

FOSSIL EVIDENCE FOR A DIVERSE BIOTA FROM KAUA‘I AND ITS TRANSFORMATION SINCE HUMAN ARRIVAL

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Abstract. Coring and excavations in a large sinkhole and cave system formed in an eolianite deposit on the south coast of Kaua‘i in the Hawaiian Islands reveal a fossil site with remarkable preservation and diversity of plant and animal remains. Radiocarbon dating and investigations of the sediments and their fossil contents, including diatoms, invertebrate shells, vertebrate bones, pollen, and plant macrofossils, provide a more complete picture of prehuman ecological conditions in the Hawaiian lowlands than has been previously available. The evidence confirms that a highly diverse prehuman landscape has been completely transformed, with the decline or extirpation of most native species and their replacement with introduced species.

The stratigraphy documents many late Holocene extinctions, including previously undescribed species, and suggests that the pattern of extirpation for snails occurred in three temporal stages, corresponding to initial settlement, late prehistoric, and historic impacts. The site also records land-use changes of recent centuries, including evidence for deforestation, overgrazing, and soil erosion during the historic period, and biological invasion during both the Polynesian and historic periods. Human artifacts and midden materials demonstrate a high-density human presence near the site for the last four centuries. Earlier evidence for humans includes a bone of the prehistorically introduced Pacific rat (*Rattus exulans*) dating to 822 yr BP (calendar year [cal yr] AD 1039–1241).

Vegetation at the site before human arrival consisted of a herbaceous component with strand plants and graminoids, and a woody component that included trees and shrubs now mostly restricted to a few higher, wetter, and less disturbed parts of the island. Efforts to restore lowland areas in the Hawaiian Islands must take into account the evidence from this study that the prehuman lowlands of dry leeward Kaua‘i included plants and animals previously known only in wetter and cooler habitats. Many species may be restricted to high elevations today primarily because these remote locations have, by virtue of their difficult topography and climate, resisted most human-induced changes more effectively than the coastal lowlands.

Key words: biological invasions; birds; diatoms; extinctions; Hawaiian Islands; human impacts; land snails; paleoecology; paleontology; plant macrofossils; pollen; tsunami.

INTRODUCTION

The major Hawaiian Islands have undergone human-induced biotic transformation on a scale to match that of any comparable-sized area of the tropics. For instance, the >1029 species of flowering plants indigenous to the archipelago are now balanced by at least 1060 naturalized species (Wagner et al. 1999a). The Holocene avifauna has experienced extinction of >50% of the resident species since initial human occupation (Olson and James 1982a, 1991, Olson 1989, James and Olson 1991). The formerly diverse assem-

blages of endemic terrestrial snails have virtually disappeared, replaced by a few exotic species (Cooke 1931, Christensen and Kirch 1986).

Although government agencies and private interests are keenly interested in carrying out ecological restorations in the Hawaiian lowlands, they have been hampered by a nearly complete ignorance of the composition and dynamics of prehuman and pre-European ecological communities. The fact that biotic transformation has been massive is apparent from the general lack of native plants and animals and the predominance of exotics in nearly all low-elevation areas except a few relatively undisturbed beach strands. Some impression of the original character of lowland environments might be gained from the better preserved forest remnants on some of the higher areas of the islands' interiors. However, the extent to which these rugged

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mesic habitats in protected areas are representative of prehistoric species composition in lower areas is uncertain.

Archaeological evidence (summarized in Athens 1997) indicates that ecosystems of the coastal lowlands were transformed centuries ago by large prehistoric human populations. Evidence for the date of first colonization by Polynesians is inconclusive, with estimates ranging from the first century BC (Beggerly 1990) to AD 800 (Athens 1997). By the time Captain James Cook initiated European influence with his first visit in 1778, the coastal zones of Kaua'i and other major islands were already cleared and heavily settled by Hawaiian fishermen and taro farmers with a complex political and economic structure (Cuddihy and Stone 1990). Since European contact, the pace of landscape modification and human-mediated biological invasion has steadily increased.

Attempts to gain insight into the nature of prehuman environments of the Hawaiian Islands have generally depended on two kinds of indirect evidence: analysis of sediment cores for fossil pollen (e.g., Selling 1948, Athens et al. 1992, Burney et al. 1995, Hotchkiss and Juvik 1999) and excavation of faunal assemblages from lava tubes, dunes, and other sites (e.g., Olson and James 1982b, James et al. 1987). More information is needed concerning ecological roles of extinct species and the timing of extirpations and exotic introductions. Pu'u Naio Cave in the Maui lowlands has been the primary source for this type of information, because this lava tube preserves paleontological and palynological records spanning most of the Holocene. This rich record has permitted inferences regarding ecological roles of large, flightless anseriforms (James and Burney 1997) and the timing of extinctions and exotic introductions (James et al. 1987).

