A Catastrophic Death Assemblage and Paleoclimatic Implications of Pliocene Seabirds of Florida

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A deposit of fossil seabirds from the late Pliocene of Florida includes more than 130 skeletons of an extinct cormorant that is related phylogenetically to Recent species currently restricted to the eastern north Pacific. Evidence suggests the birds died in a single catastrophic event, perhaps a red tide. The fossil cormorant, along with other extinct seabirds and marine mammals, supports molluscan evidence for cold-water upwelling along the Florida Gulf Coast during the Pliocene. A decline in species richness of marine vertebrates throughout the Pliocene of Florida coincides with cessation of upwelling after emergences of the Panamanian Land Bridge.

Large concentrations of vertebrate fossils that include complete and partial articulated skeletons of birds are rare. Examples include the extensive material of *Presbyornis* (Presbyornithidae) from the early Eocene Green River Shale, Wyoming, and the hundreds of complete skeletons of moas (Dinornithidae) from the late Pleistocene of New Zealand (*1*). In 1989 a deposit of fossil seabirds was discovered in Sarasota County, Florida (Fig. 1), that has produced thousands of bones and 137 skeletons of a single species of cormorant (*Phalacrocorax* sp.) that phylogenetically is related to species currently restricted to the eastern Pacific (*2*). The material is well preserved and includes complete crania, premaxillae, and other delicate bones of the skeleton. The site, located within the marine Pinecrest Beds in the upper Tamiami Formation (*3*), is of late Pliocene age [late Blancan, 2.5 to 2.0 million years ago (Ma)] on the basis of invertebrate paleontology and stratigraphic association with similar deposits of known age (*4*). The vertebrate fauna from this site supports invertebrate evidence for cold-water upwelling in the Gulf of Mexico during the Pliocene.

Besides the cormorant, the fossil site has produced 48 bones collectively of two species of grebe (Podicipedidae), egret (*Egretta* sp.), extinct pygmy goose (*Anabernicula* sp.), avocet (*Recurvirostra* sp.), sanderling (*Calidris* cf. *C. alba*), red knot (*Calidris* cf. *C. canutus*), jaeger (*Stercorarius* sp.), and two gulls (*Larus* spp.) (*2*). The fauna also includes thousands of bones, scales and otoliths of fish, and bones from an adult and juvenile seal (*Callophoca obscura*). The fish are dominated by bottom-dwelling marine species including searobin (*Prionotus* sp.), mullet (*Mugil* sp.), lizardfish (*Synodus* sp.), and eagle rays (*Myliobatis* sp.). These fish currently occur in waters offshore of Sarasota (*5*), and the entire vertebrate fauna is indicative of a shallow marine and coastal environment (*6, 7*).

Systematic analysis of the fossil cormorant indicates it is an undescribed species closely related to the living Brandt's Cormorant (*Phalacrocorax penicillatus*) and the recently extinct Pallas' Cormorant (*P. perspicillatus*) (*2*). This evidence includes similarity in the morphology of the nasal gland depression and other cranial features in the fossil and Recent species (*8*). Currently *P. penicillatus* is restricted to a cold-water upwelling system in the eastern Pacific (*9*); *P. perspicillatus* was known only from the Bering Sea and Commander Islands but became extinct in the mid-1800s (*10*).

