

THE GEOLOGICAL CONTEXT OF MIDDLE PLEISTOCENE CRATER LAKE DEPOSITS AND FOSSIL BIRDS AT ULUPAU HEAD, OAHU, HAWAIIAN ISLANDS

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Alan ZIEGLER, retired vertebrate zoologist at the B. P. Bishop Museum, Honolulu, had an abiding interest in the fossil vertebrates of the Hawaiian Islands and in fostering public education about them. He made many collecting trips to Ulupau Head and personally collected hundreds of fossils there. He died 16 September 2003, on the first day of the symposium of which this volume is the proceedings. It gives us great pleasure to acknowledge his enormous contribution and to remember his many years of unstinting generosity, collegiality, and friendship.

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Resum

Els dipòsits pleistocènics llacunars del cràter Ulupau, a Oahu, contenen les restes fòssils més antigues d'ocells conegudes a les Illes Hawaiï. Aquests fòssils són importants per documentar les taxes evolutives a una varietat de línies d'ocells terrestres i aquàtics de les illes. L'anàlisi estratigràfic detallat revela diferents cicles deposicionals que comporten dipòsits llacunars interestratificats, colluvium i paleosòls. La conca volcànica va ser oberta per l'erosió marina prèvia al pic del darrer interglacial (estadi isotòpic marí, o 'MIS' 5e), fa 125 ka, restringint l'edat dels sediments del llac al Pleistocè Mitjà. Els tres cicles de deposició (Unitats III, IV i V) semblen estar estretament lligats a pujades interglacials amb una ciclicitat de 100 ka. Donada la complexitat de la successió dels sediments del cràter i el temps requerit per a la seva formació, es probable que la conca del llac s'omplís al llarg de diferents interglacials, assolint una extensió màxima de més de 50 ha durant l'estadi MIS 11, fa uns 400 ka. Aquesta és també la màxima edat probable de les capes fòssilíferes més riques de la Unitat III, però no es pot excloure que siguin del MIS 9 (fa 300 ka). Els requeriments d'hàbitat probables de diferents elements de l'avifauna donen llum sobre la paleoecologia de la localitat durant el Pleistocè Mitjà.

Paraules clau: llacs de cràter volcànic, sedimentació llacunar, cicles de llacs, ocells fòssils, paleoecologia, racemització d'aminoàcids, Illes Hawaiï.

Summary

Pleistocene lake deposits in Ulupau Crater on Oahu contain the oldest fossil bird remains known from the Hawaiian Islands. These fossils are important for documenting evolutionary rates in a variety of lineages of land and water birds from the islands. Detailed stratigraphic analysis reveals distinct cycles of deposition involving interbedded lacustrine deposits, colluvium, and paleosols. The volcanic basin was breached by marine erosion prior to the peak of the last interglaciation (marine isotope stage or 'MIS' 5e) over 125 ky ago, constraining the age of the lake sediments to the middle Pleistocene. The three cycles of deposition (Units III, IV, and V) appear to be closely linked with interglacial highstands with 100 ky cyclicity. Given the complexity of the succession of crater sediments and the time required for their formation, it is probable that the lake basin filled over several interglacials, reaching a maximum extent of over 50 ha during MIS 11, about 400 ky ago. This is also the likely maximum age of the richest fossil beds in Unit IV, but MIS 9 (300 ky) also remains a possibility. Probable habitat requirements of the various elements of the avifauna provide insights into the paleoecology of the site during the middle Pleistocene.

Keywords: volcanic crater lakes, lacustrine sedimentation, lake cycles, avian fossils, paleoecology, amino acid racemization, Hawaiian Islands.

INTRODUCTION

The Hawaiian Islands (Fig. 1) originated as the oceanic lithosphere of the central Pacific was perforated by a hotspot plume (Wilson, 1963). The chain of islands provides classic examples of Darwin's three-stage model of island evolution, progressing from (1) volcanic eruption,

to (2) fringing reef and carbonate platform development, to (3) coral atoll. The early development of carbonate platforms is poorly documented, however, as many of these deposits are submerged, buried, or eroded on older islands, and rarely interbedded with extrusive volcanics (Hearty *et al.*, 2005). Carbonate platforms are sometimes pierced by rejuvenation (late stage) volcanoes, which may result from lithospheric flexure due to shield-

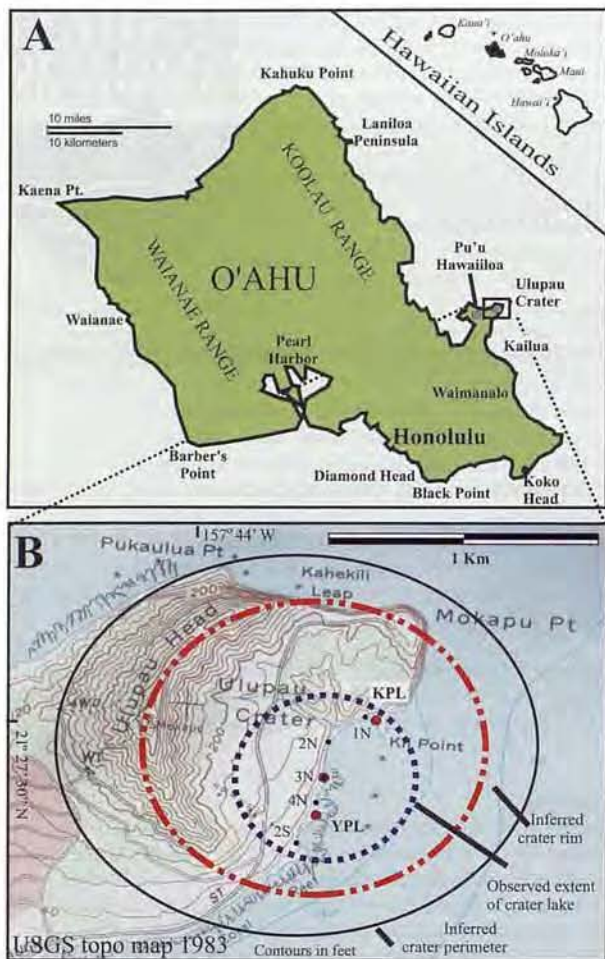


Fig. 1. A. Map of the island of Oahu showing the location of Ulupau Crater (box) and neighboring Pu'u Hawaiiiloa on the Mokapu Peninsula along the northeast coast. Inset shows the position of Oahu (solid) relative to the other Hawaiian Islands. B. Topographic map of Ulupau Crater showing reconstructed crater perimeter (solid line), crater rim (red dash-dot line), and inferred area of crater lake (blue dotted line). Small black dots identify locations of the sections in the correlation diagram (Fig. 7), while larger red circles indicate key sections. KPL = Ki'i Point Limestone. YPL = Yellow Point Limestone.

Fig. 1. A. Mapa de l'illa d'Oahu on es mostra la localització del cràter Ulupau (rectangle) i el veïnat Pu'u Hawaiiiloa a la Península Mokapu al llarg de la costa nord-est. El requadre mostra la posició d'Oahu (sòlida) respecte les altres Illes Hawaii. B. Mapa topogràfica del cràter Ulupau que mostra el perímetre reconstruït del cràter (línia sòlida), la vorera del cràter (línia vermella de punts i ratlles), i l'àrea inferida del llac del cràter (línia de punts blava). Els punts negres petits identifiquen les localitzacions de les seccions al diagrama de correlació (Fig. 7), mentre que els cercles vermells més grans indiquen seccions clau. KPL = Ki'i Point Limestone. YPL = Yellow Point Limestone.

building eruptions over the Hawaiian hotspot to the southeast (Jackson *et al.*, 1980). After eruption, volcanic craters may host bogs, lakes, or embayments. Lakes are rare and poorly understood in the Hawaiian Islands (Maciolek, 1982) and elsewhere among the Pacific islands. The crater of Ulupau Head, a tuff cone that formed during the rejuvenation stage eruptions on Oahu, may have sustained one of the longest and largest lacustrine systems in the Hawaiian Islands. The spectacular modern crater lake Rano Kau on Rapanui or Easter Island (Fig. 2; see

Flenley *et al.*, 1991) is probably a close modern analog of certain stages of development of the Ulupau crater lake. Lacustrine and colluvial sediments preserved in the crater are the source of an important assemblage of fossil birds from the Pleistocene of Oahu (Fig. 3, James, 1987).

This paper will review the complex processes that brought Ulupau Crater to its current condition, with particular attention to the formation of lakes in the crater and the occurrence of abundant avian fossils in the lacustrine and colluvial sediments (James, 1987), an aspect that was overlooked in previous geological descriptions of the crater (Stearns & Vaksvik, 1935; Wentworth & Hoffmeister, 1939). The Pleistocene bird bones from the site are a valuable resource for understanding rates of morphological evolution and species turnover in an isolated island avifauna, and providing fossil calibration points to estimate nucleotide substitution rates in avian genes. Fundamental to these research applications is a reasonably accurate knowledge of the age of the fossils.

Consequently, the overall objective of this paper is to identify constraints on the geologic age of the fossil birds through the reconstruction of the landscape evolution in and around Ulupau Head. Ancient paleoenvironments of the lake and surrounding crater are further reconstructed by inference from the habitat requirements of the birds identified in faunal assemblage.

Questions fundamental to this study include: (1) approximately when did the crater form, and how much time was required for the lacustrine and colluvial sediments to accumulate in the crater basin? (2) what geological time constraints can be implicated relative to the avian fossils contained in the lake sediments? (3) under what paleoenvironmental conditions were the fossil birds deposited? and, (4) how long ago was the crater breached, finalizing the lacustrine phase at Ulupau? Most of these questions can be addressed through interpretation of the outcrop geology, combined with new geochronologic and fossil data from the site.

EVOLUTION OF ULUPAU CRATER

Geological Setting of Ulupau Head.

Ulupau Head forms the headland of the Mokapu Peninsula along the northeast coast of Oahu (Fig. 1B) at approximately 27° 30' N Lat by 157° 44' W Long on the Marine Corps Base Hawaii at Kaneohe, about 5 km NE of the town of Kailua. After the initial shield-building phase of volcanic eruptions on Oahu (Fig. 1A), which ended c. 2 My (McDougall, 1964), the island experienced several notable geological episodes in and around Ulupau Crater. These include carbonate platform development, rejuvenation volcanics, collapse, basin formation and lacustrine sedimentation, colluvial episodes, crater breach, and coral reef development. The remnant crater is about 1300 m in diameter, with the west rim (Ulupau Head) rising to about 210 m. The Ulupau Head tuff cone is one of several dozen "rejuvenation" volcanoes on Oahu, referred to as the Honolulu Volcanic Series (HVS). Two previous studies of K-Ar dates from the HVS vents have con-



Fig. 2. Photograph of Rano Kau on Rapanui (Easter Island), a possible analog for one stage in the development and ultimate breaching of Ulupau Lake Crater. Depths are generally 5-10 m, while floating vegetation mats cover the lake surface. The eastern wall of the crater (right of photo) is near the point of breaching.

