SDSNH 22914/2971-A, right missing proximal end; SDSNH 24554/2971, left missing trochleae III and IV; SDSNH 22673/2978, distal end left.

Mancalla emlongi Olson 1981
Figs. 120, 127, 135, 138, 143, 149, 158

Holotype.—USNM 243765, a right ulna.

Referred material.—SDSNH 25236/2971-A, associated skull, mandible, and ribs; SDSNH 22853/2977, left quadrate; humeri—LACM 2670/4226, right; SDSNH 25517/3206, left; SDSNH 23585/3153, left distal end; SDSNH 21253/3031, right distal end; SDSNH 24563/3186, left distal end; SDSNH 24567/3168, proximal shaft fragment; SDSNH 25280/3006, left ulna; carpometacarpi—SDSNH 21177/3015, left; SDSNH 21442/2977, right; SDSNH 23068/2971-A, left; SDSNH 21126/3006, left proximal end fragment; SDSNH 22843/3007, right proximal end; coracoids—SDSNH 25275/3006, right; SDSNH 55529/2906, left; SDSNH 22379/3016, right missing head end; SDSNH 26242/3088-C, sternum; SDSNH 24966/3175, proximal end right scapula; pelvic bones and synsacrum—SDSNH 25552/3206; SDSNH 25230/2971; femora—SDSNH 25538/3206, left; SDSNH 23763/2971-A, right; SDSNH 25814/3181-A, left proximal end; SDSNH 24592/3184, left distal end; LACM 2694/4227, left distal end; tibiotarsi—UCMP 61011/V5566, right missing proximal end; SDSNH 25287/3006, left proximal end; SDSNH 25812/3076, left tarsometatarsus.

Description.—Skull and mandible (SDSNH 25236) schizorhinal with narrow bill tapering from craniofacial hinge to bill tip. Supraorbital grooves present, supraorbital rims lacking. Temporal fossae deep and do not meet on the midline of the skull. Short zygomatic processes extend anteriorly. Occipital plate protrudes from back of skull over foramen magnum. Opisthotic processes broad and extend externally ventrad from skull. Large opening in interorbital septum. Lachrymal (or prefrontal) descends from craniofacial hinge and fused to ectethmoid plate, which has a large medial foramen. Maxillopalatines free of prepalatine bar and thick and cup-shaped. Vomer straight and blade-like ventrally with posterior half bifurcated. Lateral crests of palatines broadly rounded and end near palatine-pterygoid articulation. Pterygoid T-shaped in cross-section. Quadrate apneumatic with long orbital process. A tuberosity occurs lateral and ventral to optic process of pterygoid just below articulating surface. Basitemporal plate lacks processes for a secondary mandibular articulation. Processes for basipterygoid articulations also absent. Premaxillary symphysis short in relation to overall length of mandible. Flange of prearticular bone extends onto surangular bone but is neither fused to it nor reaches dorsal edge of mandible. A foramen occurs in external process of mandible anterior and lateral to articulating surface. Large retroarticular processes present.

A sternum (SDSNH 26242) has a single deep sternal notch on either side of the keel. Coracoidal sulci slightly curved ventrally and ventral manubrium does not separate sulci at midline. Ventral manubrium triangular in cross-section. Sternocoracoidal processes directed anteriorly. There are seven costal processes. Four rib fragments are associated with this sternum.

Proximal end of humerus (LACM 2670) with plain or slightly grooved anconal surface below head. Median crest of pneumatic fossa extends distad and shaft near pneumatic fossa robust with small openings. Shaft relatively straight and robust.

Ulna had been described by Olson (1981:98).

Furcular facet of coracoid (SDSNH 25275) pointed and overhangs triosseal canal. Furcular facet does not reach glenoid facet.

Comparisons.—Character polarities were set using charadriiform, gruiform, procellariiform, and gaviiform birds as outgroups.

Femora are the holotypes for *Mancalla diegensis* (UCMP 33409) and *M. milleri* (LACM 2185). An ulna is the holotype for *M. emlongi* (USNM 243765) and until this study was the only known skeletal element of that species.

The femur of *Mancalla diegensis* differs from those of *milleri* and *emlongi* (SDSNH 23763 and 25538) by having a shorter and more rounded contour of the trochanteric ridge; *milleri* and *emlongi* have longer trochanteric ridges with straight anterior contours. Among the outgroups, gruiform and charadriiform birds have a proximad raised trochanter and a short trochanteric ridge. Alcids generally have long straight trochanteric ridges. Thus, the derived condition of *M. milleri* and *M. emlongi* is symplesiomorphic for alcids and the rounded contour in *M. diegensis* is an autapomorphy.