Detailed studies of "integrated sites" (sensu Burney 1999) should yield an improved understanding of the prehuman character of the Hawaiian lowlands and the history of their anthropogenic transformation. Such sites are likely to have an anoxic, nearly neutral, well-buffered sediment chemistry that (1) preserves a wide array of plant and animal remains, (2) provides a chronological record of ecological variation for several millennia prior to humans, and (3) documents the changes of the human period.

We present here a stratigraphic study of a sinkhole paleolake and associated caves at Māhā'ulepū on the south coast of Kaua'i, using evidence from sedimentology, diatom frustules, mollusc shells, bones, plant macrofossils, pollen, and human artifacts. The unusually good preservation of many kinds of fossil evidence at this integrated site permits examination of nearly 10 millennia of environmental history and species composition. In particular, this work provides evidence that the prehuman lowlands of dry leeward Kaua'i included plants and birds previously known only in wetter and cooler habitats. Also, extensive radiocarbon dating

documents many late Holocene extinctions, including previously undescribed species, and provides a basis for testing the hypothesis that the pattern of extirpation for land snails occurred in three temporal stages, corresponding to initial settlement, late prehistoric, and historic impacts.

LOCATION AND GEOMORPHOLOGY

The sizeable limestone cave system on the south coast of Kaua'i is unusual for the volcanic Hawaiian Islands. The karst features, located in the traditional land units (*ahupua'a*) of Māhā'ulepū and Pa'a, are adjacent to the sea on a broad, south-projecting peninsula. Erosion has produced sea cliffs, caves, and a large sinkhole in the Pleistocene eolianite (lithified calcareous dune deposits). The sinkhole has cave passages on its north and south ends (Figs. 1 and 2). Previous literature on the site is limited to brief treatment in various travelogues, speleological notes, and archaeological surveys. The site is referred to by a variety of names, including Limestone Quarry Cave (Howarth 1973), Grove Farm Sinkhole System (Halliday 1991), Grove Farm Cave (Ashbrook 1994), and Māhā'ulepū Caves (Kikuchi and Burney 1998). The site is State Archaeological Site #50-30-10-3097. In Hawaiian tradition, the place-names in the vicinity include Māhā'ulepū, Waiopili, and Kapunakea (map collection, Grove Farm Homestead Museum), and Makauwahi (Papers by Lahainaluna Students 1885).

Soft clastic fills, mainly dark-brown sandy silty clays, mantle the nearly level floor of the caves and sinkhole. High parts of the floor in the back of the South Cave are covered with coarse white and yellowish-white sands. Stalactites, flowstone draperies, and speleothem straws adorn the ceiling, particularly in the more remote recesses of both major caves. A few large, partially redissolved speleothems to ~0.5 m diameter also occur, notably along the walls of the sinkhole. Smaller cave passages above the basal floor on the west and south side open into the steep walls of the sinkhole. The largest of these rises diagonally through the wall and ends at a surface collapse at the edge of an adjacent limestone quarry. A walk-in entrance is on the north end of the North Cave, a triangular opening 1.2 m tall in the sheer limestone bluff facing Waiopili Stream, also known as Mill Ditch. Old maps show that, prior to the mid-20th century, a large pond (Kapunakea) existed outside this entrance.

The walls of the sinkhole range from 6 m above the level ground inside the sinkhole on the east side to a maximum of ~25 m on the west side adjacent to the Grove Farm rock quarry. Because of the generally thick overburden of modern sediments on most of the cave floor, there are no visible indications that the deep subsurface is rich with fossils and human artifacts.

The partially redissolved large speleothems on the walls of the sinkhole (which could form only in a humid cave void) indicate that the sinkhole is a collapsed cave