Fig. 2. Fotografia de Rano Kau a Rapanui (Illa de Pàsqua), un possible anàleg per a un estadi en el desenvolupament i trencament final del cràter Ulupau. Les profunditats són generalment 5-10 m, mentre que tapisos de vegetació flotant cobreixen la superfície del llac. La paret oriental del cràter (a la dreta de la foto) es troba a prop del punt de trencament.

cluded that this post-shield-building explosive volcanic phase on Oahu took place after 0.8 to 0.6 My, although the picture is clouded by several older K/Ar readings that are rejected by the original authors due to contamination by xenoliths apparently containing excess argon (Gramlich *et al.*, 1971; Lanphere & Dalrymple, 1980). The accepted dates on the HVS correlate roughly with the period of major shield building on the island of Hawaii (<0.6 My, in Macdonald *et al.*, 1983), which apparently caused lithospheric flexure beneath Oahu. Lithospheric flexure and fracturing are thought to be closely linked to the fundamental causes of rejuvenation volcanic activity (Jackson *et al.*, 1980). Carbonate platforms must have been forming between the shield-building and rejuvenation intervals of volcanism, as blocks and fragments of marine limestones are common in tuff cones around Oahu (Wentworth & Hoffmeister, 1939; Stearns, 1978). These limestone traces are evidence of HVS eruptions penetrating through carbonate deposits.

After its formation, Ulupau Crater intermittently filled with either fresh, salt, or a mixture of waters, and accumulated both colluvial and lacustrine deposits below and well above present sea level. Soils formed on these deposits during periods of stability. At its maximum size, the crater may have held a lake of up to 50-60 ha, by far the largest lake known in the Hawaiian Islands. Subsequently, the eastern half of the crater wall and lake sediments were removed, forming a sea cliff against which coral reefs of last interglacial age formed (Muhs & Szabo, 1994; Szabo *et al.*, 1994).

Post-Shield Building and Pre-eruption Phases at Ulupau

Shield building took place at different times in western and eastern Oahu. Buildup of the Waianae western shield volcano occurred between about 3.5 and 2.5 My, while the eastern Koolau volcano developed somewhat later between about 2.5 and 1.8 My (McDougall, 1964). The shield-building phases of Oahu (Waianae and Koo-



Fig. 3. Middle Pleistocene bird bones from Ulupau Head, Oahu, lake deposits, Unit IVa. A. Humerus of a small duck *Anas* aff. *wyvilliana/laysanensis*, BPBM 178731. B. Maxilla of the large extinct finch *Chloridops regiskongi*, USNM 528523. C. Coracoid of a goose *Branta* sp., BPBM 159074. D. Tarsometatarsus of the extinct flightless waterfowl *Thambetochen xanion*, BPBM 159751. E. Tarsometatarsus of a hawk *Buteo* sp., USNM 394270. F. Ulna of an extinct crow, *Corvus* sp. USNM 528524.

Fig. 3. Ossos d'ocells fòssils del Pleistocè Mitjà provinents d'Ulupau Head, Oahu, sediments lacunars, Unitat IVa. A. Húmer d'un ànneret petit *Anas* aff. *wyvilliana/laysanensis*, BPBM 178731. B. Maxil·lar del gran pinçà extingit *Chloridops regiskongi*, USNM 528523. C. Coracoid d'una oca *Branta* sp., BPBM 159074. D. Tarsometatars de l'oca avoladora extingida *Thambetochen xanion*, BPBM 159751. E. Tarsometatars d'un aligot *Buteo* sp., USNM 394270. F. Ulna d'un corb extingit, *Corvus* sp. USNM 528524.

lau Volcanic Series) ended around 1.8 My. Carbonates presumably began to accumulate soon after, leaving at least 1 My of the early and middle Pleistocene for carbonate platforms to form before the eruptive phase of the HVS. Although many carbonate and reef deposits are known from Oahu (Stearns, 1978), most of them date from middle and late Pleistocene intervals (Ku *et al.*, 1974; Szabo *et al.*, 1994; Muhs & Szabo, 1994; Hearty *et al.*, 2000). Exposed early Pleistocene platform remnants are known only from southeastern Kauai (Hearty *et al.*, in press).

Eruption

Ulupau Head is a tuff cone formed by hydromagmatic eruptions near sea level (Stearns in Macdonald *et al.*, 1983), inferring synchrony with an interglacial highstand of sea level. The tuffs overlie nephelinite lava flows from Pu'u Hawaiiiloa (a neighboring tuff cone, Fig. 1), which is thus older than Ulupau. Pu'u Hawaiiiloa is terraced at 30 m above present sea level (noted as "+30 m"), probably equating with the Kaena Highstand (Stearns, 1978), which is interpreted to have occurred during MIS 11, around 400 ky (Hearty, 2002a). Because of the K/Ar age uncertainty created by the volcanics contaminated with xenoliths of the area (Gramlich *et al.*, 1971; Lanphere & Dalrymple, 1980) the Ulupau tuff has not been directly dated, and it is only possible to infer the age of crater formation. Assuming the lake developed penecontemporaneously with the development of the volcanic basin, crater formation probably occurred toward the end of the period between about 0.6 and 0.4 My.

The Ki'i Point Limestone and the Ulupau Eruption

Near the center of the original Ulupau basin (Fig. 1B, 4) are two isolated and discontinuous outcrops of carbonate rock whose stratigraphic position and relative ages are perplexing. These two fossiliferous limestones are sedimentologically distinct and are comparable only in their high-angle bedding dipping inward toward the ancient center of the crater.

The Ki'i Point Limestone (KPL; Fig. 4A, B) is an *in situ* oyster (*Ostrea hanleyana* Sowerby) and barnacle reef with a matrix of fine-grained, parallel-bedded carbonate marl, interbedded with diatom ooze, carbonate silt and minor volcanics. The bedding dips southward at between 25° and 35°. Wentworth & Hoffmeister (1939) describe an overlying "calcareous sandstone composed of beach detritus", but we did not observe a distinct unit of this description (collapse is evident and frequent at the site).

The Yellow Point Limestone (our name, or YPL; Fig. 4C), was considered part of the Ki'i Point Formation by Wentworth & Hoffmeister (1939) despite the fact there are few similarities between the units. The YPL is a coarse-grained foraminiferal carbonate sand, containing <25% volcanics. The deposits contain large coral and well-rounded volcanic tuff fragments, and nearshore hard-substrate-associated fossils (limpets, top shells, etc). Considering the large clasts and littoral marine fossils, the YPL was probably deposited in a nearshore, moderate to high energy, shallow, subtidal sandy environment, in proximity of rocky outcrops. A rib of a small whale (*Globicephala* sp.) was also found within the YPL (Wentworth & Hoffmeister, 1939) confirming a connection of this unit with the open ocean.

Either or both of these limestone units were formed (1) as part of carbonate platforms previous to the eruption of Ulupau Crater and were subsequently rotated and incorporated into the volcanic mass; or (2) during the initial stages of volcanic eruption, and are nearly in place, with minor displacement, perhaps caused by collapse of the caldera. Stearns & Vaksvik (1935) and Wentworth & Hoffmeister (1939) concluded that the KPL and YPL were formed in place within Ulupau Crater. Without question, however, they predate and are succeeded by lake sediments.

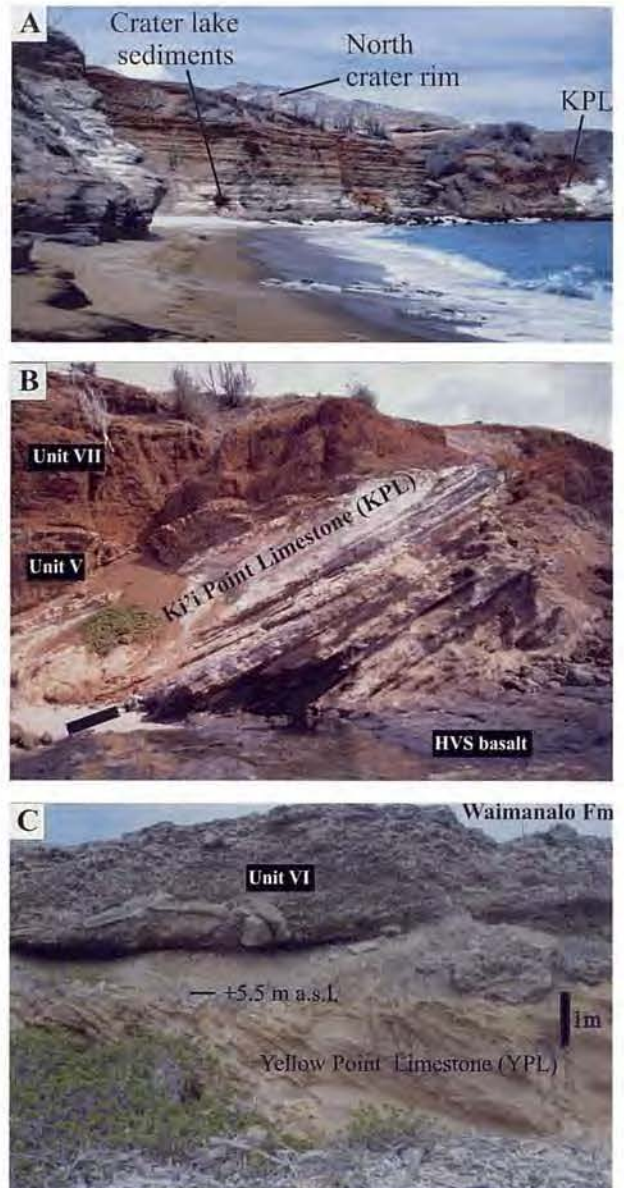


Fig. 4. Photographs of sea cliff and lake sediments at Ulupau Crater. A. View of crater rim in background and lake sediments in mid and foreground. B. Detail of the Ki'i Point Limestone and adjacent lake-filling colluvial units. C. Detail of the Yellow Point Limestone and overlying Waimanalo Fm conglomerate and reef.

Fig. 4. Fotografies del penya-segat mari i dels sediments llacunars del cràter Ulupau. A. Vista de la vorera del cràter a darrera i dels sediments llacunars enmig i a davant. B. Detall del Ki'i Point Limestone i unitats col·luvials adjacents que rebleixen el llac. C. Detall del Yellow Point Limestone i el conglomerat i esculls de la formació Waimanalo que el cobreixen.

