L'EVOLUTION DES OISEAUX D'APRES LE TEMOIGNAGE DES FOSSILES

Table Ronde internationale du CNRS
Lyon-Villeurbanne, 18-21 Septembre 1985

C. Mourer-Chauviré (Coordonnateur)

A LATE PLEISTOCENE AVIFAUNA FROM THE ISLAND OF OAHU, HAWAIIAN ISLANDS

Helen F. JAMES

Docum. Lab. Géol. Lyon, nº 99, 1987, p. 221-230, 1 fig., 1 tabl.

A LATE PLEISTOCENE AVIFAUNA FROM THE ISLAND OF OAHU, HAWAIIAN ISLANDS

UNE AVIFAUNE DU PLEISTOCENE SUPERIEUR DE L'ILE D'OAHU (HAWAII)

Helen F. JAMES *

Abstract

Fossils from an eroding sea cliff on the Mokapu Peninsula of the island of Oahu constitute the oldest vertebrate fauna known from the Hawaiian Islands. These bones apparently accumulated in a lake that once occupied the crater of the Ulupau Head tuff cone, probably during the Illinoian Glacial. The fossil avifauna from this locality comprises an ecologically diverse assortment of birds, including seabirds, shorebirds, waterfowl, and large and small land birds. At least two species of seabirds from Ulupau Head are not known historically or in Holocene fossil deposits from the Hawaiian Archipelago. The presence of migratory shorebirds and waterbirds is evidence that migratory routes of these species over the Pacific Ocean have endured for more than 120,000 years. Preliminary morphological comparisons of the land and fresh water birds from Ulupau Head with a Holocene fossil avifauna from Barber's Point, Oahu, suggest that many, if not all, of the major adaptations found in the endemic Hawaiian species had already evolved at the time the Ulupau Head fossils were deposited.

KEY-WORDS : Fossil birds, Hawaiian Islands, Late Pleistocene, migration, evolution.

Résumé

Les fossiles provenant d'une falaise érodée par la mer de la presqu'île de Mokapu, dans l'île d'Oahu, représentent la plus ancienne faune de Vertébrés connue dans l'archipel des Hawaii. Ces ossements se sont apparemment déposés dans un lac qui occupait le cratère du volcan Ulupau Head, probablement au cours de la glaciation d'Illinois. L'avifaune fossile de ce gisement comprend des formes appartenant à des biotopes variés, incluant des oiseaux de mer, de rivage, d'eau douce et des formes terrestres de grande et de petite taille. Parmi les oiseaux de mer, deux espèces au moins n'ont pas été connues durant les périodes historiques ni dans les faunes fossiles d'âge holocène de l'Archipel des Hawaii. La présence de formes migratrices parmi les oiseaux d'eau ou de rivage indique que les voies de migration de ces espèces à travers l'Océan Pacifique étaient déjà établies il y a plus de 120.000 ans. Les premières comparaisons morphologiques entre les formes terrestres et d'eau douce et l'avifaune fossile holocène de Barber's Point, Oahu, suggèrent que la plupart sinon toutes les adaptations majeures trouvées dans les espèces endémiques des Hawaii étaient déjà apparues au moment de la formation du gisement d'Ulupau Head.

MOTS-CLES : Oiseaux fossiles, Iles Hawaii, Pléistocène supérieur, Migration, Evolution.

* Dept. of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

Table of Contents

Annotated Faunal List 224
Procellariidae 224
Oceanitidae 226
Fregatidae 226
Sulidae 226
Anatidae 226
Accipitridae 227
Rallidae 227
Charadriidae 227
Scolopacidae 227
Strigidae 227
Corvidae 227
Myiagridae 227
Meliphagidae 228
Fringillidae (Drepanidini) 228
Mammalia 228
Discussion 229
Literature 229

Over the past decade and a half, approximately 100,000 specimens of fossil vertebrates have been collected in the Hawaiian Islands and added to the collections of the Bernice P. Bishop Museum in Honolulu and the National Museum of Natural History, Smithsonian Institution, in Washington, D.C. Significant fossil deposits have been found on five of the eight main Hawaiian islands, in various geologic contexts including lava tubes, karstic sinkholes, and eolian dunes. Evidence provided by fossils has led to a vastly improved record of the natural diversity and distribution of birds in the Hawaiian Archipelago (Olson and James, 1982a, 1982b, 1984). However, the fossil material that has previously been studied is apparently not sufficiently old to add the perspective of geologic time to knowledge of the Hawaiian avifauna. Radiocarbon ages and other evidence indicate that most known vertebrate fossil localities in the archipelago date to the Holocene ; indeed, some of the material has been found in archaeological contexts (Olson and James, 1982b). The only Pleistocene radiocarbon date obtained so far from a Hawaiian vertebrate fossil locality is that of 25,150 ± 1,000 ybp (Stearns, 1973) for snail shells associated with the fossil goose later described as the type of *Thambetochen chauliodons* OLSON and WETMORE (1976). This date may not be valid since snails living in carbonate dunes can incorporate environmentally dead carbon into their shells during life, producing radiocarbon dates that are fallaciously old.