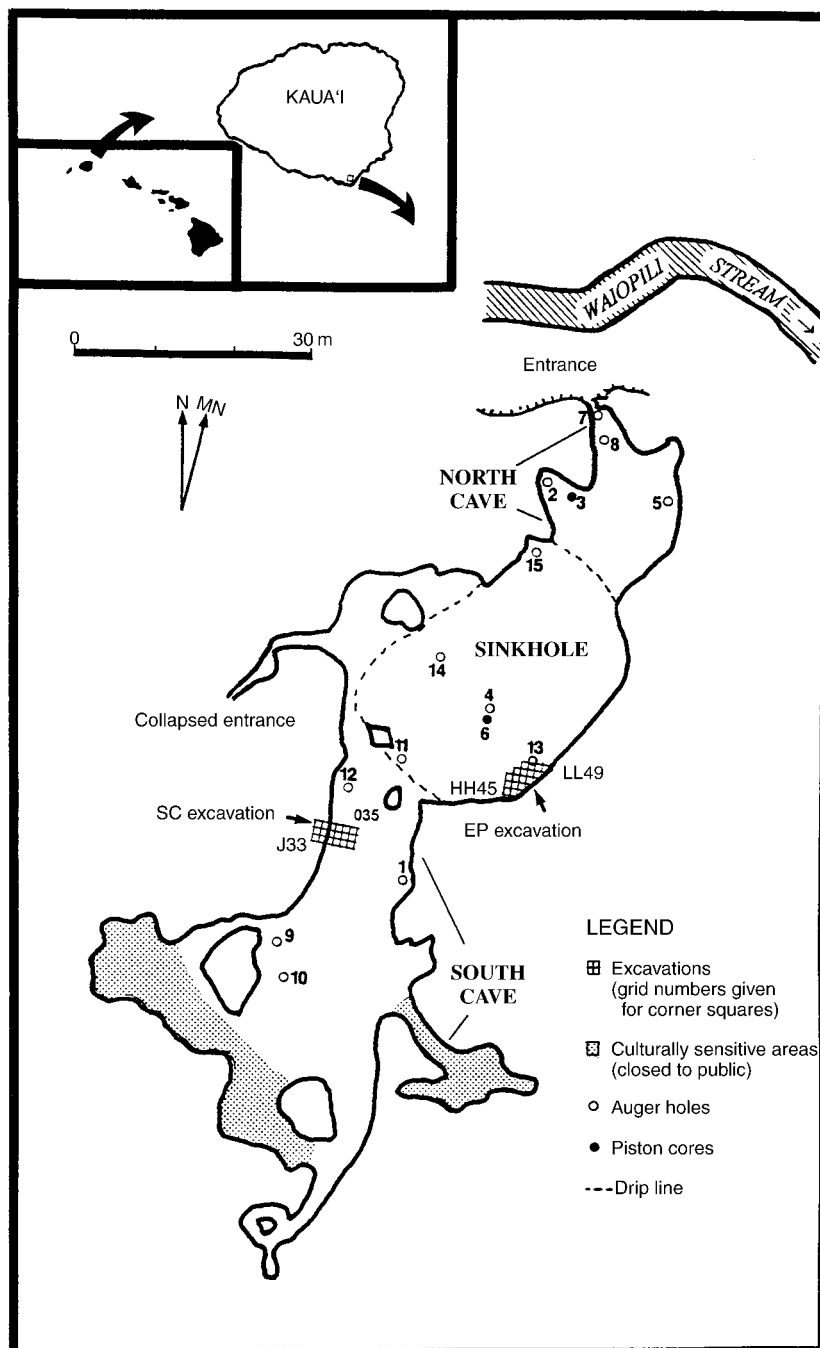


FIG. 1. Map of the Māhā'ulepū Caves and Sinkhole on the south coast of Kaua'i, Hawaiian Islands (N21°53'30", W159°25'17"). Grove Farm rock quarry is adjacent to the western edge of the map. Waiopili Spring is ~200 m northwest of the map's northwest corner.

passage. Measuring $\sim 35 \times 30$ m, the surface opening was formed when the roof dropped into a cave floor, which is now mantled with enough sediment that the large blocks that composed the roof are exposed only in a few places around the edges. Because the present floor is only 1–2 m above sea level in most places, it is likely that a lake or marsh was present in the site

until sediment filled the basin to and above the water table. The combination of strong freshwater recharge from the aquifer of the adjacent Waiopili Spring, which feeds the Waiopili Stream, and Ghyben-Herzberg buoyancy (Linsley et al. 1958) where this water meets the marine aquifer, would have created a hydrographic window that forms a shallow karst lake or *cenote* in the



FIG. 2. View of the Māhā'ulepū Sinkhole from the north rim. The entrance to the South Cave and the SC excavation pit are in the upper center of the photo. The EP excavation is against the wall on the left (note pump hoses leading from the pit). Sediments are wet-screened in the inflatable swimming pool (under pavilion) in the left foreground. The eolianite walls of the sinkhole extend to the top of the photo. (D. Burney, photographer.)

sinkhole whenever sea level is at or near its present height.

METHODS

Sediments were mapped inside the cave and sinkhole system using coring transects, as in Bliley and Burney (1988) and Burney et al. (1997). Fifteen cores were taken systematically throughout the site to characterize subsurface layers. Two of these were taken with a 5 cm diameter Livingstone-sampler piston corer for dating purposes, sediment description, and pollen, diatom, and other microfossil analyses. The other cores were taken with a 7.5 cm diameter bucket auger for sediment description.

Initial coring results and sediment mapping led to the choice of two areas for large-scale excavation, one along the east wall of the sinkhole (designated EP) and the other inside the drip line and extending beneath the west wall of the South Cave (designated SC). Detailed work was carried out from 1997 to 1999. Fossils and artifacts were recorded by depth below datum and by grid location. The grid system was oriented to magnetic north, with increasing numbers indicating distance north of a point in the southwest corner of the site (designated A1) and letter designations advancing eastwards by 1-m increments. Areas east of Z (i.e., >26 m east) were designated by doubled letters, starting at AA. In artifact-rich layers above the water table in SC, grid locations were recorded to 0.5 m, and features were plotted to 1 cm, described, and photographed. In all other excavations, depth control was at 10-cm intervals below datum, with 1.0-m grid control. Excavation by natural layers was employed above the water table. All

elevational data were measured relative to the top of a large rock at grid R40, near the center of the site, determined by transit measurement to be ~ 1.82 m above sea level.