Numerous species of seabirds and marine mammals with modern counterparts

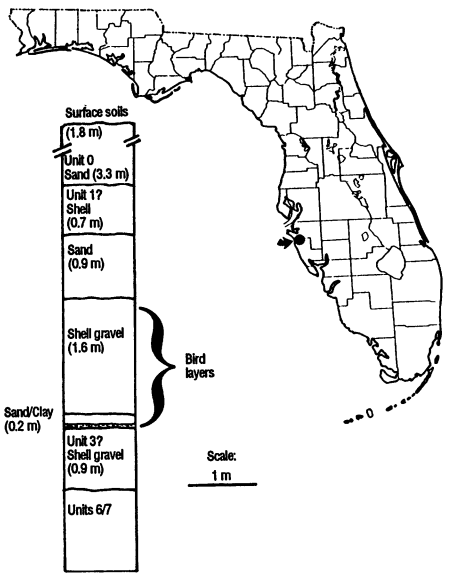

Fig. 1. Location and stratigraphic section of the upper Pinecrest Beds, Tamiami Formation, Richardson Road Shell Mine, Quality Aggregates, Incorporated, Sarasota County, Florida. Unit designations for the Pinecrest Beds (*3*) are provided in the sections where known. The shell gravel, sand, and clay are localized within the Pinecrest Beds, have no unit designation, and constitute the extent of the bird layers throughout which the cormorant skeletons were deposited.

Table 1. Stratigraphic distribution of extinct seabirds (*2, 11*) and marine mammals (*7*) in the Pliocene of Florida. The taxa listed occur in two formations of Pliocene age: Bone Valley (BV) Formation (early Pliocene, 5.2 to 4.5 Ma) and Tamiami (T) Formation (late Pliocene, 3.4 to 2.0 Ma). The seabirds and marine mammals from the Tamiami Formation occur in two stratigraphic units that differ in age. The marine mammals are derived from a lower unit of early late Pliocene age (3.4 to 3.0 Ma), whereas the seabirds occur in the Pinecrest Beds in an upper unit of late Pliocene age (2.5 to 2.0 Ma).

Taxon	Formation	
	BV	T
Seabirds		
Albatross (*Diomedea* cf. *D. anglica*)	X	
Shearwater (*Puffinus* sp.)	X	
Pelican (*Pelecanus* sp.)	X	
Gannet (*Morus peninsularis*)	X	
Booby (*Sula guano*)	X	
Booby (*Sula phosphata*)	X	
Booby (Sulidae, sp. 1)	X	
Cormorant (*Phalacrocorax wetmorei*)	X	
Cormorant (*Phalacrocorax idahensis*)	X	
Cormorant (*Phalacrocorax* sp. 1)		X
Jaeger (*Stercorarius* sp.)		X
Gull (*Larus elmorei*)	X	
Gull (*Larus* sp. 1)		X
Gull (*Larus* sp. 2)		X
Auk (*Pinguinus* sp.)	X	
Auk (*Australca grandis*)	X	
Auk (Alcidae, sp. 1)	X	
Auk (Alcidae, sp. 2)	X	
Auk (Alcidae, sp. 3)	X	
Marine Mammals		
"River" dolphin (Pontoporiidae, sp. 1)	X	
"River" dolphin (*Goniodelphis hudsoni*)	X	
Dolphin (Delphinidae, sp. 1)	X	
Dolphin (Delphinidae, sp. 2)		X
Dolphin (Delphinidae, sp. 3)		X
Beaked whale (*Mesoplodon* sp.)	X	
Beaked whale (*Ninoziphius platyrostris*)	X	
Sperm whale (*Kogiopsis floridanus*)	X	
Sperm whale (*Physeterula* sp.)	X	X
Right whale (Balaenidae, sp. 1)		X
Rorqual (*Balaenoptera floridana*)	X	X
Rorqual (*Balaenoptera* sp.)		X
Humpback whale (*Megaptera* sp.)		X
Rorqual (Balaenopteridae, sp. 1)	X	
Walrus (*Trichechodon huxleyi*)	X	X
Seal (*Callophoca obscura*)*	X	X
Seal (*Phocanella pumila*)	X	
Seal (Phocidae, sp. 1)	X	
Dugong (*Corystosiren varguezi*)	X	
Dugong (Dugongidae, sp. 1)*		X

*Denotes taxa that occur in both upper and lower units of the Tamiami Formation.