The fossil record of Hawaiian terrestrial vertebrates now extends into the Pleistocene through the discovery of an older fossil deposit on the island of Oahu. This deposit accumulated in the crater of Ulupau Head, a tuff cone forming the northeast salient of the Mokapu Peninsula (fig. 1). The fossils are now being exposed by marine and subaerial erosion of the sea cliff that runs along the beach south from Kii Point. Vertebrate fossils were first noticed here by Gustav Paulay in 1982, while in the course of collecting fossil mollusks from the overlying Waimanalo Formation (see Kohn, 1980). Subsequent collections were made for the Bishop Museum and the Smithsonian Institution, so that about 750 recognisable fossil bones are now available.

Ulupau Head was formed by one of a series of pyroclastic eruptions on southeastern Oahu known collectively as the Honolulu Volcanic Series (Macdonald and Abbott, 1970). Although no direct radiometric date is available for the eruption of Ulupau Head, potassium-argon ages of 12 other eruptive vents of the Honolulu Volcanic Series, obtained by Gramlich *et al.* (1971), range from about 800,000 ybp for the oldest member date to about 30,000 ybp for the youngest. In a study of the probable relative ages of the various vents of the Honolulu Volcanic Series based on ancient shorelines and other geologic evidence, Winchell (1947) places Ulupau Head as one of the earlier eruptions.

Alternating high and low sea levels have affected the physiography of Ulupau Head, so that in its modern form most of the original crater rim and a large portion of the eastern side of the crater floor have been stripped away by erosion (fig. 1). After the eruption of the tuff cone, Ulupau Head was submerged 45 feet (13.7 meters) to 70 feet (21.4 meters) more than at present, and the crater was inundated after the sea breached the east rim (Stearns and Vaksvik, 1935 ; Wentworth and Hoffmeister, 1939). Wentworth and Hoffmeister (1939) postulate that the most severe marine and fluvial erosion of Ulupau Head took place during this first period of relative submergence, which left, among other evidence, a limestone deposit consisting mainly of well-preserved oyster and barnacle shells lying directly on the indipping beds of tuff exposed in the seacliff at Kii Point (fig. 1).