LAKE FORMATION AND SEDIMENTATION

Lake Depositional Model

Maciolek (1982) identified three types of lakes in the Hawaiian Islands: (1) high altitude (elevations are 2040 m for Wai'e'ele, and 3969 m for Waiau) perched aquifers; (2) salt lakes or ponds in topographic depressions adjacent to the sea, and receiving a regular supply of marine phreatic water; and (3) fresh to salt water lakes or embay-

Crater Lake Facies Model

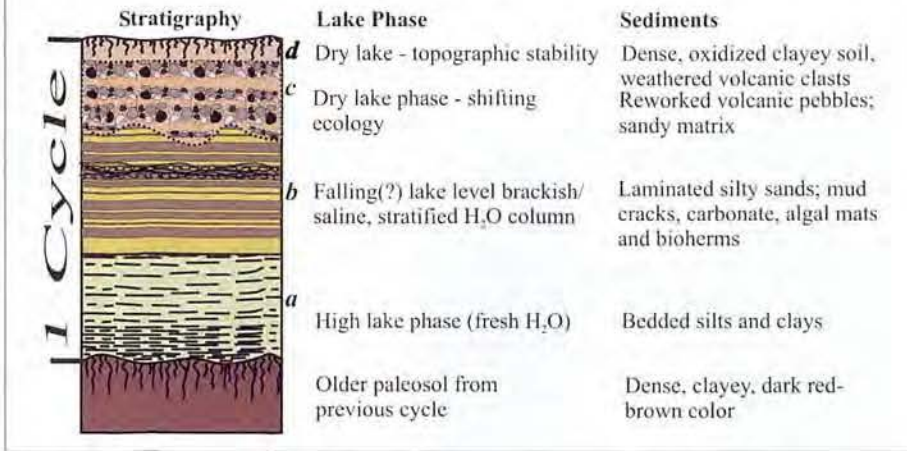


Fig. 5. Crater lake facies model. Units reflect a cyclical sedimentation progressing from (a) high fresh lake; (b) high saline lake; (c) dry lake with erosion and deposition of colluvium (shifting ecology); and (d) dry lake with topographic stability (forested?) and soil development.

Fig. 5. Model de facies llacunar a un cràter. Les unitats reflecteixen una sedimentació cíclica progressant des de (a) un llac d'aigua dolça alt; (b) un llac salí alt; (c) un llac sec amb erosió i deposició de col·luvium (ecologia canviant); i (d) un llac sec amb una estabilitat topogràfica (forestal?) i amb desenvolupament de sòl.

ments in craters lying at or near the sea, with the local or regional groundwater table dictated by sea level. Ulupau Crater would fall in the last category. Because of the permeable nature of the volcanic tuff, it would be unlikely that a lake at Ulupau could be perched at an elevation significantly above sea level. There are no perched lakes at lower elevations anywhere in the Hawaiian Islands today. Therefore it is reasonable to assume that rising and falling sea levels would have dominated the hydrology of the Ulupau crater lakes, and that such lakes would tend to fill the crater basin during stable highstands.

It is possible to infer some of the conditions in the lakes of Ulupau Crater by comparison with Wai a Pele (or Green Lake), currently the largest freshwater lake in Hawaii, located 2 km inland of Cape Kumukahi in a windward position on the easternmost point of the Big Island of Hawaii. The lake, which occupies the inactive Kapoho Crater, is about a hectare in area, over 6 m deep, and rises to an elevation of about +1 m (Maciolek, 1982). Wai a Pele occurs in an area of moderate precipitation (250 cm per yr), and has a dissolved mineral content of 300 mg per liter. The lake is stratified between 22° and 25°C, and becomes anoxic at a thermocline about 3 m deep. The hydrologic stratification persists most of the year, turning over with cooler winter temperatures. We assume that the Ulupau lakes may have operated similarly in the earlier stages of development of the basin. Later stages of development in Ulupau basin may have resembled Rano Kau on Rapanui (Fig. 2), which currently supports a 8-m-deep lake with floating vegetal mats, and is near the point of breaching on its southern rim (right of photo in Fig. 2).

Lake and Colluvial Sedimentation in Ulupau Crater

Despite the limitations of the geochronological methods and less than optimal sample material, it is still possible to understand the history of basin filling in Ulupau Crater by interpretation of the exquisite exposures in the cliffs. Furthermore, we recognize and have dated various sea-level highstands from the Hawaiian Islands (e.g., Hearty *et al.*, 2000; Hearty, 2002a), and seek to corre-

late them with high lake stands. With these considerations, we developed a facies model representing the major elements of crater basin sedimentation (Fig. 5) based on an extensive survey of the strata exposed in Ulupau Crater. The stratigraphic evidence indicates rapidly shifting and diverse environments of deposition within the crater. The sediments indicate deposition in fresh, salt, and mixed lake waters, with significant fluxes of colluvium on slopes during unstable (thinly vegetated?) intervals, and stable intervals of soil formation. Analyses have identified four main types of sediments (as per Fig. 5): (a) massive or weakly stratified, fissile and compact greenish (reduced anoxic conditions?) silts and clays = high fresh water lake phase, anoxic with depth; sea-level highstand, but sufficiently separated by stratigraphic barriers to influence, but not dominate the lake water chemistry. The presence of abundant carbonate sediments and rocks in the KPL and YPL as well in pre-existing carbonate platform beneath the crater, would have provided ample buffering in the subsequent lake sediments; (b) laminated and oxidized silty sands with carbonate bioherms = high level anoxic lake with input of marine groundwater; (c) volcanic colluvium = low sea level; no lake, and unstable crater landscape and slope wash due to shifting plant ecology; and (d) dense, oxidized soil development = stable landscape; vegetated, perhaps forested. It appears that the deposition of these types of sediments occurred in a cyclical succession from lacustrine sediment, to colluvium, to soil.

A representative stratigraphic section logged from near the center of the Ulupau Crater basin (Section OKP3N, Fig. 6) contains a variety of sediment types and sedimentary structures related to different processes. This section has been subdivided into units from the base to the top of the section. Five units (III to VII) have been identified within OKP3N and adjacent sections (Fig. 7). Each of the units contains facies variations and subunits, indicative of changing environments within larger sedimentary cycles. Some subunits are missing locally due to topographic irregularities in the basin. In all crater-filling units, colluvial beds become finer and thinner toward the center of the basin, while lake sediments are thickest in

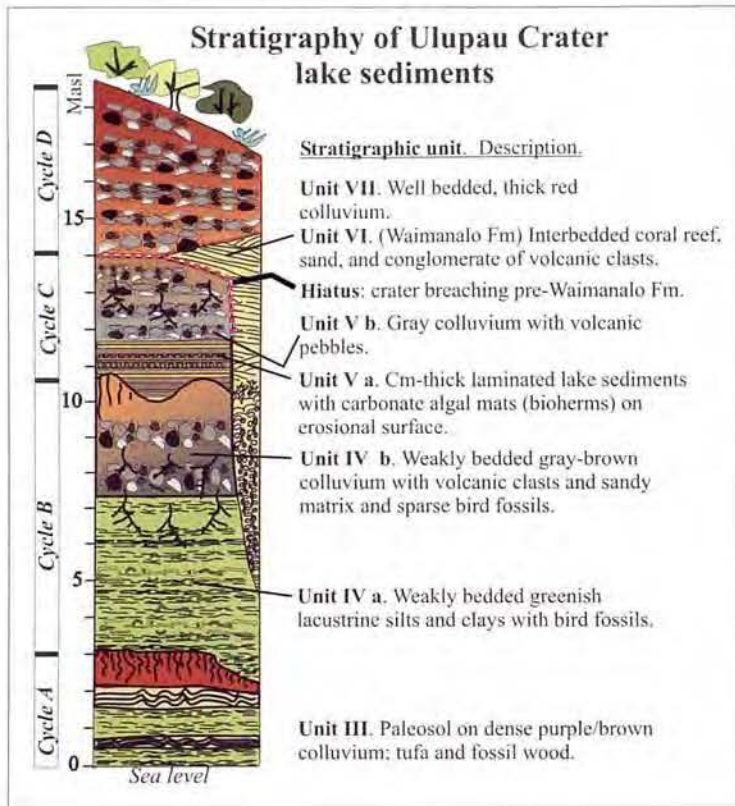


Fig. 6. Interpretation of representative stratigraphy of lake sediments (Section OKP3N) in Ulupau Crater illustrating three cycles of lake deposition. The earliest lake level was near present sea level (Unit III), followed by a deep-lake phase over +15 m (Unit IV), and a final high lake phase (Unit Va) to around +12 m. Removal of the eastern rim and breaching of the crater wall occurred previous to MIS 5e. Unit VII (Cycle D) represents only a colluvial cycle as no lake sediments are present.

Fig. 6. Interpretació de l'estratigrafia representativa dels sediments lacunars (Secció OKP3N) al cràter Ulupau, il·lustrant tres cicles de deposició lacunar. El nivell lacunar més primerenc estava a prop del nivell marí actual (Unitat III), va ser seguit per una fase lacunar fonda a devers +15 m (Unitat IV), i una fase final de llac alt (Unitat Va) a devers +12m. La substracció de la vorera oriental i el trencament de la paret del cràter va ocórrer abans del MIS 5e. La Unitat VII (Cicle D) representa només un cicle col·luvial ja que no s'hi troben sediments lacunars.

the center of the basin, and thin laterally (Fig. 7). Facies transitions (lake to colluvial) are generally conformable with the exception of minor cut and fill probably associated with the development of small gullies within the basin formed during heavy rainfall events.

1. *Unit III, 1st lake, colluvial, and pedogenic cycle.* The lowest deposit exposed in the crater is Unit III, which, along with Units IV and V, onlap the Ki'i Point Limestone in angular unconformity (Fig. 4B). Subunit IIIa is a dense clayey colluvium, interbedded with tufa beds (IIIb). The colluvium thickens considerably in more northerly sections. The tufa beds on the southern edge of the lake basin expose organic structures (root traces and algal mat) as well as fossil wood. The succession of deposits is capped by a dense, dusky-red mature clayey paleosol found across the basin (Figs. 7 and 8). The lower beds exhibit short-term switching of lake and colluvial deposition, perhaps indicating the waning phases of the crater lake. This cycle of deposition is marked by a substantial, well-developed paleosol suggesting an extended interval of topographic and ecologic stability, perhaps under forest cover.

2. *Unit IV, 2nd lake and colluvial cycle.* This comprises two subunits, with Subunit IVa consisting of lake sediments. Its five meters of green to buff colored silts and clays form Subunit IVa and the base of the second cycle of lake deposition. There is weak, compact, fissile bedding but no profound visual lamination of the sediments. Thin lenses of pebbles and some whitish hardpans are observed. Before compaction, the sediments of Unit IVa may have been considerably thicker, indicating

a much greater height of the lake level during deposition, than indicated by their current height of +7 to +8 m.

Unit IVa contains bones of seabirds, shorebirds, waterbirds, land birds, and bats, but few other macrofossils (James, 1987). Because abundant bird bones are preserved in the unit, it is evident that the pH of the lake was sufficiently basic to prevent their dissolution, so the lake waters apparently were buffered either by marine phreatic groundwater leaking through the crater walls, or by the influence of carbonates within and beneath volcanic tuff. Root traces are observed in the uppermost beds penetrating the lacustrine unit, indicating growth of vegetation probably in the overlying colluvial deposit. The uppermost beds of Subunit IVa grade conformably to the overlying colluvium.