Mancalla emlongi differs from *diegensis* and *milleri* by having the autapomorphic condition of a short fibular condyle and having a notched external contour of the distal end; *diegensis* and *milleri* share the symplesiomorphic condition (with alcids) of a more evenly rounded external contour of the distal end, and the fibular condyle equal to the external condyle in height. The outgroup has a much deeper external condyle than the fibular condyle. *Mancalla emlongi* also has a more distally pointed internal condyle in lateral contour, whereas *M. diegensis* and *M. milleri* have a rounded internal condyle, the primitive condition in the outgroups.

A partial associated skeleton of *Mancalla diegensis* (SDSNH 21086) includes left femur, pelvic bones, and synsacrum. The synsacrum has five transverse processes which fuse to the preacetabular ilium, which I think is primitive. Referred synsacra for *emlongi* (SDSNH 15552 and 25230) are longer and have the derived condition of six fused transverse processes, with seven sacral vertebrae in the synsacrum. A more rigid back is an adaptive specialization of the vertebral column in wing-propelled swimmers such as *Mancalla,* a convergence with penguins. Small synsacra (SDSNH 23077, 33804, 23757) with doubled transverse processes at their mid-length resembling *emlongi,* might belong to *milleri* rather than *diegensis.*

Two specimens with associated leg elements allow a composite leg of *Mancalla milleri* to be assembled. LACM 2681, associated right femur, right tibiotarsus, and distal end of a left tibiotarsus, and LACM 2177, associated right tibiotarsus and tarsometatarsus, show that the femur of *milleri* goes with a tibiotarsus that is anteroproximally flattened, the cnemial crests are on the lateral edges of the shaft, and there is a slight notch between the proximal articulating surfaces (Howard 1970:9). The flattened tibiotarsus in turn goes with a tarsometatarsus that has distinct internal and external anterior edges, and the anterior surface is deeply grooved (Howard 1970:9). Additionally, the external edge of the tarsometatarsus in *M. milleri* is distinct and continuous with the distal foramen. The distal foramen is more slit-like than round. *Mancalla diegensis* differs from *M. milleri* by having a more rounded proximal tibiotarsus shaft and the converging cnemial crests, which I consider plesiomorphic. The tarsometatarsus of *M. diegensis* I consider primitive in its shallow anterior surface with lateral edges poorly defined. Also, the external edge is not merged in the lateral border of the distal foramen, and the foramen is round and open. *Mancalla emlongi* has larger leg bones than *M. diegensis* and *M. milleri*; the tibiotarsus, however (SDSNH 25287), resembles *M. milleri,* with a small notch (plesiomorphic condition) between proximal articulating surfaces, and has a primitive rounded shaft (UCMP 61011) as in *M. diegensis.*

A specimen (SDSNH 25236) with associated skull, mandible, and ribs is tentatively referred to *Mancalla emlongi,* based strictly on size. The skull is smaller than that of the Great Auk, *Pinguinus impennis* (Table 28). In general, the skull is very primitive: cup-shaped maxillopalatines, straight and blade-like vomers, and vomer bifurcated for half of its length, are primitive characteristics for alcids. An autapomorphy of the quadrate is a lateral tuberosity below the articulating surface on the opisthotic process.

Discussion.—The family Mancallidae (Miller 1946:34) was reduced to subfamily status Mancallinae by Brodkorb (1967:217). The separation of *Mancalla* from the other genera in Alcidae is its adaptation for flightlessness.

Alcidae gen. et sp. indet.

Material.—SDSNH 24938/3176, right coracoid missing the furcular facet.

Description.—Procoracoid level within internal contour of shaft and not fenestrated near shaft. Neck narrow and shaft narrow along internal contour below furcular facet. Bone sloped toward the internal side and sternal facet thin and curved.

Comparisons.—I consider the narrow back and shaft along the internal contour derived in SDSNH 24938 (*Brachyramphus*) and *Mancalla* with the accompanying elongation of the head to the furcular facet; a broad area below the head and the furcular facet with a short length between them I consider primitive in other alcids and the outgroups. The glenoid facet is long and narrow as in *Brachyramphus*. The procoracoid is not fenestrated, which is derived, and most like *Brachyramphus, Mancalla, Aethia, Ptychoramphus,* and *Cyclorrhynchus*. A straight sternal facet, the primitive condition in alcids and the outgroups, is best shown by *Mancalla*. SDSNH 24938 has a curved sternal facet like *Ptychoramphus* and not as curved as in *Brachyramphus*. The procoracoid is even with the internal contour of the shaft. This condition I consider derived; it is seen in *Ptychoramphus* and *Cyclorrhynchus* but not in *Brachyramphus pliocenum* or the other alcids, which have the procoracoid more medial on the inside of the shaft.