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associated with cool ocean temperatures or upwelling systems were present in the early to late Pliocene (Bone Valley Formation and Tamiami Formation, 5.2 to 2.0 Ma) of Florida (Table 1) but are absent from latest Pliocene (Caloosahatchee Formation, 2.0 to 1.6 Ma) and late Miocene marine deposits (*6, 7, 11*). The late Pliocene of Florida is also characterized by rich deposits of marine invertebrates (*12*). The new vertebrate faunas add to a growing body of paleoceanographic, invertebrate paleontologic, isotopic, and geochemical evidence indicating that Florida's Gulf Coast was once characterized by cold-water upwelling. Evidence for this upwelling is correlated with periods of high sea level and submergence of the Panamanian isthmus (*4, 12, 13*).

Taphonomic study of the fossil cormorants and the stratigraphy suggest long-term deposition for much of the material, but that a single catastrophic event added a large number of skeletons to the deposits at one time. Evidence for long-term deposition includes hundreds of isolated cormorant bones that are abraded and worn or that have fossil invertebrates (barnacles and oysters) attached to their surface that indicate that they were resting in shallow water for a long period before burial in the sediments. The stratigraphy of the deposit includes more than 1 m of high-angled and cross-bedded sediments with a distinct basal layer of greenish clay (Fig. 1). This clay suggests the presence of a lagoon in association with the fossil accumulation.

The whole and partial skeletons of cormorants show similar preservation and patterns of articulation (Fig. 2). Bird carcasses tend to separate from decay in a specific sequence, with the hindlimbs becoming disarticulated before the wings (*14*). Further decay results in disarticulation of all bones in the skeleton. The pattern of skeletal articulation in the fossil sample is biased toward wing elements. Most carcasses (70.8%) consist of pectoral or major wing bones and indicate that a large number of carcasses were in a similar state of decay before they were rapidly buried. The precise articulation of most wing and leg elements further indicates that soft tissue was present on the bone when buried (Fig. 2).

The cause of death of these birds is unknown, although mass mortality in cormorants often occurs from toxic poisoning in red tides (*15*), disease, and loss of food resources. Another possible explanation is that the cormorant skeletons accumulated at a rookery; however, adults rarely die in rookeries. Nearly all of the bones from the fossil site are completely ossified and represent adult individuals, and thus it is unlikely that the deposit is a fossil rookery. The abundance of bottom-dwelling fish in the same deposits suggests that red tide may have been responsible for the death of the birds. These fish also are highly susceptible to mass mortality from red tides (*16*), though intense blooms may kill all fish in a region.

The high-angled layers in the sediments are composed primarily of broken shells and shell gravel that indicate high-energy deposition (*4*). Few whole or articulated shells are present in these layers. The Florida Gulf Coast currently experiences seasonal landfall of hurricanes which, in unusually strong events, are associated with storm surges that produce characteristic sedimentary facies (*17*). The densely packed bioclastic features of the fossil deposits suggest that a strong storm or storm surge caused their formation (*4, 18, 19*). Intense hurricanes and storm surges are rare on the west coast of Florida (*17*) but are associated with unusual rainfall patterns in Africa (*20*) and perhaps with the El Niño Southern Oscillation (ENSO) (*21*). The fossil deposit may have resulted from such an event.

The decline in species richness of seabirds and marine mammals in the Pliocene of Florida (Table 1) coincides with an end to upwelling and an increase in ocean temperatures after separate emergences of the Panamanian Land Bridge at approximately 3.5 to 3.0 and 2.4 to 2.0 Ma (*13, 22*). Before the time of these closures, populations of the fossil cormorant or a closely related species may have extended into the Gulf of Mexico from the eastern Pacific. Emergence of the isthmus was followed by an increase in seabird diversity in the eastern Pacific, particularly in the number of cormorants (*23*), while species richness continued to decline in the Gulf of Mexico.

Fig. 2. One of over 130 skeletons of an undescribed species of cormorant (*Phalacrocorax* sp.) recovered from the bird layers. The feet of the bird are to the right and have digits in articulation indicating rapid burial of the carcass before complete decay and loss of soft tissues.

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