The sediments of Subunit IVb are composed of alternating lenses of weakly to strongly bedded, very coarse volcanic breccia and medium sand and pebble textures. Fossil bird bones occur in this subunit but are less common than in subunit IVa. Trace fossils of root structures are abundant throughout this subunit and extend into the lower subunit. At OKP3N, the upper contact of the colluvial unit exposes an undulating surface showing scouring and removal by erosion. Although absent in this section, a moderately-developed paleosol capping IVb is observed in more northerly sections OKP1N and OKP2N (Figs. 7 and 8).

Deep lake levels persisted over a considerable time period during the deposition of Subunit IVa. The 5 m of tightly compacted sediment may represent a much greater

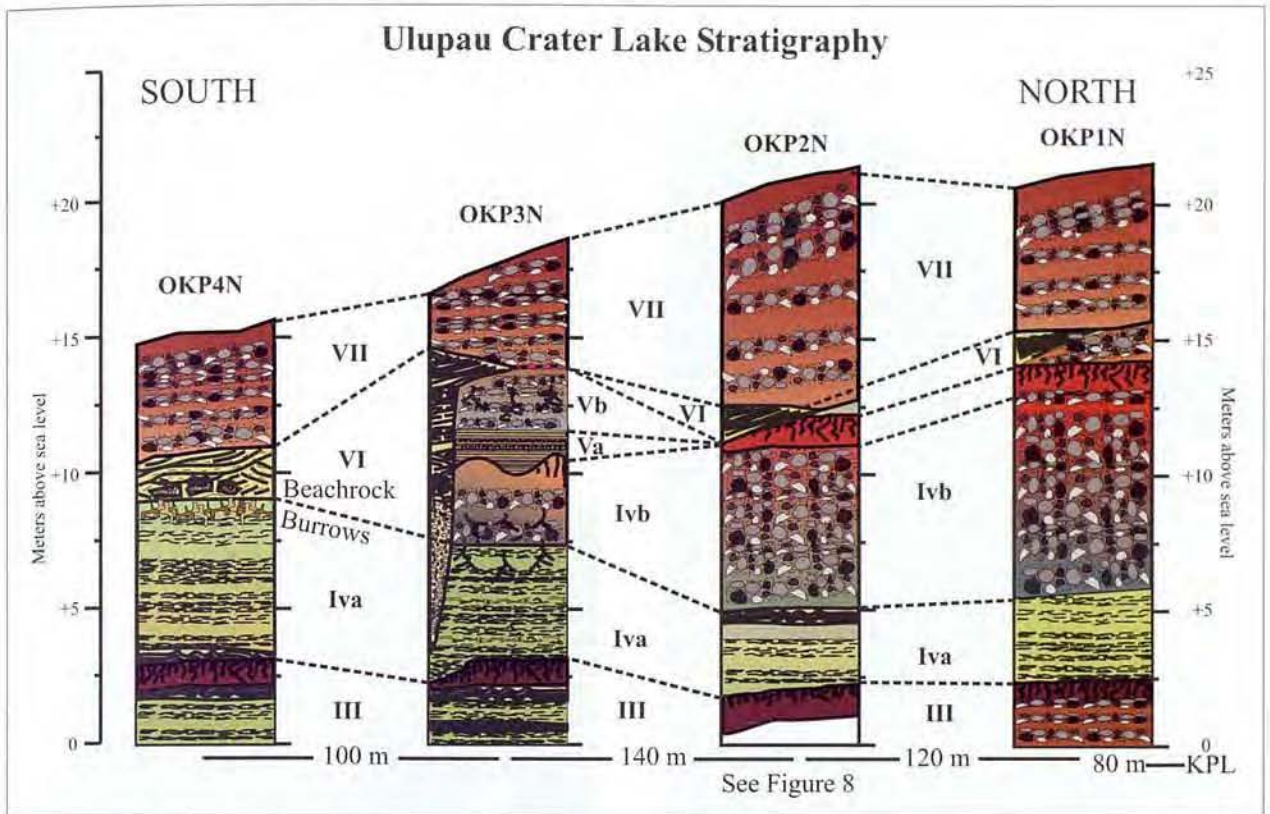


Fig. 7. Correlation of four logged stratigraphic sections in lake sediments of Ulupau Crater. The sections transit the lake exposure from north to south, representing most of the existing strata and units.

Fig. 7. Correlació de quatre seccions estratigràfiques en columna dels sediments llacunars del cràter Ulupau. Les seccions recorren l'exposició del llac de nord a sud, representant la majoria d'estrats i unitats existents.

ter original thickness (perhaps double), and thus significantly higher elevation of the lake level of perhaps between +15 to +20 m. A stratified water column and generally anoxic conditions produced a reducing environment. It is reasonable to assume that anoxia occurred at similar depths of -3 m as in the modern Wai a Pele. The area attracted abundant bird life, whose fossil remains accumulated primarily in the lake sediments in Unit IVa, and less so in the colluvium of Unit IVb. The presence of root casts indicates termination of the lake phase, growth of vegetation, and ecological transition from the high lake to dry lake and colluvial phases. Colluvial Subunit IVb represents a major depositional event within the crater walls. It is apparent that lake levels fell quickly, after which there was rapid flux of colluvial debris from the flanks, thinning near the center of the crater. According to our model, this transition occurred at the onset of a glacial period as sea level fell. Rapid drying of the lake accompanied marine regression, which lowered the level of the Ghyben-Herzberg lens, so that the crater no longer functioned as a hydrographic window.

3. *Unit V, 3rd lacustrine phase and colluvium.* Subunit Va overlies an erosional contact and is characterized by thinly-laminated silty and clayey layers averaging about 5 mm thick (Fig. 9A) and rising to about +10 to +12 m. These lake facies are present only near the center of the basin at OKP3N (Figs. 6 and 7). The laminations contain lenses and intercalations of carbonate algal structures and desiccation cracks (Figs. 9B and 9C). A sample of

the algal material has been dated by the ICPMS U/Th method (discussed below). A red oxidation stain fills an irregular and undulating zone in the upper 1 to 2 m of the unit. The laminated lake sediments make a conformable and thinly-interbedded transition to the overlying colluvial unit.

The grey colluvium of Subunit Vb is 2 to 3 m thick and gray in color. The deposits are moderately to strongly bedded and contain multiple-cm thick lenses of pebbles.

The laminations in Unit Va indicate stratified anoxic (brackish?) water ranging from dry (mudcracks) to ca. 2 m deep. Unit Va is absent from OKP1N, 2N, and 4N logs (Fig. 7), indicating that the lake was much smaller than during Unit IVa, as the basin had largely filled with sediments from previous higher highstands. The clast-supported coarser sediments would have been compacted less than the matrix-supported silts and clays of Unit IV. Because of their carbonate composition, the algal mats may have formed by the leakage of marine phreatic water through the perhaps thinning eastern crater wall. Further support of this inference comes from the reddening by oxidation of the volcanic minerals in Unit Va. This may indicate that the sediments, rich in ferric minerals, were initially deposited in a reducing lake environment (deeper water), and subsequently exposed to marine waters and occasional desiccation. This partial marine incursion by percolation or piping may have also contributed to the sustained higher pH of the groundwaters in the crater.

CRATER BREACHING AND SUBSEQUENT EROSIONAL AND DEPOSITIONAL EVENTS

Crater Breaching

1. *Premises and givens.* A high eastern rim of Ulupau Crater must have been present in order for the lake sediments to accumulate to nearly +20 m thickness. Assuming a circular or slightly oblong crater geometry, as inferred from the remaining structure (Fig. 1), and similarly shaped HVS volcanoes of Oahu, it is possible to estimate that between 300 and 500 m of horizontal erosion from the eastern flank has taken place. Holocene and recent erosion would account for only a fraction of the removal. The existing sea cliff exposes lake sediments for approximately 0.5 km along a N-S axis. Coral reef, shore and marine conglomerate of the Waimanalo Fm abut the sea cliff (Fig. 10) and armor it from erosion, particularly along the southern part of the crater. Once reef deposits are removed, however, erosion of the friable lake sediment occurs quickly, as observed along more northerly reaches of the coastline.

2. *Interpretation of timing of crater breaching events.* At some point in Oahu's history, an enormous landslide ripped a major portion of the island away from the northeastern coast, leaving a dramatic headwall, the Nuuanu Pali. The "Nuuanu Debris Avalanche" was one of the most massive of the submarine slides described in the Hawaiian Islands by Moore *et al.* (1989), covering 23,000 km², and extending about 230 km from the headwall on Oahu across the Hawaiian Deep (depth 4600 m) and up the opposite rising flank. Those authors propose that the largest and most extended slides occurred during "the final stages of the shield building cycle when volcanic production peaks" (Moore *et al.*, 1989, p. 17,482), probably around 2.5 My ago. Thus, the entire HVS, coastal plain development, and carbonate platform construction, and breaching of Ulupau Crater all most likely occurred subsequent to the Nuuanu Debris Avalanche.

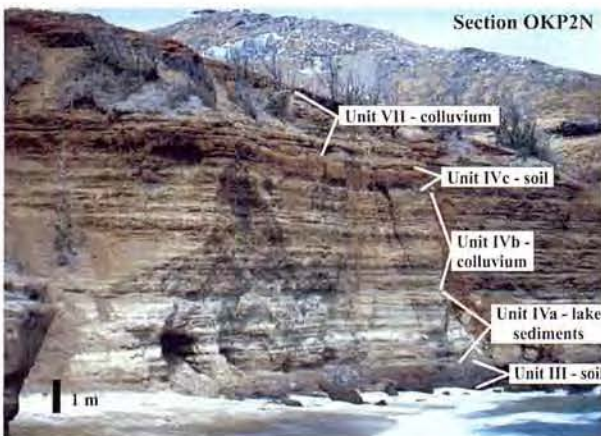


Fig. 8. Photograph of OKP2N (noted as "2N" on Fig. 1) showing a full cycle of deposition (paleosol → lake sediments → colluvium → paleosol).

Fig. 8. Fotografia de OKP2N (indicada com a "2N" a la Fig. 1) que mostra un cicle complet de deposició (paleosòl → sediments lacustres → col·luvium → paleosòl).

The modern shelf, about 6 km wide (to 100 m depth) east of Ulupau Crater, is intact and does not indicate any bathymetric evidence of mass wasting. Relatively shallow platform and islands surround Ulupau Head on all sides (Fig. 1), additional evidence that no significant mass wasting events have affected the peninsula during the latter part of the Quaternary. Inspection of USGS Pacific Seafloor Mapping shaded relief and backscatter images of the ocean floor east of Ulupau Head (<http://wrgis.wr.usgs.gov/dds/dds-55/pacmaps/ou>) provides further confirmation of this view.