Discussion.—Although I am not referring SDSNH 24938 to any specific alcid genus, the derived condition of the neck and internal contour in combination with an unfenestrated procoracoid suggests that this bone is from an individual with some affinities to *Brachyramphus*.

Order PASSERIFORMES
Family MUSCICAPIDAE
Subfamily TURDINAE
Genus *Turdus* Linnaeus
Turdus sp.

Referred material.—SDSNH 31357/3088-C, a left tarsometatarsus.

Discussion.—This is the earliest fossil record for this subfamily (Brodkorb 1978: 179). The fossil tarsometatarsus is longer but more slender than that of the American Robin, *Turdus migratorius*.

I am currently studying this specimen and expect to describe it later.

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SUMMARY

This study brings the recorded avifauna of the San Diego Formation to more than 24 species level taxa, 14 previously described, 10 new ones, and a small number—no more than 15—certainly or probably additional but referable at present only to genus. These species represent a marine assemblage of 13 families, plus 1 terrestrial family. Compared with the living fauna off the coast of southern California, the San Diego Formation fauna is richer in marine species of groups such as sulids and alcids.

Podiceps discors and *Aechmophorus elasson,* two of the grebes identified in the San Diego fauna, have been identified from other contemporary Pliocene localities, *P. discors* from the Rexroad local fauna of Kansas and the Hagerman local fauna of Idaho, *A. elasson* from the Hagerman local fauna.

Diomedea howardae n. sp. is the first fossil albatross known from the late Pliocene of North America. *Puffinus gilmorei* n. sp. represents the first Pliocene record of the shearwater subgenus *Thyellodroma.* All other fossil shearwaters from the west coast of North America are in the subgenus *Puffinus* except *P. inceptor* Wetmore, which probably should be placed in its own subgenus.

The reevaluation of sulid *Miosula recentior* and *Sula humeralis* has led to their inclusion in *Morus,* which extends the fossil record of this genus by showing that some species occurred in the North Pacific from the middle Miocene to the late Pleistocene. Gannets (*Morus*) are now absent from this area. Based on the fossil record and the biogeography of the family, the sulids most likely had a Pacific origin. Gannets perhaps emigrated to the North Atlantic at the same time, early Miocene, as did other seabird groups, e.g., the alcids.

Melanitta ceruttii n. sp. (Anseriformes, Mergini) provides the oldest record of this genus and is its first extinct species.

A plover the size of the Recent Killdeer is identified and assigned to the genus *Charadrius,* the second shorebird species to be identified. This is the second late Tertiary record attributed to the genus, the other being from the middle Oligocene of Colorado.

Rissa estesi n. sp. (Charadriiformes, Laridae) is the first fossil species and the oldest record of *Rissa* for North America. Also, the identification of a tern as *Sterna* sp. provides the oldest North American record for this genus.

The three species of flightless auks recorded in the San Diego Formation have been redefined on the basis of synapomorphies to show that the two species *Mancalla diegensis* and *M. milleri* show extensive overlap in size. *Mancalla emlongi* is the largest species found in the deposit. Associated leg bones of the two overlapping species have been identified, and large size and autapomorphic char-

acters allow *M. emlongi* to be separated from the other two species. Remaining specimens of other body parts of the two overlapping species are unidentifiable to species because there are no known associations (e.g., between leg and wing bones or even among different wing bones).

The importance of associated fossil skeletal parts is crucial to completing the descriptive analysis of various species found in the San Diego Formation, as it is elsewhere. Because most of the material found in this formation is unassociated, bones not found in association of congeneric species of similar size are impossible to assign to a species (e.g., *Mancalla diegensis* and *M. milleri*).

Two new species of murrelets are described for the San Diego Formation; *Synthliboramphus rineyi* n. sp. is the first fossil species in this genus. Rea's puffin, *Cerorhinca reai* n. sp., is the third fossil species in this genus, and like *C. minor* from the late Miocene-early Pliocene, Cedros Island, Baja California, it is approximately three-quarters the size of the Recent species *C. monocerata,* the Rhinoceros Auklet or, better, Puffin.

The first record of a passerine bird is also the first record of the subfamily Turdinae and the genus *Turdus* in the paleontological record earlier than the late Pleistocene.