Phreatic-zone excavation required modification of standard excavation techniques and site-specific innovations in order to cope with the ever-present ground water. Water was constantly pumped from the excavation pit. This created a temporary cone of depression in the water table below the layer being excavated, thereby permitting controlled excavation. When not excavating, we stopped the pump; the pit would fill with water again in less than an hour. In this project, we used small, gasoline-powered pumps (Honda WH15X and WB20X, Honda Motor Company, Tokyo, Japan) with a shielded suction hose placed in a 20 cm diameter, PVC-cased sump hole in the corner of the excavation.

Surfaces were leveled with standard surveying instruments. Sediment particle size analysis was carried out by nested sieving and dry-weighing, and the coarse-gravel-to-boulder fractions in a 1-m² subsample from EP grid KK47 were identified to rock type and weighed in 10-cm contiguous intervals.

In excavations below the water table, sediment was removed in 10-cm lifts with trowel, small scoop, or by hand, and was carried to the surface in labeled plastic buckets. The investigators and trained local volunteers wet-screened the material in nested 6-mm and 1.5-mm mesh screen boxes. All fossils, artifacts, and allochthonous stones were examined, labeled, and cataloged. Bones and shells were air-dried, and perishable wood, seeds, and wooden artifacts were refrigerated wet in sealed plastic containers. In richly fossiliferous

levels, fine concentrate from the 1.5-mm screens was dried in mesh bags and later rewashed, dried, and sorted under low magnification for small bones, shells, and seeds.

Bulk sediment samples were collected from excavation walls in 10-cm contiguous samples. Piston cores were sampled in units 1 cm thick at 5-cm intervals, and the intervening 4 cm were dried and stored for future analyses. An undisturbed voucher half of each core was photographed, described, wrapped, and refrigerated. Subsamples (0.5 cm³) were treated for pollen and spore analyses according to the procedures outlined in Faegri et al. (1989), and for diatoms using 30% H₂O₂ (Reyes 1993). Pollen and spores were identified by reference to Selling (1946, 1947) and comparison to a collection of >8000 pollen and spore reference slides in the senior author's laboratory, prepared from vouchered herbarium specimens. Botanical nomenclature follows Wagner et al. (1999b); diatom nomenclature follows Patrick and Reimer (1966).

Fossil seeds and fruits were identified by comparison to herbarium material at the National Museum of Natural History, Smithsonian Institution, and the National Tropical Botanical Garden in Lawa'i, Kaua'i. Bird bones were compared with fossil and modern reference collections in the Departments of Vertebrate Zoology and Paleobiology of the National Museum of Natural History (Smithsonian Institution). Molluscs were identified by comparison to private collections on Kaua'i (belonging to R. Gage, P. Sutter, and M. Genre) and specimens at the Bernice P. Bishop Museum in Honolulu. Artifacts were identified and cataloged, and placed in temporary storage in the Science and Mathematics Division, Social Science Building, at Kaua'i Community College.

Thirty-four ¹⁴C dates were obtained from the site, all but one of which are stratigraphically consistent (Table 1). Of these, 27 are accelerator mass spectrometer (AMS) dates on macrofossils or 1–4 cm thick vertical segments of acid/alkali-treated sediments. Five others are radiometric dates on large plant macrofossils. The other two dates are acid/alkali-treated sediment radiometric dates on vertical intervals of ≤10 cm. Dates are reported as radiocarbon years ± 1 σ (years before present), followed by the dendrocalibrated range at 2 σ (cal yr BP or cal yr AD). Calibrations were calculated with INTCAL98 (Stuiver et al. 1998).

Stratigraphic diagrams were plotted with TILIA version 2.0b4 (Eric Grimm, Illinois State Museum, Springfield, Illinois, USA). To establish zonation in particle size and diatom analysis, we used stratigraphically constrained, incremental sum-of-squares cluster analysis (CONISS) to construct dendrograms, employing Orloci's Chord Distance as the dissimilarity coefficient. Orloci's is often used for this type of data because it gives a higher signal-to-noise ratio than most other algorithms (Overpeck et al. 1985).

SEDIMENTOLOGY AND DATING

The sedimentology and biostratigraphy of the sinkhole and caves at Māhā'ulepū record a Holocene history driven by marine, hydrological, climatic, biotic, and human events (Figs. 3 and 4). Correlation of the stratigraphies of 15 cores and two excavations is not complete: missing layers in some areas, and difficulty penetrating sediments to the limestone floor in others, necessitate some extrapolation, but the internal consistency of 33 out of 34 ¹⁴C dates provides a plausible chronology for the geomorphological reconstructions that we will outline. Detailed stratigraphic descriptions and radiocarbon evidence are provided in the Appendix.