Removal of one-third to one-half of the crater diameter (300 - 500 m) of Ulupau Crater and exposure of lacustrine beds must have occurred prior to the deposi-

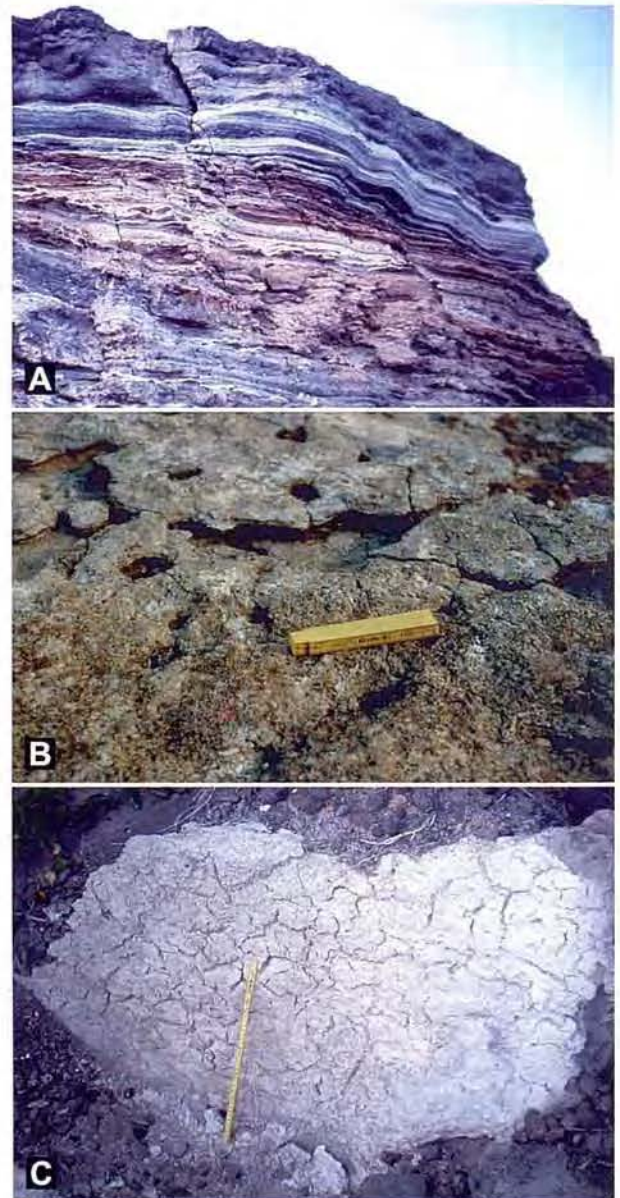


Fig. 9. Photographs showing detail of Unit V. A. Laminated lake sediments and colluvium. B. Carbonate algal mat (dated at 240 ± 10 ka by U/Th). C. Mud cracks in algal mat in Unit V.

Fig. 9. Fotografies que mostren detalls de la Unitat V. A. Sediments lacustres laminats i col·luvium. B. Tapis algal carbonatats (datats a 240 ± 10 ka by U/Th). C. Crrulls de fang a el tapis algal a la Unitat V.

tion of the Waimanalo Fm. Wave erosion would require a long period of time to accomplish this work, while large-scale mass wasting could have effectively removed the material very quickly. Opportunities for removal by marine erosion occurred during highstands post-dating the formation of the crater 0.3 to 0.5 My and preceding MIS 5e. The most likely highstands involved in erosion of the Ulupau crater wall would thus have been MIS 11, 9, and 7. Removal of the eastern rim and lake sediments by marine erosion may have taken more than one interglacial (>100 ka). Within the lake sequence, the removal of the eastern rim is represented by a major angular unconformity between Units III, IV and V, and Unit VI the Waimanalo Fm (Figs. 4B and 10). Vertical reef growth and accumulation of sediments built a wall plastered against sub-horizontal lake beds (Fig. 8).

Unit VI, Waimanalo Erosion and Marine Highstand Cycle

A coral reef (Waimanalo Fm) and cemented sediments abut directly against a sea cliff eroded in Ulupau lake sediments (Units IV and V) in the southern part of the study area (Fig. 10). Unit VI consists of laterally discontinuous lenticular geometry of coral reef, coral rubble, volcanic conglomerate facies with some fossil mollusk and calcareous algae, marine sands, and minor eolian deposits. Our new MC-ICPMS U/Th ages on corals from this unit range in age from 131 to 115 ka (Table 3), largely in agreement with previous U-series determinations (Szabo *et al.*, 1994; Muhs & Szabo, 1994). Coral reefs rise to +5 and +8.5 m, while marine subtidal sands are present to +11 m (Hearty *et al.*, 2000). The Waimanalo deposits are succeeded by Unit VII. Remnants of the bioconstructional coral reef and shore deposits still remain along the sea cliff, indicating that Holocene events have removed only a small fraction of the lake deposits over the past 6,000 to 7,000 years (see below). A flat shelf surface at less than 6 m below sea level c. 200 to 300 m wide (USGS 1:24,000 topographic maps) east of Ulupau Crater, marks the extent of what is probably the cumulative erosion from both MIS 5 and 1.

Unit VII – Final Colluvial/Alluvial Phase

Subunit VIIa is an accumulation of more than 10 m (over 20 m in places) of interbedded fine to coarse colluvium. Throughout the crater, these deposits are oxidized to a reddish brown color (Fig. 4B). The red colluvium slopes at low angles <10° to the east in amphitheater form within the existing half of the Ulupau Crater. This unit buries all previous sediments except in the modern sea cliff. This final phase of sedimentation occurred after the Waimanalo highstand, and may be active up to the present. Multiple weak soils (Subunit VIIb) are interbedded within the unit, with greater soil development near the top of the unit.

It appears that this major colluvial event was initiated soon after the Waimanalo highstand, and continued throughout the following glacial lowstands (MIS 4 to 2) and into the Holocene. Most of this sediment flux could probably be attributed to ecological disturbance in the transition between wetter interglacial vegetation and more xeric types during glacial periods (Hotchkiss *et al.*, 2000). The degree of influence of anthropogenic changes

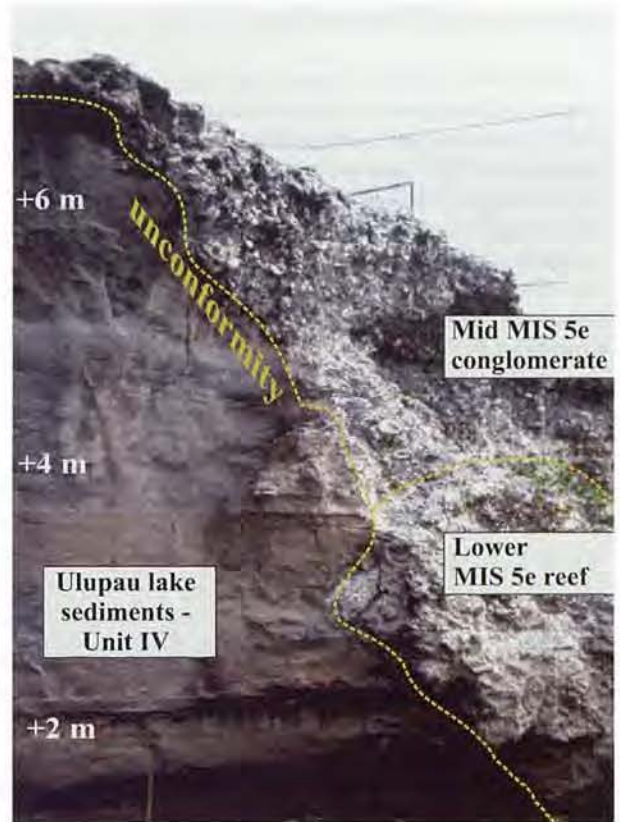


Fig. 10. Detailed stratigraphic log of the Waimanalo Fm plastered against the Ulupau Crater lake sediments at OKP2 (section 2 in Fig. 1). The section shows lake sediments adjacent to a near vertical plaster of reef/conglomerate-reef of Waimanalo age (134 to 118 ky). Between 300 and 500 m of crater wall and lake sediments were removed from the eastern margin of Ulupau Crater *previous to* initiation of deposition of Waimanalo deposits.

Fig. 10. Columna estratigràfica detallada de la Formació Waimanalo enfront dels sediments llacunars del cràter Ulupau a OKP2 (secció 2 a la Fig. 1). La secció mostra els sediments llacunars adjacents a un pegat quasi vertical de escull/conglomerat-escull d'edat Waimanalo (134 a 118 ka). Entre 300 i 500 m de la paret del cràter i sediments llacunars varen ser tretes de la vorera oriental del cràter Ulupau abans de començar la deposició dels dipòsits Waimanalo.

in plant cover on the sediment flux is unknown, but by analogy with other Hawaiian basins, this could have been a significant source of colluvial flux (Burney *et al.*, 2001; Burney, 2002).

APPARENT AGE OF ULUPAU LAKE SEDIMENTS, CARBONATES, AND FOSSILS

The isotope curve from ODP Site 677 (Shackleton *et al.*, 1990) provides a template and time frame for the geological events and evolution of Ulupau Crater over the past half-million years (Fig. 11). The curve also serves as a *relative* sea level indicator based largely on ice volume changes. *Measured* sea-level highstands from stable carbonate platforms (Hearty & Kaufman, 2000) are compared to those of Oahu (Hearty *et al.*, 2000; Hearty, 2002b) over the past half-million years, the interval when high lake stands occurred (Table 1).

Age Sequence of Ulupau Crater

No direct dating of Ulupau volcanics has been successful (Gramlich *et al.*, 1971; Lanphere & Dalrymple, 1980). Based on the extent of weathering and erosion, Winchell (1947) concluded that Ulupau Crater and neighboring Pu'u Hawaiiola were among the oldest of the HVS, perhaps approaching 0.6 My. Amino acid racemization (AAR) analyses of whole-rock carbonate sand from the YPL and oysters from the KPL indicate ages between 0.3 and 0.6 My (Table 2). The equilibrium ratio from the KPL ($A/I = 1.30 \pm 0.03$) is beyond the range of age calculation by apparent parabolic kinetics (Mitterer & Kriaušakul, 1989). It thus constrains a *minimum* age of 0.4 to 0.6 My. The estimated age of the whole-rock sample from the YPL, determined from $A/I = 0.80 \pm 0.09$, is between 0.3 and 0.5 My. In summary, the AAR data from the KPL and YPL, which are stratigraphically older than lake sediments of Units III to V, give a general estimate of lake sedimentation beginning somewhere between 0.3 and 0.5 My. These independent age estimates fit well with the succession of events interpreted from the physical geology of Ulupau crater.