FOSSIL BIRDS OF THE SAN DIEGO FORMATION

- Order Gaviiformes
  - Family Gaviidae
    - *Gavia howardae* Brodkorb 1953
    - *Gavia* sp.
- Order Podicipediformes
  - Family Podicipedidae
    - *Podiceps subparvus* Miller and Bowman 1958
    - *Podiceps arndti* n. sp.
    - *Podiceps* cf. *P. discors* Murray 1964
    - *Podiceps* sp. Miller and Bowman 1958
    - *Aechmophorus elasson* Murray 1967
- Order Procellariiformes
  - Family Diomedeidae
    - *Diomedea howardae* n. sp.
    - *Diomedea* sp. A
    - *Diomedea* sp. B
  - Family Procellariidae
    - *Puffinus gilmorei* n. sp.
    - *Puffinus kanakoffi* Howard 1949
    - *Puffinus* sp.
    - Procellariidae gen. et sp. indet.
  - Family Hydrobatidae
    - *Oceanodroma* sp.
- Order Pelecaniformes
  - Family Sulidae
    - *Morus recentior* (Howard 1949)
    - *Morus humeralis* (Miller and Bowman 1958)
    - *Sula clarki* n. sp.
    - *Sula* sp.
  - Family Phalacrocoracidae
    - *Phalacrocorax kennelli* Howard 1949
    - *Phalacrocorax* sp.
    - *Stictocarbo kumeyaay* n. sp.
    - Phalacrocoracidae gen. et sp. indet.
- Order Anseriformes
  - Family Anatidae
    - *Melanitta ceruttii* n. sp.
    - Tribe Mergini gen. et sp. indet.
- Order Charadriiformes
  - Family Charadriidae
    - *Charadrius* sp.
  - Family Scolopacidae
    - Shorebird? Howard 1949
  - Family Laridae
    - *Rissa estesi* n. sp.
    - *Larus* sp.
    - *Sterna* sp.
  - Family Alcidae
    - *Brachyramphus pliocenum* Howard 1949
    - *Brachyramphus dunkeli* n. sp.
    - *Synthliboramphus rineyi* n. sp.
    - *Ptychoramphus tenuis* Miller and Bowman 1958
    - *Cerorhinca reai* n. sp.
    - *Cerorhinca* sp.
    - *Mancalla diegensis* (Miller 1937)
    - *Mancalla milleri* Howard 1970
    - *Mancalla emlongi* Olson 1981
- Order Passeriformes
  - Family Muscicapidae
    - *Turdus* sp.

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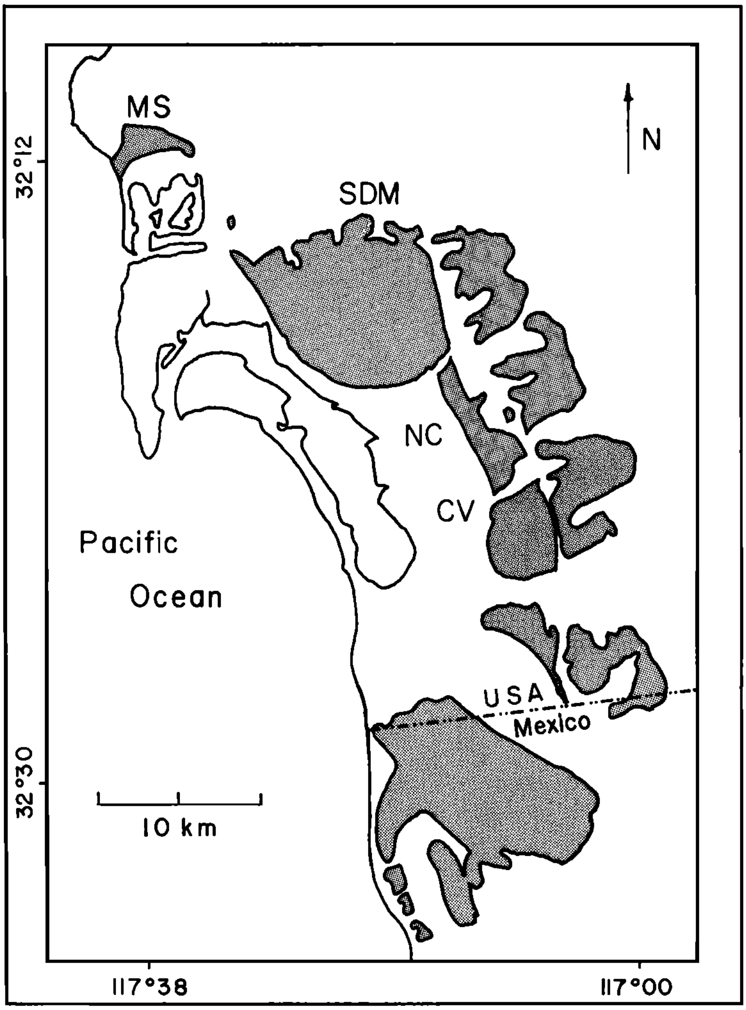

MAP 1. Index map of the San Diego Formation Outcrop distribution (stippled) in San Diego County, California. Abbreviations: CV = Chula Vista; MS = Mount Soledad; NC = National City; SDM = San Diego Mesa.

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