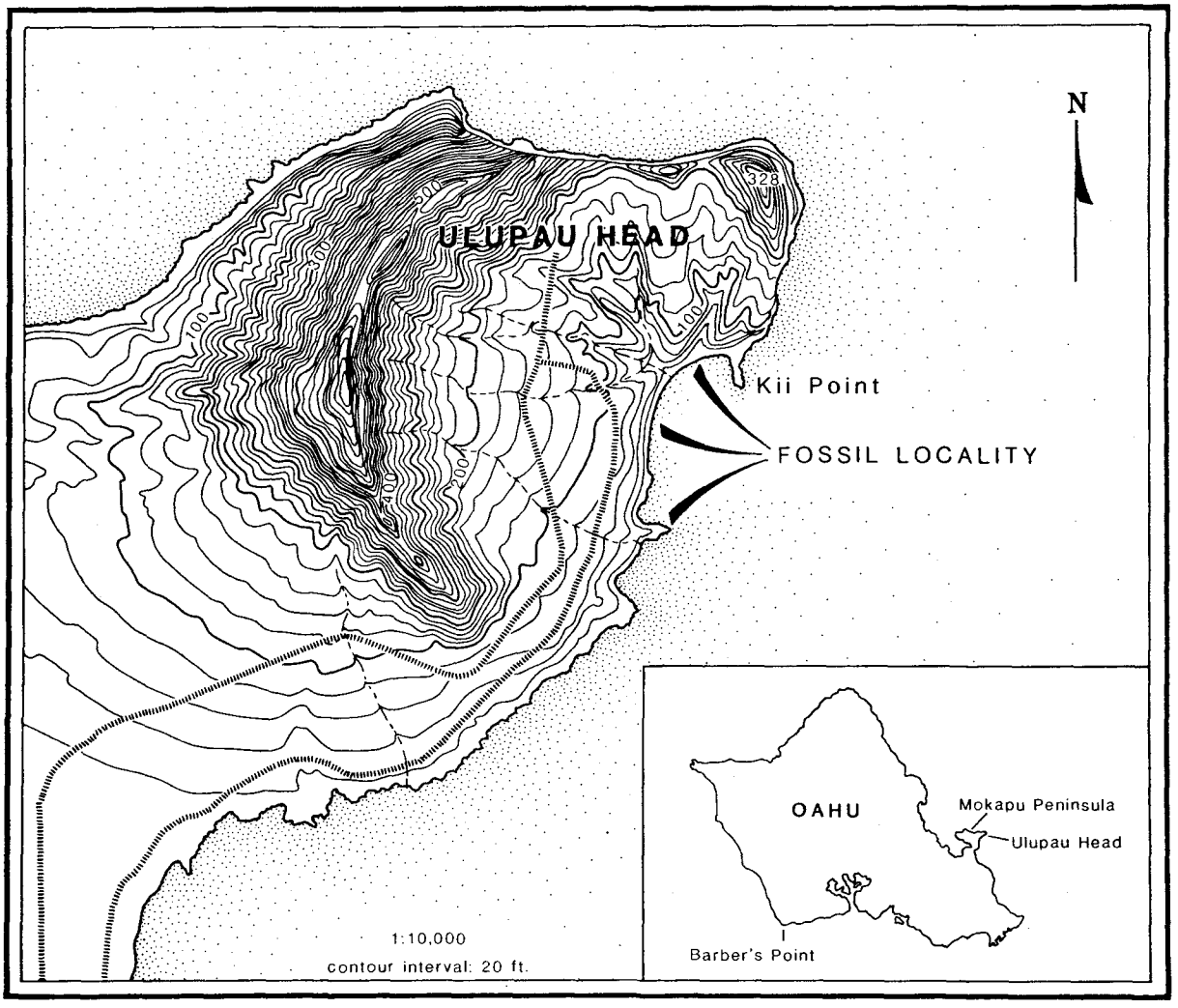

Fig. 1 – **Topographic map of Ulupau Head, Oahu, showing the vertebrate fossil locality.**
Fig. 1 – **Carte topographique d'Ulupau Head, Ile d'Oahu, montrant le gisement de vertébrés fossiles.**

Deposition of the limestone at Kii Point was followed by a period of relative emergence of Ulupau Head. The sea receded from the crater, and a thick deposit of tuffaceous silt accumulated on the crater floor, overlying the limestone at Kii Point. It was in this tuffaceous silt, described by Wentworth and Hoffmeister (1939) as «older alluvium» resulting from «fluviatile and colluvial» erosion of the crater walls, that Paulay and others later found fossil birds. In his notes based on several visits to the site in 1982, Paulay suggests that the silt is primarily a lacustrine rather than an alluvial deposit. This implies that the eastern wall of the crater was not completely removed by marine erosion during the preceding high sea level, so that enough of a depression remained to hold at least a semi-permanent lake when the terrestrial vertebrate fossils were accumulating in Ulupau Crater. Paulay's reinterpretation accounts for the fossilization of bones in the deposit, and for the occurrence of waterbirds in the fauna, including ducks, geese, and coots. The presence of indurated calcareous layers within the tuffaceous silt and the extensive, uninterrupted parallel bedding, are consistent with sedimentation in a permanent or semi-permanent crater lake. In places the sediment is more cobbly, suggesting that sheetwash from the surrounding crater walls has also contributed to the deposit. Vertebrate fossils occur rarely in the cobbly sediments. They also occur rarely in an indurated marine deposit at the southern part of the fossil locality which may have accumulated contemporaneously with the Kii Point limestone.

After the vertebrate fossils were deposited, the sea rose to about 7.6 m (25 feet) above the present level and again entered the crater, leaving behind a beach deposit on top of the «older alluvium». This was the Waimanalo stand of the sea, which is well marked around the periphery of Oahu by fossil reefs, beach deposits, and wave-cut notches and benches (Stearns and Vaksvik, 1953 ; Stearns, 1978). Ku *et al.* (1974) found a high degree of concordance in uranium-thorium ages of fossil corals from various exposures of the Waimanalo Formation around Oahu, yielding a date of 120,000 ybp for this sea level. The Waimanalo Formation therefore correlates with the Sangamon Interglacial, or oxygen isotope stage 5e (Shackleton and Opdyke, 1973). Ku *et al.* (1974) included samples in their study from the beach deposit directly overlying the «older alluvium» where it is exposed in the eastern sea cliff of Ulupau Head, as well as samples from elevated fossil reef taken *in situ* on the northern side of Ulupau Head. Hence, the fossil vertebrates from Ulupau Head must antedate the last significant transgression of the sea before the modern one.

How much older the vertebrate fossils are than the Waimanalo Formation cannot be precisely determined without radiometric dates for the high and low sea stands that preceded deposition of the Waimanalo Formation. A reasonable hypothesis is that the first submergence of Ulupau Head, when marine limestone was laid down inside the crater of Ulupau Head, occured during the eustatic high sea levels associated with the Yarmouth Interglacial ; and the subsequent emergence of Ulupau Head, when lacustrine sediment and most of the vertebrate fossils accumulated in the crater, occurred during the eustatic low sea levels associated with the Illinoian Glacial. These tentative correlations assume that during the time period in question, Oahu has not been subjected to isostatic movements of sufficient magnitude to greatly alter the impact of eustatic sea level fluctuations.