Late Pleistocene events at the site are extremely sketchy; the eolianite deposits (Unit I, Fig. 4) probably represent dune formation during a previous interglacial. Phreatic dissolution of the layers of eolianite that produced the main cave passages (North and South Caves) probably occurred later than that of the smaller upper passages, which must have formed at a time when the water table (and presumably sea level) was several meters higher than in the Holocene. Whether the main cave passages are early Holocene or from a previous interglacial (e.g., Isotope Stage 5e) has not been determined. However, if these passages formed in the Holocene, they must have formed soon after sea level was within ~10 m of the present level in order for Ghyben-Herzberg buoyancy effects to have played a role in raising the water table to the height of the limestone base of the cave floor. Alternatively, phreatic-zone dissolution here might not be tied to sea level (e.g., an aquaclude perches the water table in the vicinity even when sea level is much lower). If this were the case, large cave passages could have formed here at any time in the late Quaternary when the top of the phreatic zone was eroding eolianite.

Around 9500 cal yr BP, terrestrial sediments (Unit II) were being deposited subaerially on the floor of the central portion of the cave. By about 7000 cal yr BP, the sea penetrated the cave, depositing intact marine shells along the east wall of the sinkhole (Unit III). At or before this time, the roof collapsed in the central part of what is now the sinkhole, and the postulated opening to the sea on the south end was blocked by collapse and sand deposition. The collapse had spread to the edge of the sinkhole on the east side within about one millennium. Through the middle Holocene, a fresh-to-oligohaline lake occupied the site, with water levels generally stable at some time in the period at ~0.5–1.5 m below present sea level. The lake infilled with a complex sequence of bands and lenses of algal gyttja, humic sand, and sandy peat over subsequent millennia (Units IV and V).

This gradual sedimentation was truncated by an extremely high-energy sedimentation event (Figs. 5 and 6). About four or five centuries ago (cal yr AD 1430–1665), a severe marine overwash of the site, probably

TABLE 1. ¹⁴C dating and calibrations for the Māhā'ulepū Caves, Kaua'i (Hawaii, USA).

Lab no.	Material	Type	Grid location	Depth†	Unit	¹⁴ C yr BP ± 1σ‡	Calibrated age range at 2σ§
β-110270	<i>Aleurites</i> seed	AMS	N35 (SC)	142–146	IX	10 ± 40	too recent
β-67394	Humic silty clay	AMS	KK82 (core 3)	112–113	IX	[2145 ± 55]	not applicable (date rejected)
β-122587	<i>Aleurites</i> seed	radiometric	J34 (SC)	275–285	VIII	modern	too recent
β-122586	<i>Aleurites</i> seed	radiometric	J34 (SC)	305–315	VIII	20 ± 60	AD 1685–1735, 1810–1925, 1950–1955+
β-122588	<i>Aleurites</i> seed	radiometric	J34 (SC)	245–255	VIII	100 ± 50	AD 1665–1955
β-116527	<i>Aleurites</i> seed	radiometric	O33 (SC)	155–160	VIII	160 ± 60	AD 1645–1955
β-116526	<i>Aleurites</i> seed	radiometric	N33 (SC)	150–155	VIII	220 ± 60	AD 1515–1590, 1620–1885, 1910–1950
β-122585	<i>Lagenaria</i> rind	AMS	J34 (SC)	325–335	VII	180 ± 50	AD 1645–1950
β-110271	<i>Aleurites</i> seed	AMS	LL49 (EP)	225–235	VII	90 ± 40	AD 1675–1765, 1800–1940, 1945–1955
β-110272	<i>Aleurites</i> seed	AMS	LL49 (EP)	245–255	VI	340 ± 40	AD 1450–1650
β-110273	<i>Aleurites</i> seed	AMS	LL49 (EP)	275–285	VI	300 ± 40	AD 1480–1660
β-116189	<i>Aleurites</i> seed	AMS	KK46 (EP)	235–245	VI	380 ± 50	AD 1430–1645
β-115789	<i>Lagenaria</i> rind	AMS	JJ46 (EP)	285–295	VI	410 ± 40	AD 1425–1520, 1575–1625
NZA 10058	bone (<i>R. exulans</i>)	AMS	LL49 (EP)	305–315	V	822 ± 60¶	AD 1039–1241
NZA 10056	bone (<i>Grallistrix</i>)	AMS	KK46 (EP)	245–255	V	2328 ± 60	2485–2299, 2265–2178, 2168–2157 cal BP
β-67395	humic sandy clay	AMS	KK82 (core 3)	296–297	V	2705 ± 55	2910–2745 cal BP
NZA 10057	bone (<i>Buteo</i>)	AMS	KK46 (EP)	245–255	V	3416 ± 60	3830–3475 cal BP
β-128626	sandy peat	AMS	EE54 (core 6)	356–358	V	3760 ± 70	4380–3915 cal BP
β-110275	sandy peat	radiometric	LL49 (EP)	305–315	V	3670 ± 60	4155–3845 cal BP
β-110274	sandy peat	radiometric	LL49 (EP)	365–375	IV	4310 ± 60	5035–5005, 4990–4820 cal BP
β-115788	<i>Cordia</i> fruit	AMS	KK46 (EP)	265–275	IV	4680 ± 50	5580–5515, 5490–5305 cal BP
β-115790	<i>Cordia</i> fruit	AMS	KK47 (EP)	305–315	IV	4960 ± 50	5875–5820, 5755–5600 cal BP
β-56647	humic sandy clay	AMS	KK82 (core 3)	398–399	IV	4470 ± 70	5315–4860 cal BP
β-64124	sandy peat	radiometric††	KK82 (core 3)	477–481	IV	4780 ± 110	5730–5300 cal BP
β-115786	<i>Cordia</i> fruit	AMS	KK47 (EP)	375–385	IV	4700 ± 50	5585–5310 cal BP
β-115785	<i>Cordia</i> fruit	AMS	KK46.5 (EP)	495–505	IV	4980 ± 50	5890–5805, 5770–5605 cal BP
β-115787	<i>Cordia</i> fruit	AMS	JJ46 (EP)	355–365	IV	5010 ± 50	5900–5620 cal BP
β-115783	<i>Cordia</i> fruit	AMS	KK46.5 (EP)	475–485	IV	5030 ± 50	5910–5645 cal BP
β-128627	<i>Cordia</i> fruit	AMS	EE54 (core 6)	672–673	IV	5020 ± 70	5920–5605 cal BP
β-115784	<i>Cordia</i> fruit	AMS	KK46.5 (EP)	425–435	IV	5120 ± 50	5945–5740 cal BP
β-93000	sandy peat	AMS	EE54 (core 6)	832–836	IV	5860 ± 50	6760–6545 cal BP
β-128625	marine bivalve	AMS	II45 (EP)	600–630	III	6550 ± 90‡‡	7190–6660 cal BP
β-128628	clay	AMS	EE54 (core 6)	899–901	II	8520 ± 80	9580–9425 cal BP
β-128629	silty clay	AMS	EE54 (core 6)	944–946	II	8490 ± 80	9560–9405, 9345–9320 cal BP