Based on the complexity and time-requirements for formation and development of the units (particularly deep paleosols), the lack of "perched" low-elevation lakes in Hawaii, and probable modulation by sea-level highstands, we suggest that lake cycles are tied to 100 ka sea-level cycles (Fig. 11). The dense and well-developed capping paleosol and complex stratigraphy of Unit III supports a significant length of time of development, far more than could be accomplished during shorter obliquity or precession cycles (20-40 ka duration). Likewise, the >5 m accumulation of fine silts in Sub-unit IVa, source of the greatest concentration of bird fossils, alone must encompass a significant interval of time. We suggest up to 25 ka for this unit to form.

Given that the 125 ka Waimanalo reef abuts a cliff of lake sediments located midway across the lake basin (Fig.10), and the estimated maximum age of the crater,

all of the lake sediments must be of middle Pleistocene age. Based on the complex stratigraphy, including three lake phases, three colluvial phases, and well-developed paleosols between, the duration of the entire lake sequence must have encompassed multiple sea-level cycles.

MIS 7 was a less influential highstand on the lake evolution as growth-position corals from the west coast of Oahu, dated at ca. 225 ka, indicate maximum MIS 7 sea level was below -10 m (Sherman *et al.*, 1999), too low to support a groundwater lake in the crater. Tectonic uplift was not factored into the MIS 7 datum, implying that original sea level may have been even lower. Indeed, considering that the marine platform created by marine erosion is less than 6 m below current sea level, we can infer that the bulk of erosion of the crater must have occurred before MIS 7.

We have obtained a U/Th age of 240 ± 10 ka on algal carbonate material from Unit V. Because the sample contained a small fraction of detrital material, we can consider the age only an estimate (Table 3). Despite this, it appears to fit reasonably well with other data. Most importantly, the date indicates the lake represented by Unit V was intact up until the upper-middle Pleistocene.

If the 240 ka age were taken at face value, it would indicate the lower part of Unit V was formed at the onset of MIS 7. However, because MIS 7 sea level probably never attained an elevation greater than -10 m in Oahu (Sherman *et al.*, 1999), it is highly unlikely that the algal mat formed during this particular highstand. There are no known tectonic processes on the island that can raise the highstand deposits 20 m in 200 ka, and a younger age is not an option for reasons discussed below. However, given an uplift rate of 3 m/100 ka, generally accepted for Oahu (Muhs & Szabo, 1994; Hearty *et al.*, 2000), combined with an approximate +3 m sea level during MIS 9, relative sea level would have been about +12 m. This level for the algal mat in Unit V would be in better agreement with a late MIS 9 correlation (Hearty & Kaufman, 2000). If this is the case, then the older and thicker lake deposits

Isotope Stage	Oahu, HI (Stearns, 1978; Hearty <i>et al.</i> , 2000; Hearty, 2002a)	Bahamas (Hearty & Kaufman, 2000)	Bermuda (Hearty, 2002b; Hearty <i>et al.</i> 1999)	Uplift Rate (m/ky)
Late 5e	+9 to +11 m (Waimanalo)	+6 to 8.5 m	+6 to +9.2 m	0.025 ± 0.005
Mid 5e	+5.5 m (Waimanalo)	+3.0 m	+2.5 m	0.024 ± 0.003
7?	-10 to -20 (Olomana?)	0 to +1 m	<0m	Insufficient data
9?	+12 m (Waialae?)	+3	Above present	Insufficient data
Late 11	+28 m (Kaena)	+21 m	+20 m	0.020 ± 0.003
Mid 11	+13.5 m (Kaena)	+7.5 m	+5 to +7m	0.015 ± 0.001
Early 11	+5 to +6 m (Kaena)	0 to +1.5 m	+1m	0.012 ± 0.005

Table 1. Comparison of sea-level indicators between Oahu, Bermuda, and the Bahamas used to estimate uplift rates since MIS11. These data indicate that a fairly consistent or slightly increasing uplift rate averaging 0.020 m/ky has affected Oahu over the past 410 ky. Uplift rates calculated in previous studies (Muhs & Szabo, 1994; Grigg & Jones, 1997) were greater by a factor of 2 to 3, attributing all 30 m elevation of the Kaena deposits to uplift, rather than only 8 to 10 m, given a global highstand of sea level at 400 ky at +20 m.

Taula 1. Comparació dels indicadors de nivell marí entre Oahu, Bermuda i les Bahames emprats per estimar les taxes d'aixecament des de l'estadi MIS11. Aquestes dades indiquen que una taxa d'aixecament bastant consistent o lleugerament incrementada d'un promig de 0,020 mlka va afectar Oahu durant els darrers 410 ka. Les taxes d'aixecament calculades a estudis anteriors (Muhs & Szabo, 1994; Grigg & Jones, 1997) eren més grans per un factor d'entre 2 i 3, i atribueixen totes una elevació del 30 m al dipòsit de Kaena, enlloc que només 8 a 10 m, donat la situació més alta del nivell marí, a +20m, a nivell global fa 400 ka.

of Unit IV may either have formed during early MIS 9 (c. 320 ka), or more likely during the previous MIS 11 (c. 400 ka). The MIS 11 highstand is known to have risen to 18–20 m on stable coastlines (Hearty *et al.*, 1999), and is found up to 30 m during the Kaena Highstand of Oahu at 400 ka (Hearty, 2002a) because of a 3 m/100 ka uplift rate. No traces of the Kaena Highstand are evident on the flanks of Ulupau Head, although preservation of such geomorphology would be unlikely in the friable and unstable volcano-clastic materials of the crater. We conclude therefore that the evolution of lakes in Ulupau Crater was in synchrony with, and modulated by 100 ka sea-level oscillations (Fig. 12) from MIS 13 onward.

AVIFAUNA OF ULUPAU CRATER LAKE.

Twenty-six species of birds were identified in a preliminary study of approximately 750 bones from Unit IV (James, 1987). Subsequent collecting has increased the number of fossil bones from the site considerably, although further morphological and systematic studies of the collection have not been completed. The fossil collections from Ulupau Head are accessioned primarily at the B. P. Bishop Museum, Honolulu, with a smaller number of bones accessioned at the National Museum of Natural History, Smithsonian Institution, Washington, DC.

Lab #	Sample type	Sample #	Run 1	Run 2	Average	$\pm 1\sigma$	N
Mokapu – Waimanalo Formation (c. 125 ka) – <i>Ostrea</i>							
2507A	<i>Ostrea</i>	OKP2a	0.980	0.940	0.960	0.028	2
2507B	<i>Ostrea</i>	OKP2a	0.716	0.719	0.718	0.002	2
Mean: 0.84 ± 0.17 (n = 4)							
Ki'i Point Limestone (KPL) – age unknown – <i>Ostrea</i>							
2506A	<i>Ostrea</i>	OKP1a	1.279		1.279		1
2506B	<i>Ostrea</i>	OKP1b	1.313	1.329	1.321	0.011	2
Mean: 1.30 ± 0.03 (n = 3)							
Mokapu – Waimanalo Formation (c. 125 ka) – Whole-rock							
2511A	W-R	OKP2a	0.550	0.532	0.541	0.013	2
2511B	W-R	OKP2a	0.532		0.532		1
Mean: 0.54 ± 0.01 (n = 3)							
Yellow Point Limestone (YPL) – age unknown – Whole-rock							
4267A	W-R	OKP3aa	0.722	0.751	0.737	0.021	2
4267B	W-R	OKP3aa	0.858	0.868	0.863	0.007	2
Mean: 0.80 ± 0.09 (n = 4)							

Table 2. Amino acid ratios (D-alloisoleucine/L-isoleucine or A/I) from oyster and whole-rock samples from last interglacial Waimanalo, Ki'i Point and Yellow Point Limestone units. Mollusks (*Ostrea* in this case) epimerize at substantially faster rates compared to whole-rock samples (Hearty *et al.*, 1992; Hearty, 2002b), as indicated from the equal-age samples from the Waimanalo Formation. Age estimates are based on "apparent parabolic kinetics" (Mitterer & Kriausakul, 1989).

Taula 2. Proporcions d'aminoàcids (D-alloisoleucina / L-isoleucina o A/I) de mostres d'ostres i de roques senceres del darrer interglacial, Ki'i Point and Yellow Point Limestone. Els mol·luscs (*Ostrea* en aquest cas) epimeritzen en taxes substancialment més altes, en comparació a les mostres de roques completes (Hearty *et al.*, 1992; Hearty, 2002b), com s'indica a partir de mostres d'edat idèntica de la Formació Waimanalo. Les estimes d'edat estan basades en la "cinètica parabòlica aparent" (Mitterer & Kriausakul, 1989).

Sample number	Material	U ppm	^{230}Th ppt	$\delta^{234}\text{U}$	$\delta^{234}\text{U}$	$^{230}\text{Th}/^{238}\text{U}$	$^{230}\text{Th}/^{238}\text{U}$	$^{230}\text{Th}/^{232}\text{Th}$	Age (ka)	$\pm 1\sigma$	Initial	$\delta^{234}\text{U}$
OHE 1c	Coral	2.506	30.74	114.85	0.71	0.7547	0.0022	20917	119.4	0.6	161.1	0.93
OHE 2a 1	Coral	2.275	27.38	115.21	1.55	0.7403	0.0042	38643	115.4	1.2	159.8	2.01
OHE 2a 2	Coral	2.204	26.82	111.94	1.23	0.7487	0.0031	135934	118.3	0.9	156.6	1.59
OKP 2a	Coral	2.216	28.78	119.63	0.87	0.7987	0.0012	53242	131.2	0.4	173.6	1.16
OKP 2c	Coral	2.449	32.13	111.5	0.81	0.791	0.0013	273	130.9	0.5	161.6	1.07
OKP 3c	Coral	2.482	31.83	108.39	0.79	0.7887	0.0015	18865	131.0	0.5	157.1	1.05
OKP3n Unit V	Algal mat	1.694		28.210	2.140	0.922	0.016	4	240	15	55.7	4.4

Table 3. New U/Th ages of corals and algal limestone on Oahu¹. All corals from OHE and OKP are from Unit VI, the last interglacial Waimanalo Formation. The algal mat is from Unit V.

Taula 3. Noves edats U/Th de coralls i calcàries algals a Oahu¹. Tots els coralls de OHE i OKP són de la Unitat VI, la Formació Waimanalo del darrer interglacial. El tapís algal és de la Unitat V.

¹ Analyses were performed on a multi-collector, inductively coupled plasma mass spectrometer (MC-ICPMS) at The Australian National University (Canberra, ACT).