Polynesians arrived in the Hawaiian Islands about 1500 years ago (Kirch, 1974), and these original colonists were joined by western peoples about 200 years ago (Kirch, 1985). In the aftermath of these two colonizations, most of the endemic birds of the Hawaiian Islands became extinct (Olson and James, 1982a, b, 1984). Nowhere has this extinction been better documented than on Oahu, where a large collection of fossil birds was recovered from Holocene deposits in karstic sink holes near Barber's Point. The fossils from Barber's Point apparently post-date human colonization of Oahu (Kirch and Christensen, 1981 ; Olson and James, 1982b), yet these fossils include 23 species of endemic land birds that were extinct before they could be discovered on Oahu by westerners. The avifauna of Oahu has continued to diminish during historic times, so that six additional endemic land birds have become extinct over the past 200 years. All told, the surviving native land and fresh water birds of Oahu represent no more than 27.5 percent of the species that occurred there naturally before the tragic period of extinction began (tabl. 1). For this reason, the extant avifauna of Oahu does not provide an adequate basis for comparison with the fossils from Ulupau Head. It is fortunate that the fossils from Ulupau Head are found on the same island where the naturally occurring recent avifauna is best known, through the Holocene remains at Barber's Point.

ANNOTATED FAUNAL LIST

Many species in the fossil fauna from Ulupau Head are known from only one or a few bones, and more species undoubtedly remain to be collected. Preliminary identifications of the fossil vertebrates are given below. The nomenclature in this paper follows Olson and James (1982b) as closely as possible, including the informal names used for as yet undescribed species known from other Hawaiian fossil deposits.

PROCELLARIIDAE

Pterodroma cf. *hypoleuca* : A single proximal end of a humerus probably belongs to the Bonin Petrel, or possibly to an as yet undescribed species of *Pterodroma* found in Holocene fossil deposits at Barber's Point, Oahu. In either case, this humerus represents a species that has not bred in the main Hawaiian Islands in historic times, since the Bonin Petrel now breeds only in the Northwest Hawaiian Islands, and the fossil petrel from Barber's Point is believed to be extinct.

Puffinus puffinus newelli : A nearly complete coracoid establishes the presence of Newell's Shearwater in the Ulupau Crater deposit. The known breeding range of Newell's Shearwater has been restricted to Kauai since 1908, although it probably once bred on all of the main Hawaiian Islands (King and Gould, 1967). Bones of Newell's Shearwater have been found in Holocene deposits at Barber's Point and in an archaeological context at Kuliouou Shelter on Oahu.

	Historic Avifauna	Holocene Barber's Pt.	Pleistocene Ulupau Head
Nycticorax nycticorax	x		
Branta sp., non-migratory		x	
Thambetochen sp.		x	x
Supernumerary Oahu Goose		x	
Anas wyvilliana	x	x	x
Haliaeetus sp.		x	
Buteo sp.			x
Accipiter sp.		x	
Small Oahu rail		x	x
Medium-large Oahu rail		x	x
Gallinula chloropus	x	x	
* *Fulica americana*	x	x	x
Himantopus himantopus	x		
Asio flammeus	x	x	
Long-legged Oahu owl		x	x
Corvus, raven-sized		2 sp.	x
Phaeornis obscurus	e	x	
Chasiempis sandwichensis	x	x	x
Moho apicalis	e	x	
Chaetoptila cf. *angustipluma*		x	x
Psittirostra (Telespyza) cf. *cantans*		x	
Psittirostra (Telespyza), medium species		x	
Psittirostra (Loxioides) bailleui		x	
Psittirostra (Rhodacanthis) sp.		x	x
P. (Chloridops), lesser Oahu sp.		x	x
P. (Chloridops), giant Oahu sp.		x	x
P. (Psittirostra) psittacea	e	x	
Ridge-billed finch		x	
Additional Oahu finch		x	
Heterorhynchus lucidus	e	x	
Hemignathus obscurus	e	?	?
Paroreomyza maculata	x	x	x
Hoopoe-like sickle bill		x	?
* Icterid-like gaper		x	x
Sickle-billed gaper		x	
Loxops virens	x	x	x
Loxops coccinea	e		
Himatione sanguinea	x	x	
Vestiaria coccinea	x	x	
Ciridops sp.		x	

Tabl. 1 – **Distribution through time of the native land and fresh water birds of Oahu.**
x = present ; e = became extinct since 1778 ; ? = not positively identified. * See text.