† Depth in cm below datum in excavations (EP and SC), and cm below surface in cores. The core 3 surface is 30 cm below datum; core 6 is 80 cm below datum.

‡ Corrected for isotopic fractionation.

§ Based on Stuiver et al. (1998).

|| Date rejected. Sediments in this unit contain old carbon derived from erosion of the channelized lake basin.

¶ Gelatin fraction of *Rattus exulans* pelvis. Insoluble residue (probably sediment-derived organic acids) was dated to 3038 ± 60 yr BP (NZA 10132).

†† Small sample, given four times the normal counting time.

‡‡ Applied local reservoir correction for marine samples (Stuiver and Braziunas 1993) of 115 ± 50 yr.

a tsunami, deposited allochthonous stones and fractured eolianite in a lens up to 1 m thick at the lowest point of the sinkhole rim along the east wall, thinning out in the far reaches of the caves as turbidite fans and gravel beds (Unit VI). Late Holocene sinkhole sediments were stripped or mixed by this event, but less sediment was removed in the North Cave.

After the tsunami, a shallow pond or marsh persisted in the center of the sinkhole and in the North Cave

(Unit VII). A stream resurgence flowed along the west wall of the South Cave, and water flow in this vicinity has disturbed all subsequent deposition there. Polynesians left artifact and midden evidence of their visits to the seasonally drier areas on sandy deposits inside the South Cave and along the east wall of the sinkhole. In the late 19th or early 20th century, aeolian dune sand (Unit VIII) poured over the east wall, probably as a result of livestock overgrazing of the surrounding