Taxon	Habitat characteristics
SEABIRDS	
<i>Pterodroma</i> cf. <i>hypoleuca</i>	Nests near the sea in burrows that it excavates in sandy or other soft substrates (Seto & O'Daniel, 1999).
<i>Puffinus newelli</i>	Nests in excavated burrows or crevices usually at higher elevations. Recorded between 160 and 1200 m asl. in open canopy forest with dense understory (Ainley <i>et al.</i> , 1997). Fossils of <i>P. newelli</i> are rare in lowland sites (Olson & James, 1982), suggesting that the species has always preferred to nest in upland forest.
Procellariidae, undetermined large species	Unknown.
<i>Nesofregata fuliginosa</i>	Nests in burrows that it excavates in sandy substrates with low vegetation, or in natural crevices in rocky substrates (BirdLife International, 2000).
<i>Fregata</i> cf. <i>minor</i>	<i>Fregata minor</i> nests in colonies on remote islands, usually near shore but sometimes up to 8 km inland (Metz & Schreiber, 2002). Nests are preferably placed in the tops of bushes such as beach naupaka (<i>Scaevola</i>). A few pairs currently nest on Moku Manu Island near Ulupau Head.
<i>Sula</i> sp.	Species undetermined but possibly conspecific with <i>Sula sula</i> , which currently has a breeding colony on the crater rim of Ulupau Head. <i>Sula sula</i> places nests in shrubs or trees.
SHOREBIRDS	
<i>Pluvialis</i> cf. <i>fulva</i>	In the Hawaiian Islands, winters in open habitats of many varieties, such as grasslands, mudflats, beaches, salt marshes, and small clearings in forest, and is found from seashore to at least 2,500 m asl (Johnson & Connors, 1996).
<i>Numenius tahitiensis</i>	During winter occurs on Pacific islands in a variety of habitats, both near shore and inland, including wetlands, salt pans, open grassy areas, vegetated dunes, and coconut groves (Marks <i>et al.</i> , 2002). Feeds on marine and terrestrial invertebrates, small vertebrates, seabird eggs, carrion, and fruits.
WATERBIRDS	
<i>Branta</i> sp.	The bones from Ulupau Head are similar in morphology to those of <i>Branta canadensis</i> , which winters in North America in coastal wetlands, wet grasslands, freshwater marshes, lakes, rivers, and agricultural fields (Mobray <i>et al.</i> , 2002). <i>Branta canadensis</i> feeds on aquatic plants, grazes on grasses and other terrestrial plants, and takes seeds and berries.
<i>Anas</i> aff. <i>uyvilliana</i> / <i>laysanensis</i>	<i>Anas uyvilliana</i> prefers freshwater habitat, including coastal and ephemeral wetlands, upland rivers, streams, bogs, and pools at the base of waterfalls (Engilis <i>et al.</i> , 2002). Its upland haunts can be heavily forested. It feeds mainly on aquatic invertebrates and plants. <i>Anas laysanensis</i> currently inhabits Laysan Atoll, where brine shrimp and brine flies in a hypersaline lake are important foods (Moulton & Marshall, 1996). <i>Anas laysanensis</i> is not strictly a wetland bird, as it formerly occurred in upland forest in the main Hawaiian islands (Cooper <i>et al.</i> , 1996), where it may have fed on terrestrial invertebrates such as snails and arthropods.
<i>Fulica</i> sp.	The coot from Ulupau Head is probably a distinct species from <i>Fulica americana</i> (James, 1987). To breed, <i>Fulica americana</i> requires freshwater wetlands with heavy emergent vegetation at least partly surrounded by open, standing water. When not breeding coots also make use of coastal brackish and marine wetlands. <i>Fulica americana</i> feeds primarily on aquatic vegetation, and also takes aquatic invertebrates and vertebrates (Brisbin & Mowbray, 2002).
TERRESTRIAL BIRDS	
† <i>Thambetochea xanion</i>	Bones of the species are common in Holocene sites in karstic pits and caves on the lowland `Ewa Plain of Oahu (Olson & James, 1991). Fossils of its sister species, <i>Thambetochea chauliodous</i> , of Maui, Molokai and Lanai, occur in a wide variety of terrestrial habitats from seaside dunes to upland forest (James & Burney, 1997).
†? <i>Buteo</i> sp.	The hawk from Ulupau Head is similar in morphology to the extant <i>Buteo solitarius</i> though somewhat larger. <i>Buteo solitarius</i> occurs in a variety of upland habitats from pastures to tall forest on the island of Hawaii, where it feeds on rodents, birds, and invertebrates (Clarkson & Laniawe, 2000).
† <i>Porzana</i> spp., two species of flightless rails	Flightless insular rails may occur in wetlands but are also often found in broad range of terrestrial habitats. Of the two Hawaiian species of flightless <i>Porzana</i> that survived into historical times, one inhabited Laysan Atoll where it fed on insects, seabird eggs and carrion, and the other inhabited Hawaii Island, where it reportedly was found in open and bushy habitat below the closed canopy forest belt (Olson, 1999b).
† <i>Grallistrix orion</i>	Owl pellet accumulations in Holocene fossil sites indicate that members of this endemic genus of owls specialized in eating forest birds and flightless rails (Olson & James, 1982, 1991).
† <i>Corvus</i> sp.	Bones of <i>Corvus</i> are common in Holocene sites in the `Ewa Plain of Oahu. On Hawaii Island, the only surviving species of Hawaiian <i>Corvus</i> lives in native dry to wet forest, where fleshy fruits are important in its diet, and it also takes seeds, nectar and flowers, arthropods, and eggs and nestlings of smaller forest birds (Banko <i>et al.</i> , 2002).
<i>Chasiempis sandwichensis</i>	Most abundant in tall, mesic forest with well developed understory; absent from dry scrubland (Vanderwerf, 1998). Occurs as a fossil in Holocene sites on the lowland `Ewa Plain of Oahu (Olson & James, 1982). Feeds on arthropods.
† <i>Chaetoptila</i> sp.	Fossils of the species are abundant in the Holocene sites on the `Ewa Plain (Olson & James, 1982). The species was probably primarily nectarivorous.
† <i>Rhodacanthis</i> sp.	This represents an extinct species of a koa finch (James & Olson, 2005). The two species of koa-finches (<i>Rhodacanthis</i>) that survived into historical times on the island of Hawaii fed mainly on pods and seeds of the koa tree <i>Acacia koa</i> (Olson, 1999a).
† <i>Chloridops wahi</i>	The only species in the genus of koa finches that survived into historical times, <i>C. kona</i> of the island of Hawaii, fed mainly on seeds of the naio tree <i>Myoporum sandwicense</i> (Olson, 1999a).
† <i>Chloridops regiskongi</i>	Fossils of the species are fairly common in Holocene sites on the `Ewa Plain of Oahu. The large and robust finch-like bill of this species indicates that it was able to crack hard seeds (James & Olson, 1991).
† <i>Akialoa</i> sp.	Species undetermined, but possibly <i>Akialoa ellisianus</i> , which survived into historical times on Oahu. The akialoa that were observed in life inhabited mesic to wet forest, although the distribution of fossils suggests that lowland shrublands were also used (Lepson & Johnston, 2000). Fed on beetle larvae and other arthropods and on nectar, primarily by probing with the long, decurved bill.
† <i>Aidemia</i> sp.	Holocene fossils of <i>Aidemia</i> occur in sites in the coastal lowlands of Oahu and Molokai and on the leeward slope of East Maui (James & Olson, 1991). Based on bill morphology the species is thought to have been insectivorous.
<i>Paroreomyza maculata</i>	Currently occurs in mesic to wet forest and shrubland (Baker & Baker, 2000). Holocene fossils of the species occur on the dry leeward `Ewa Plain of Oahu (Olson & James, 1982). The species feeds on invertebrates, primarily by probing in bark and dead wood and gleaning from leaves.
<i>Loxops [virens] chloris</i>	Currently occurs in dry and wet forest and more rarely in shrubland (Lindsey <i>et al.</i> , 1998). Feeds omnivorously on arthropods, nectar, and fruit. Fossils occur in Holocene sites on the lowland `Ewa Plain of Oahu.

Table 4. Habitats used by the birds in the Ulupau Head fossil assemblage (James, 1987). Daggers identify extinct species that have never been observed in life in historical times and whose habitat preferences must be inferred by analogy.

Taula 4. Habitats emprats pels ocells del conjunt fòssil Ulupau Head (James, 1987). Les creus identifiquen les espècies extingides que mai s'han observat en vida en temps històrics, i les seves preferències d'hàbitat s'han hagut d'inferir a partir d'analogies.

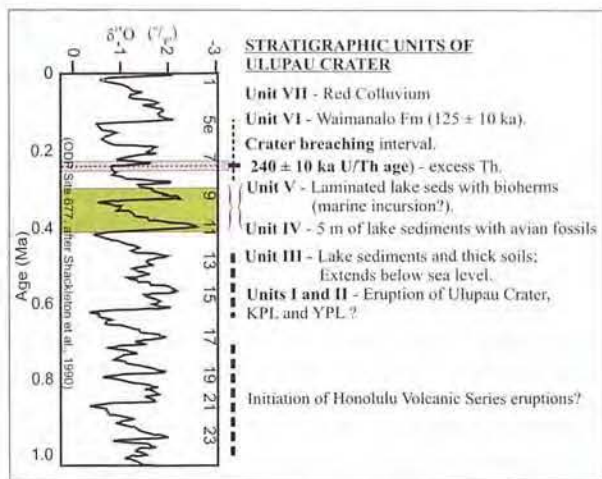


Fig. 11. Isotope curve from ODP 677 (Shackleton *et al.*, 1990) showing climate cycles and relative ice volume changes over the past million years. Events at Ulupau Crater are noted on the right of the graph.

Fig. 11. Corba isotòpica de ODP 677 (Shackleton *et al.*, 1990) que mostra els cicles climàtics i els canvis relatius del volum de gel al llarg dels darrers milions d'anys. A la dreta de la gràfica s'indiquen els esdeveniments al cràter Ulupau.

In the present paper, we assess the paleoecological setting of Unit IV by evaluating the habitat requirements of the 26 avian taxa identified by James (1987). The habitat requirements and diets of the avian taxa are summarized in Table 4, in which the taxonomic nomenclature has been updated to reflect the names for Hawaiian fossil birds introduced by Olson & James (1991) and James & Olson (1991). In the light of findings by Cooper *et al.* (1996), the bones formerly referred to *Anas cf. wyvilliana* are now identified as belonging to *Anas laysanensis* or *A. wyvilliana*. A species of goose previously listed as *Anserinae sp.* is now assigned to *Branta sp.* In the revised faunal list we also grant full species status to the Pacific Golden Plover (*Pluvialis dominica* emended to *P. fulva*, see Connors *et al.*, 1993), and to Newell's Shearwater (*Puffinus puffinus newelli* emended to *P. newelli*).

Bones of seabirds are uncommon in the deposit in proportion to those of waterbirds and terrestrial species, suggesting that seabird breeding colonies were not situated near the lake shore. However, it is likely that the lake was not far from the sea, because the seabirds in the assemblage include taxa that rarely stray inland (*Sula sp.*, *Fregata minor*). *Sula sula* and *Fregata minor* breed near the site at the present time. If we assume these species were nesting nearby when the fossils were accumulating, we can infer that the surrounding habitat probably included their preferred nesting habitat of shrubland or low trees. The two species of shorebirds in the deposit still winter in the Hawaiian Islands, where they are found along the coast and also inland in open habitats including various types of wetlands.