Tabl. 1 – **Distribution dans le temps des oiseaux terrestres et aquatiques, indigènes, de l'île d'Oahu.**
x = présent ; e = éteint depuis 1778 ; ? = identification incertaine. * Voir le texte.

Procellariidae sp. : The distal end of one humerus and the proximal end of another humerus from Ulupau Crater represent a species of procellariid larger than *Pterodroma phaeopygia* or *Puffinus pacificus*, these being the largest members of the family breeding in the archipelago now. The Ulupau fossils also include one abraded tarsometatarsus that belongs either to the same species as the humeri, or to a somewhat smaller species of *Puffinus*. Although not positively identified, it is certain that these bones do not belong to any species that occurs in Holocene deposits at Barber's Point, or that now breeds in the archipelago.

OCEANITIDAE

Nesofregetta fuliginosa : A nearly complete humerus and the distal end of a tarsometatarsus of the White-throated Storm-Petrel from Ulupau Head constitute a new record for the Hawaiian Islands, as there is no previous fossil or recent record of this species in the archipelago (Pyle, 1983). *Nesofregetta fuliginosa* breeds widely in the southwest Pacific, from the Marquesas to the New Hebrides (Jouanin and Mougin, 1979). The wide, dorso-ventrally compressed tarsometatarsus of this genus is highly diagnostic (Olson, 1985).

FREGATIDAE

Fregata cf. *minor* : The Great Frigatebird nests on Moku Manu Islet near Ulupau Head, as well as on Kauai, Maui, and Kaula, and in the Northwest Hawaiian Islands. Frigatebirds apparently also frequented the area of Ulupau Head during the Illinoian Glacial, as they are represented by the proximal end of a humerus and a wing phalanx. These are the first fossils of frigatebirds to be identified from the Hawaiian Islands.

SULIDAE

Sula sp. : The Red-footed Booby (*Sula sula*) has a breeding colony on the remnant crater wall of Ulupau Head, and boobies also breed on nearby Moku Manu Islet, where the Brown Booby (*S. leucogaster*), and occasionally the Masked Booby (*S. dactylatra*), also nest. A humerus of a booby from Ulupau Head apparently belongs to *S. sula*, although the specimen cannot yet be positively identified because most of it is still embedded in matrix.

ANATIDAE

Anserinae sp. (migratory goose) : Bones of flying geese are fairly common among the fossils from Ulupau Head. The proportions of these bones are not similar to the endemic Hawaiian Goose, *Branta sandvicensis*. Instead, the pectoral appendage is relatively well developed, as it is in various migratory geese that visit the Hawaiian Islands, such as *Branta canadensis*.

Thambetochen sp. : This extinct genus of goose-like bird was originally described from a fossil from Molokai (Olson and Wetmore, 1976), and additional species were later found in fossil deposits on other islands, including those at Barber's Point, Oahu (Olson and James, 1982b). The tooth-like processes of the mandible and extreme modifications of the post-cranial skeleton for flightlessness that characterize the genus are evident in the bones from Ulupau Head. In fact, specimens of *Thambetochen* from Ulupau Head and Barber's Point do not differ from one another.

Anas cf. *wyvilliana* : A small duck with proportions similar to those of the endemic Hawaiian (*A. wyvilliana*) and Laysan (*A. laysanensis*) Ducks is the commonest bird among fossils from Ulupau Head. These bones are generally smaller than those of *A. wyvilliana*, so that statistical analysis may show them to resemble *A. laysanensis* more closely. For the present I adopt the biogeographically more conservative altemative in referring the Ulupau bones to *A. wyvilliana*, which occurs in the main Hawaiian islands, rather than to *A. laysanensis*, which is known historically only from Laysan Atoll.

ACCIPITRIDAE

Buteo sp. : Although the Hawaiian Hawk, *Buteo solitarius*, occurs only on the island of Hawaii at present, the natural range of the genus included other islands in the archipelago. Fossils of *Buteo* had previously been found on Molokai (Olson and James, 1982b), and they are surprisingly common in the collection from Ulupau Head. The hawk bones from Ulupau Head are markedly larger than in two skeletons of *B. solitarius* available for comparison. However, both comparative skeletons are males, and the fossils may be within the size range of females of *B. solitarius*.

RALLIDAE

Fulica sp. : Bones of a large coot are more common in the Ulupau Head deposit than in any other Hawaiian fossil locality. These fossils are large and robust compared to skeletons of the Hawaiian Coot, *Fulica americana alai*. Further study is needed to ascertain whether the fossil and modern forms are consubspecific.

Porzana sp., medium flightless rail : Bones of a medium-sized flightless rail from Ulupau Head are similar to the «medium flightless rail» from the Barber's Point deposits.

Porzana sp., small flightless rail : An undescribed «small flightless rail» is found in fossil deposits at Barber's Point and at Ulupau Head. The tarsometatarsi of the small rails do not differ between the deposits.