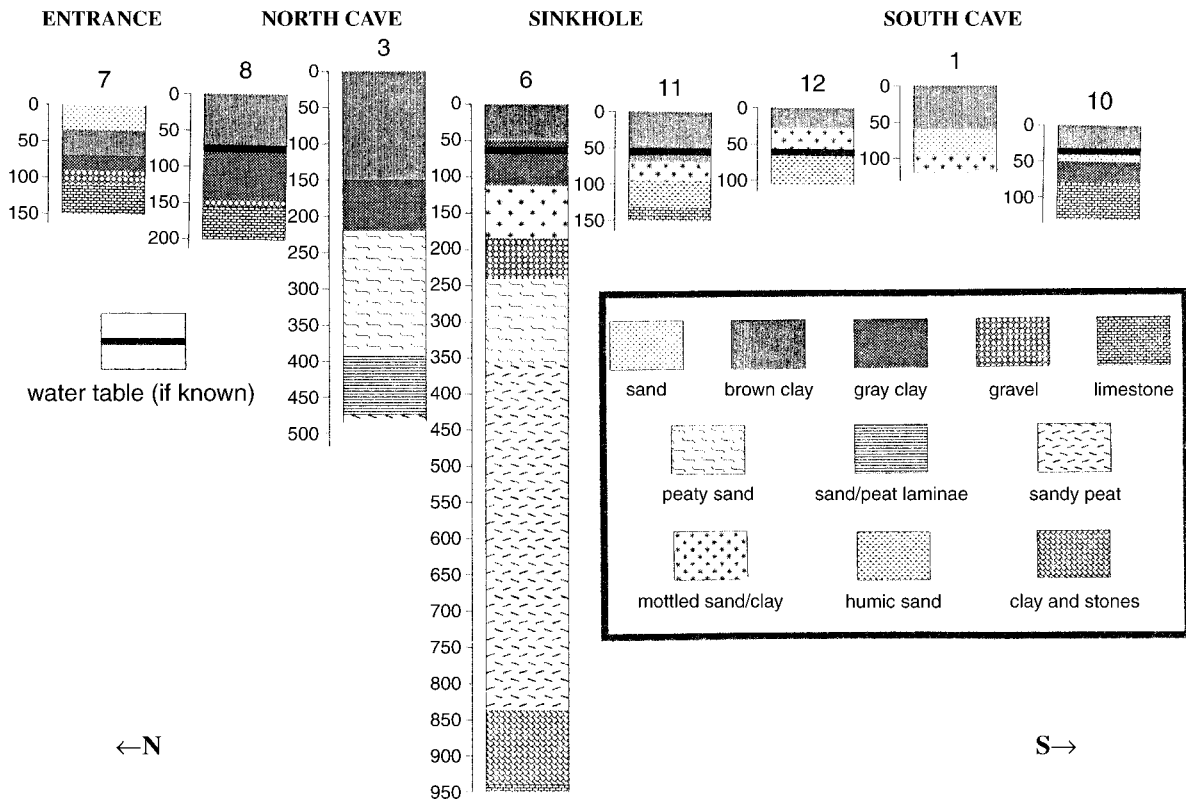


FIG. 3. N-S transect of sediment cores through the caves and sinkhole. It is not to scale horizontally, but all stratigraphies follow the same vertical scale, and the tops of cores reflect the relative position of the modern surface below datum.

vegetation and subsequent dune reactivation. In the last 50 years, upland erosion from agricultural activity, quarry development, and stream rechannelization has resulted in deposition of clay, silt, sand, and woody debris over the entire North Cave and sinkhole, and at the front of the South Cave (Unit IX). The initial clay deposition filled the remaining areas still below the water table. More recent deposition has been highly episodic, aggrading the surface throughout the cave to its present height, as much as ~2.0 m above present sea level. The most recent sedimentation occurred during Hurricane Iniki in 1992, when flooding and strong winds added patches of clay, silt, sand, and woody debris to the surface (Unit X).

BIOSTRATIGRAPHY AND INTERPRETATION

Diatoms, paleolimnology, and groundwater

Core 3 from the North Cave was analyzed for fossil diatom frustules. Forty-nine taxa were identified to genus and 18 tentatively to species. Three assemblage zones were identified using stratigraphically constrained cluster analysis (CONISS), employing Orloci's Chord Distance as the dissimilarity coefficient (Fig. 7). Although they show major differences in diversity, all three zones are characterized primarily by oligohalobitic types (preferring fresh to only slightly brackish waters, <500 mg/L salt concentration). No marine diatoms

were identified, and brackish-adapted taxa identified were ubiquitous types found in a wide range of salt concentrations, including dilute and euryhaline waters.

Zone 1, from the base of the core at 483 cm to 310 cm bs (below surface), is bracketed by ^{14}C dates of 4780 ± 110 (5730–5300 cal yr BP) and 2705 ± 55 yr BP (2910–2745 cal yr BP). This zone has higher species richness than the other two, and a prevalence of benthic freshwater types such as *Fragilaria brevistriata* and *F. construens* as well as ubiquitous types such as *Nitzschia frustulum* and *Amphora ovalis*. The lower part of this zone is part of stratigraphic Unit IV. At ~400 cm, dated to 4470 ± 70 yr BP (5315–4860 cal yr BP), sediments make a gradual transition to Unit V and diatom diversity declines, with the virtual disappearance of some major types of Unit IV, including *Anomoeoneis sphaerophora*, *Cyclotella* spp., *Cymbella* sp., *Navicula radiosa*, and several other species of *Navicula*, and *Synedra* spp. This loss of diversity and the contemporaneous change to coarser sediments suggest a shallowing of the lake.