A small duck that is similar in morphology to the two extant species of endemic Hawaiian ducks is the most abundant species in the Ulupau Head assemblage. Bones of the duck, a goose *Branta sp.*, and a coot *Fulica sp.*, probably represent birds that fed or rested in the lake. Modern taxa that closely resemble the fossils are *Fulica americana* and *Branta canadensis*, which may feed in

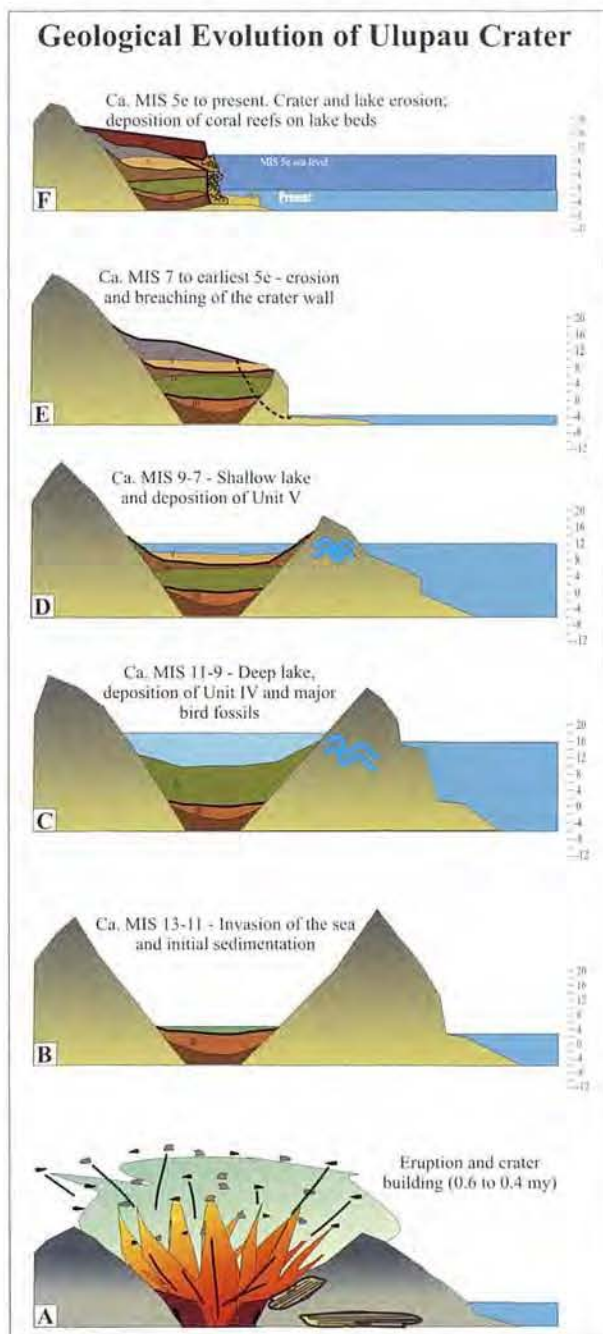


Fig. 12. Schematic evolution of Ulupau Crater encompassing eruption, lake phases, and breaching over the past several hundred thousand years.

Fig. 12. Evolució esquemàtica del cràter Ulupau, que inclou l'erupció, les fases llacunars, i l'obertura d'una bretxa al llarg dels darrers centenars de milers d'anys.

water or on adjacent dry land. Modern populations of *Anas wyvilliana* and *A. laysanensis* feed primarily on aquatic invertebrates, especially insects, and secondarily on aquatic plants. The numerical dominance of birds that feed in freshwater habitats in the faunal assemblage supports the inference that a lake and perhaps at times a shallow wetland existed when Unit IV was accumulating. However, waterbirds have a tendency to expand their ranges into terrestrial habitats after colonizing islands that lack native mammalian ground-dwelling predators.

Holocene fossils of *A. laysanensis* occur in upland lava tubes on the island of Hawaii, far from coastal wetlands, for example (Cooper *et al.*, 1996). For this reason, we rely on the abundance of birds that prefer to feed in lakes, rather than their mere presence, to support our paleoecological interpretation of Unit IV.

A species of hawk *Buteo* is common in the assemblage (Olson & James, 1997). By analogy with the extant species of *Buteo* from the island of Hawaii, the Pleistocene hawk of Oahu may have occurred in a wide range of terrestrial habitats from grassland to canopy forest. An abundance of hawk bones appears to be a taphonomic signature of lake deposits in the Hawaiian Islands. The only other avian fossil assemblage in the islands with abundant hawk bones is from the lake deposit in Makauwahi Cave on Kauai (Burney *et al.*, 2001). Both the hawk and an extinct bird-eating owl, *Grallistrix orion*, probably contributed to the fossil assemblage by depositing prey remains of smaller forest birds and flightless rails.

The ground-dwelling terrestrial birds in the Ulupau Head assemblage include two species of flightless rails *Porzana* spp., and a flightless goose-like duck *Thambetochen xanion*. If *T. xanion* were similar in habit to *Thambetochen chauliodous*, a very similar species known from the islands of Molokai, Maui and Lanai, then it was a widely distributed browsing herbivore that fed on broadleaf understory vegetation (James & Burney, 1997). The ground-dwelling birds in the assemblage, and likewise the predatory species, are not particularly helpful for characterizing the plant communities near the site, because they tend to make use of a broad range of habitats. Although avian faunal assemblages are useful for paleoenvironmental reconstructions on continents (Olson & Rasmussen, 1986; Behrensmeyer *et al.*, 2003), the tendency of endemic island birds to have broad habitat tolerances may reduce their informative value for ecological purposes.

Five of the small forest birds in the assemblage belong to the insectivore or nectarivore/insectivore feeding guilds. The presence of this suite of birds suggests that the habitat surrounding the lake included forest or at least shrubland with nectar-producing plants, and habitat for insects. Some of the insectivorous birds in the assemblage forage by probing in bark, plant bracts, and epiphytes (*Akialoa* sp., *Paroreomyza*). Crow bones in the deposit may indicate that plants with fleshy fruits grew in the area, considering that fruit is an important part of the diet of the extant *Corvus hawaiiensis* on the island of Hawaii. Finally, the three species of finches in the assemblage indicate that plants with hard seeds grew in the area. The koa-finch (*Rhodacanthis* sp.) may have been feeding on koa pods, or perhaps on pods of kanaloa (*Kanaloa kahooolawensis*), a leguminous shrub that no longer occurs on Oahu but is abundant in the Holocene lowland pollen record of the island (Athens, 1997). The two species of *Chloridops* in the deposit are finches with very robust bills, suggesting that other trees or shrubs with hard yet nutritious seeds were present near the lake.

In one respect the vertebrate assemblage from Unit IV is distinctly different from the only other vertebrate assemblage from a lake deposit in the Hawaiian Islands, that from the central sinkhole of Makauwahi Cave on Kauai (Burney *et al.*, 2001). Fish bones are abundant in

the Makauwahi deposit, whereas they are all but absent from the lacustrine sediments at Ulupau Head, indicating that fish failed to colonize the Ulupau lakes. Marine and freshwater shells are also absent, or nearly so, although one worn and fragmentary bone of a marine mammal was found (James, 1987). The virtual absence of marine shell supports the interpretation that the lake of Unit IVa had no surface connection to the ocean, and was protected from overwash by either a high crater wall or a more distant shoreline.

In summary, the vertebrate assemblage provides support for interpreting Unit IV and as lake and wetland sediments, particularly because waterbirds and hawks are common. The seabird bones in the lake deposit are suggestive that breeding colonies were present although probably not adjacent to the lake. From the species of seabirds represented we can infer that the site was not far from the ocean and that scrublands or low trees were probably nearby. We cannot infer that open habitat such as grassland or herbland was present, because the birds in the deposit that favor such areas can also be expected to occur near lakes and other wetlands and along shorelines. The forest birds in the deposit indicate that the local plants provided nectar, seeds, and probably fleshy fruits, as well as habitat for bark-dwelling insects. A leguminous tree or shrub, either koa or kanaloa, was probably present. Ulupau Head most likely supported mixed forest and perhaps shrublands surrounding a lake when Unit IV was deposited.

The Ulupau Head tuff cone lies on the windward side of Oahu, where it currently receives enough rainfall to support mesic lowland forest (c. 900 cm per yr). Weakening of the trade winds during glacial periods may have reduced precipitation at the site (Hotchkiss & Juvik, 1999; Hotchkiss *et al.*, 2000), so that forest and shrubland might have been replaced with dry grassland or herbaceous groundcover, which could not have sustained the forest birds present in the assemblage. The paleoecological evidence from the avian assemblage is thus consistent with our sedimentological arguments in favor of interglacial timing of high lake stands, although it is by no means decisive.

SUMMARY OF EVOLUTION OF ULUPAU CRATER AND ITS FOSSIL AVIFAUNA

1. The extensive exposures of lake sediments, colluvium, and paleosols in Ulupau Crater allow the interpretation and reconstruction of paleoenvironments in the basin over several hundred thousand years. The deposits show cyclicity and complexity indicating a dynamic setting with periodic lakes, floods of colluvium, and intervals of ecological stability (Fig. 12) marked by thick, well-developed soils. The primary modulating agent was the rise and fall of sea level during multiple middle Pleistocene events.

2. High lake levels appear to coincide with sea-level highstands. Three major cycles of lacustrine sedimentation occurred in Ulupau Crater. The largest lake may have occupied 50-60 ha during late MIS 11 (c. 400 ka) or early

MIS 9 (c. 300 ka), but was greatly reduced as the basin had filled with sediments, and as sea-level highstands progressively lowered during MIS 9 and 7 interglacials.

3. Crater breaching occurred previous to MIS 5e as the result of progressive attack of the eastern rim by marine erosion over multiple sea-level highstands.

4. If taken at face value, the U/Th age of 240 ka would constrain the age of the three lake cycles between about 400 and 200 ka. However, if we consider the amplitude of sea-level cycles that would best correspond with a succession of high lake levels, and the optimal times of crater breaching, the "best fit" scenario equates Units IV and V with either two separate highstand episodes during MIS 11, or MIS 11 and 9, respectively. Thus, the concentration of bird fossils at the base of Unit IV would have been deposited between 400 and 300 ka.

5. The fossil bird remains from Ulupau Crater are the oldest known for the Hawaiian archipelago and may be among the oldest recovered from any relatively small oceanic island. Their significance derives in part from the fact that they constitute a large fossil assemblage representing many species lineages with diverse ecological and trophic specializations. A few of the species appear to be closer to continental ancestral taxa that may have given rise to endemic Hawaiian species in the interval since the fossils were deposited, which could provide one of the most precise estimates of divergence times for any vertebrate lineage in the fossil record. This could potentially be extremely valuable for calibrating molecular divergence times. On the other hand, numerous other lineages appear not to have changed at all morphologically over several hundred thousand years and provide striking examples of evolutionary stasis.

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