CHARADRIIDAE

Pluvialis dominica : Various bones of the Golden Plover were found in the Ulupau Head fossil deposit. This species also occurs in fossil deposits at Barber's Point, Oahu, and on other Hawaiian Islands, and is still a common wintering shorebird in the archipelago.

SCOLOPACIDAE

Numenius tahitiensis : Like the above species, the Bristle-thighed Curlew winters in the Hawaiian Islands, and has been found as a fossil at Barber's Point, and on Kauai and Molokai. Its bones also occur in the fossil deposit at Ulupau Head.

STRIGIDAE

Long-legged owl : There are at least five post-cranial bones of owls in the collection from Ulupau Crater, and these are identical to the extinct «long-legged owl» previously known from the fossil deposits at Barber's Point.

CORVIDAE

Corvus sp. : The fossils from Ulupau Crater include at least eleven post-cranial bones of extinct raven-sized corvids similar to those found as fossils at Barber's Point and on Molokai. Whether the bones from Ulupau Crater represent only one or both of the two species that occur at Barber's Point has not been determined.

MYIAGRIDAE

Chasiempis sandwichensis : The presence of one articular end of a mandible among Ulupau Head fossils is sufficient to establish the occurrence of the Elepaio in the deposit. The Elepaio also occurs in

the Holocene deposits from Barber's Point, and is still fairly common in montane forests on Oahu.

MELIPHAGIDAE

Chaetoptila sp. : This genus barely survived into the historic period, being known from only four skin specimens taken on the island of Hawaii between 1840 and 1859. The genus occurs in Holocene fossil deposits on Oahu and Maui (Olson and James, 1982b and pers. obs.), and probably occurred on other of the main islands as well. It is represented by cranial and post-cranial bones among the Ulupau Head fossils.

FRINGILLIDAE (DREPANIDINI)

Psittirostra (Rhodacanthis) sp. : Remnant populations of two species of Koa finches occurred on the island of Hawaii during historic times, but both were presumably extinct by 1900 (Berger, 1981). Holocene fossils from Oahu (Olson and James, 1982b) and Maui (pers. obs.) have shown that this subgenus was once more widespread in the main Hawaiian Islands. Three partial mandibles of Koa finches are present among the fossils from Ulupau Head. As is true of the fossil Koa finch from Barber's Point, these mandibles are more similar to the smaller *P. flaviceps* than to *P. palmeri.*

Psittirostra (Chloridops), lesser Oahu species : This is one of two species of Hawaiian grosbeak finch previously known only from Holocene fossils at Barber's Point, Oahu. A nearly complete rostrum and a piece of mandible establish its presence in the Ulupau Head deposit.

Psittirostra (Chloridops), giant Oahu species : The largest of the Hawaiian grosbeak finches was also known only from Barber's Point fossils until it was collected in the Ulupau Head deposit, where it is represented by two well-preserved rostra and two quadrates.

Psittirostra sp. : One small articulation of a mandible among the Ulupau Head collection belongs to an as yet unidentified species in this genus.

cf. *Hemignathus obscurus* : The Oahu race of Akialoa (*H. o. lichtensteini* is known historically from a single specimen in the Berlin museum. It has not been positively identified among Barber's Point fossils. I have tentatively identified two partial rostra from Ulupau Crater as *H. obscurus,* with the reservation that these rostra could also belong to the undescribed «hoopoe-like sickle bill» that occurs in fossil deposits at Barbers's Point and on Kauai, but that is known so far by the mandible only.

Icterid-like gaper : Two undescribed species of «icterid-like gapers» have been found in the Holocene deposits at Barbers' Point, and one species of this type also occurs as a fossil on Molokai. The fossils from Ulupau Head include three broken mandibles of «icterid-like gapers». Better material is needed before the specific affinities of these fragments can be determined.

Paroreomyza maculata : The Alauwahio is represented in the Ulupau head fossil collection by a single broken mandible. This species still survives in montane forests on Oahu, but it is extremely rare. It also occurs as a fossil at Barber's Point.

Loxops virens : The Amakihi is present in Holocene fossil deposits at Barber's Point, and is still fairly common in the relatively undisturbed native forests of Oahu. One articular portion of the mandible of an Amakihi was found at Ulupau Head.

MAMMALIA

Several bones of bats (*Lasiurus* spp.) and one small fragment of a marine mammal bone have also been found in the fossil deposit at Ulupau Head.

DISCUSSION

The fossils from Ulupau Head include remains of at least 28 species of birds, although some of them could not be positively identified at the specific level. This total includes representatives from all major habitats exploited by birds in the Hawaiian islands, with 6 seabirds, 2 shorebirds, 4 waterbirds, 2 predatory species, 3 terrestrial flightless species, and 11 to 12 passerine species. The size of the current fossil collection from Ulupau Head is small compared to other major Hawaiian collecting localities (Olson and James, 1982b), and there can be little doubt that more species will be found as collecting at the site continues. Future collecting should also fill in morphological details for many taxa in the fauna that are at present known from only one or a few skeletal elements. With sufficient fossils from Ulupau Head, it should be possible to study turnover and morphological evolution in the endemic avifauna of Oahu over a period of more than 120,000 years.

Even this preliminary study has yielded much useful information about the history of Hawaiian birdlife. Relatively few seabird bones have been collected from Ulupau Head so far, yet these include *Nesofregetta fuliginosa* and at least one other species of seabird that has not bred in the Hawaiian Islands during history. Pleistocene turnover in breeding seabirds of oceanic islands has already been observed on St. Helena (Olson, 1975) and Bermuda (S. L. Olson, pers. com.), and fossils from Ulupau Head may eventually show that the phenomenon was not restricted to the Atlantic. The fossils of *Numenius tahitiensis, Pluvialis dominicensis,* and migratory geese in the deposit constitute the oldest available evidence for the antiquity of the migratory routes of these species over the Pacific Ocean. As for the endemic land birds of Oahu, which are well represented in this preliminary fossil collection, no striking examples of morphological evolution were found in comparing the Pleistocene and Holocene avifaunas. Although *Anas wyvilliana* has possibly become larger, and the species of «icterid-like gaper» may not be the same in the Ulupau Head and Barber's Point deposits, these apparent changes are minor and perhaps illusory, since they could also be explained as artifacts of sampling or of recent human-caused extinctions. The weight of the evidence here indicates that remarkably little morphological evolution or turnover in species composition has occurred in the endemic avifauna of Oahu during the Late Pleistocene and Holocene.

Most vertebrate fossil sites that have been found on volcanic, oceanic islands date to the Wisconsinan Glacial or the Holocene (e.g. Olson and James, 1982b ; Steadman and Olson, 1986 ; Steadman, 1986). In fact, I do not know of another fossil vertebrate site on a volcanic, oceanic island that would compare with Ulupau Head as a well-documented older deposit containing remains of birds from all major habitats found on the island. In view of the important role islands have played in the development of modern evolutionary and ecological principles, more effort should be spent in locating and studying ancient fossil sites on these and other oceanic islands.

ACKNOWLEDGEMENTS

Permission to collect fossils at Ulupau Head was kindly granted by the Commander of the United States Marine Corps Air Station at Kaneohe Bay. I am particularly grateful to Diane Drigot for helping scientists gain access to the site. Gustav Paulay discovered the vertebrate fossils at Ulupau Head, and originated the reinterpretation of the «older alluvium» as a lacustrine sediment. I thank Carla Kishinami, Alan Ziegler, and Allan Allison of the Bishop Museum for collecting and loaning many of the specimens used in this study. My research at Ulupau Head is part of an ongoing research project under the direction of Storrs L. Olson at the Smithsonian Institution. Jonathan Becker, Gustav Paulay, Storrs L. Olson, and David Steadman provided helpful criticisms of a previous draft of the manuscript.

LITERATURE

BERGER A.J. (1981). – Hawaiian Birdlife. Second edition. *Univ. Press Hawaii,* Honolulu, XV + 260 p., 137 fig.

GRAMLICH J.W., LEWIS V.A. & NAUGHTON J.J. (1971). – Potassium-Argon Dating of Holocene Basalts of the Honolulu Volcanic Series. *Geol. Soc. America Bull.*, Boulder, Colorado, vol. 82, p. 1399-1404, 1 fig.

JOUANIN C. & MOUGIN J-L. (1979). – Order Procellariiformes. *In* Mayr E. & Cottrell G.W., eds.; Check-list of Birds of the World, vol. 1, second edition, *Museum Comparative Zoology,* Cambridge, Massachusetts.

KING W.B. & GOULD P.J. (1967). – The Status of Newell's race of the Manx Shearwater. *Living Bird,*

Ithaca, New York, vol. 6, p. 163-186.
KIRCH P. V. (1974). – The Chronology of Early Hawaiian Settlement. *Archaeology and Physical Anthropology in Oceania,* Sydney, vol. 9, p. 110-119, 1 fig., 2 tab.
KIRCH P. V. (1985). – Feathered Gods and Fishhooks. *Univ. Hawaii Press,* Honolulu, x + 349 p., 8 tab., 245 fig.
KIRCH P. V. & CHRISTENSEN C. C. (1981). – Nonmarine Mollusks and Paleoecology at Barber's Point, O'ahu. *In* Hammat H. H. and Folk W. H., Archaeological and Paleontological Investigation at Kalaeloa (Barbers' Point), Honouliuli, Ewa, O'ahu, Federal Study Area 1a adb 1b, and State of Hawaii Optional Area 1, p. 242-286. (Unpublished typescript deposited in Smithsonian Institution and Bishop Museum libraries).
KOHN A.J. (1980). – *Conus kahiko,* a New Pleistocene Gastropod from Oahu, Hawaii. *J. Paleontol.,* Tulsa, vol. 54, n° 3, p. 534-541, 3 fig.
KU T-L., KIMMEL M.A., EASTON W.H. & THOMAS J.O. (1974). – Eustatic Sea Level 120,000 Years Ago on Oahu, Hawaii. *Science,* Washington, vol. 183, p. 959-962, 1 fig., 1 tab.
MACDONALD G.A. & ABBOT A.T. (1970). – Volcanoes in the Sea. *Univ. Press Hawaii,* Honolulu, x + 441 p., 60 fig., 13 tab.
OLSON S.L. (1975). – Paleornithology of St. Helena Island, South Atlantic Ocean. *Smiths. Contrib. Zoology,* Washington, n° 23, 49 p., 10 fig., 6 pl., 8 tab.
OLSON S.L. (1985). – Early Pliocene Procellariiformes (*Aves*) from Langebaanweg, South-western Cape Province, South Africa. *Ann. South African Mus.,* Cape Town, vol. 95, n° 3, p. 123-145, 7 fig., 5 tab.
OLSON S.L. & JAMES H.F. (1982a). – Fossil Birds from the Hawaiian Islands : Evidence for Wholesale Extinction by Man before Western Contact. *Science,* Washington, vol. 217, n° 4560, p. 633-635, 1 fig., 1 tab.
OLSON S.L. & JAMES H.F. (1982b). – Prodromus of the Fossil Avifauna of the Hawaiian Islands. *Smiths. Contrib. Zoology,* Washington, n° 365, 59 p., 12 fig., 5 tab.
OLSON S.L. & JAMES H.F. (1984). – The Role of Polynesians in the Extinction of the Avifauna of the Hawaiian Islands. *In* Martin P. S. and Klein R. G., eds., Quaternary Extinctions, A Prehistoric Revolution, *Univ. Arizona Press,* Tucson, p. 768-780, 3 fig., 2 tab.
OLSON S.L. & WETMORE A.W. (1976). – Preliminary Diagnoses of Two Extraordinary New Genera of Birds from Pleistocene Deposits in the Hawaiian Islands. *Proc. Biological Soc. Washington,* vol. 89, n° 18, p. 247-258, 6 fig.
PYLE R.L. (1983). – Checklist of the Birds of Hawaii. *Elepaio,* Honolulu, vol. 44, n° 5, p. 47-58.
SHACKLETON N.J. & OPDYKE N.D. (1973). – Oxygen Isotope and Paleomagnetic Stratigraphy of Equatorial Pacific Core V28-238 : Oxygen Isotope Temperatures and Ice Volumes on a 10^5 Year and 10^6 Year Scale. *Quaternary Research,* Seattle, vol. 3, p. 39-55, 9 fig., 4 tab.
STEADMAN D.W. (1986) – Fossil birds, reptiles, and mammals from Isla Floreana, Galapagos Archipelago. *Smiths. Contrib. Zoology,* Washington, n° 413, 103 p., 25 fig., 11 tab., 4 pl.
STEADMAN D.W. & OLSON S.L. (1986). – Bird remains from an archaeological site on Henderson Island, South Pacific : Man-caused extinctions on an «uninhabited» island. *Proc. Nation. Acad. Science USA,* Washington, vol. 82, p. 6191-6195.
STEARNS H.T. (1973). – Geologic Setting of the Fossil Goose Bones Found on Molokai Island, Hawaii. *Occas. Papers Bernice P. Bishop Museum,* Honolulu, vol. 24, n° 10, p. 155-163, 7 fig.
STEARNS H.T. (1978). – Quaternary Shorelines in the Hawaiian Islands. *Bull. Bernice P. Bishop Museum,* Honolulu, n° 237, 57 p., 21 fig., 6 tab.
STEARNS H.T. & VAKSVIK K.N. (1935). – Geology and Ground Water Resources of the Island of Oahu, Hawaii. *Hawaii Divis. Hydrography Bull.,* Honolulu, n° 1, 479 p.
WENTWORTH C.K. & HOFFMEISTER J.E. (1939). – Geology of Ulupau Head, Oahu. *Geol. Soc. America Bull.,* Boulder, Colorado, vol. 50, p. 1553-1572, 3 fig., 2 pl.
WINCHELL H. (1947). – Honolulu Series, Oahu, Hawaii. *Geol. Soc. America Bull.,* Boulder, Colorado, vol. 58, p. 1-48, 7 fig., 2 pl.