Diatom Zone 2 shows further decline in species richness, with the decrease of *Achnanthes* spp., *Diploneis* spp., and all species of *Fragilaria*. Other types, notably *Anomoeoneis sphaerophora*, *Campylodiscus* cf. *clypheus*, *Gyrosigma* sp., and *Navicula radiosa* reach maximum abundances in at least one of the three dissimilar

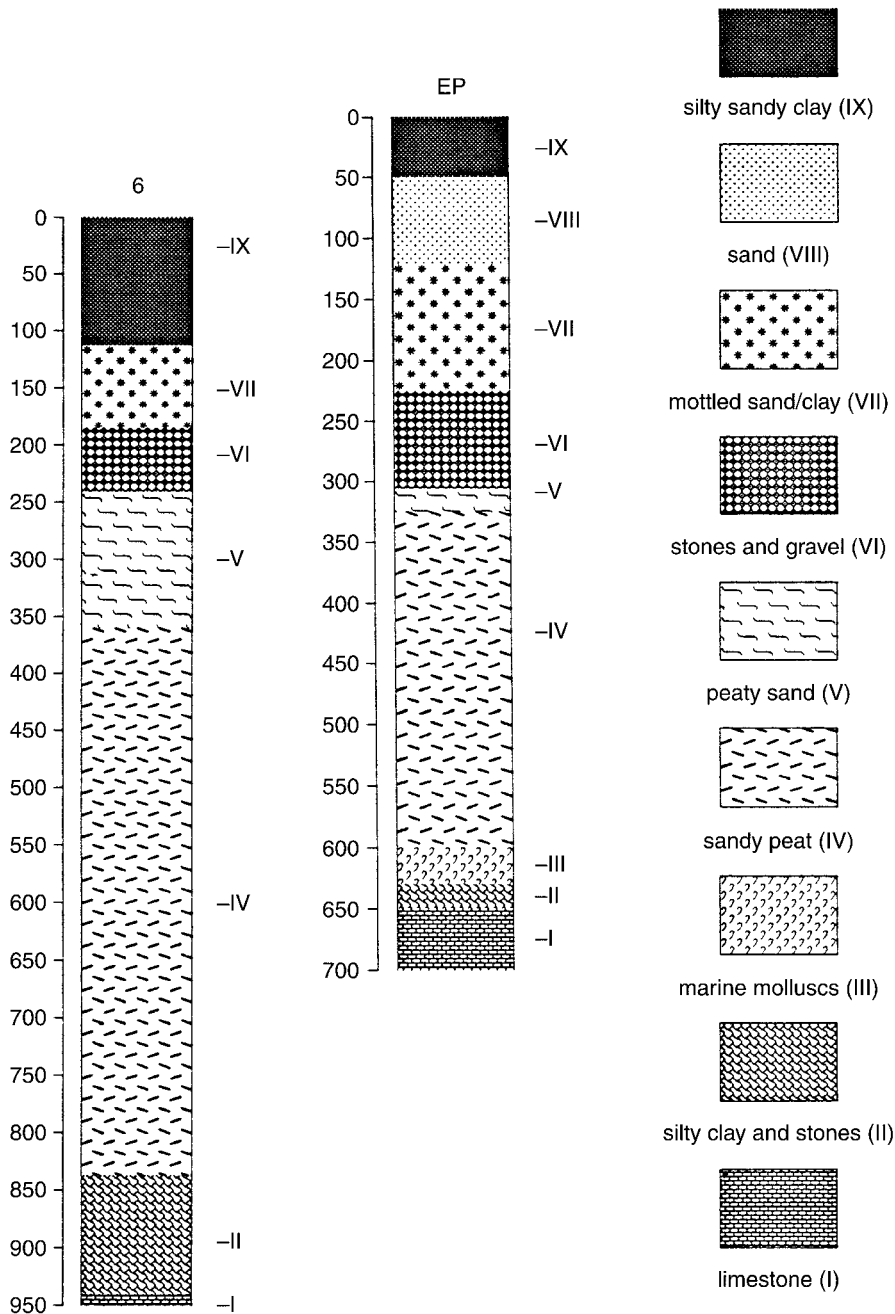


FIG. 4. Comparison of stratigraphy of the center (Core 6) and southeastern edge (EP, grid II45) of the sinkhole. The tops of cores reflect the relative position of the modern surface at or below datum.

levels comprising this zone. Diatom preservation is generally poor in this zone, with an insufficient count of diatoms for inclusion of some intervals in the analysis. Diatom preservation is especially poor above the weakly resolved transition from Unit V to Unit IX around 220 cm, except for low counts obtained at 110 cm and at the modern surface.

Zone 3 consists of the two diatom counts obtained in Unit IX. These counts of only about 300 frustules

each were very different from those of the other two zones, consisting primarily of *Melosira* sp. and traces of other generalist taxa, typical of intermittent ponding and muddy substrates (Patrick and Reimer 1966).

The prevalence of diatoms preferring freshwater to slightly brackish conditions throughout this core is in marked contrast to the results from a coastal pond studied for diatoms on O'ahu by D. W. Blinn (Athens et al. 1995). At 'Uko'a Pond, Blinn found evidence for

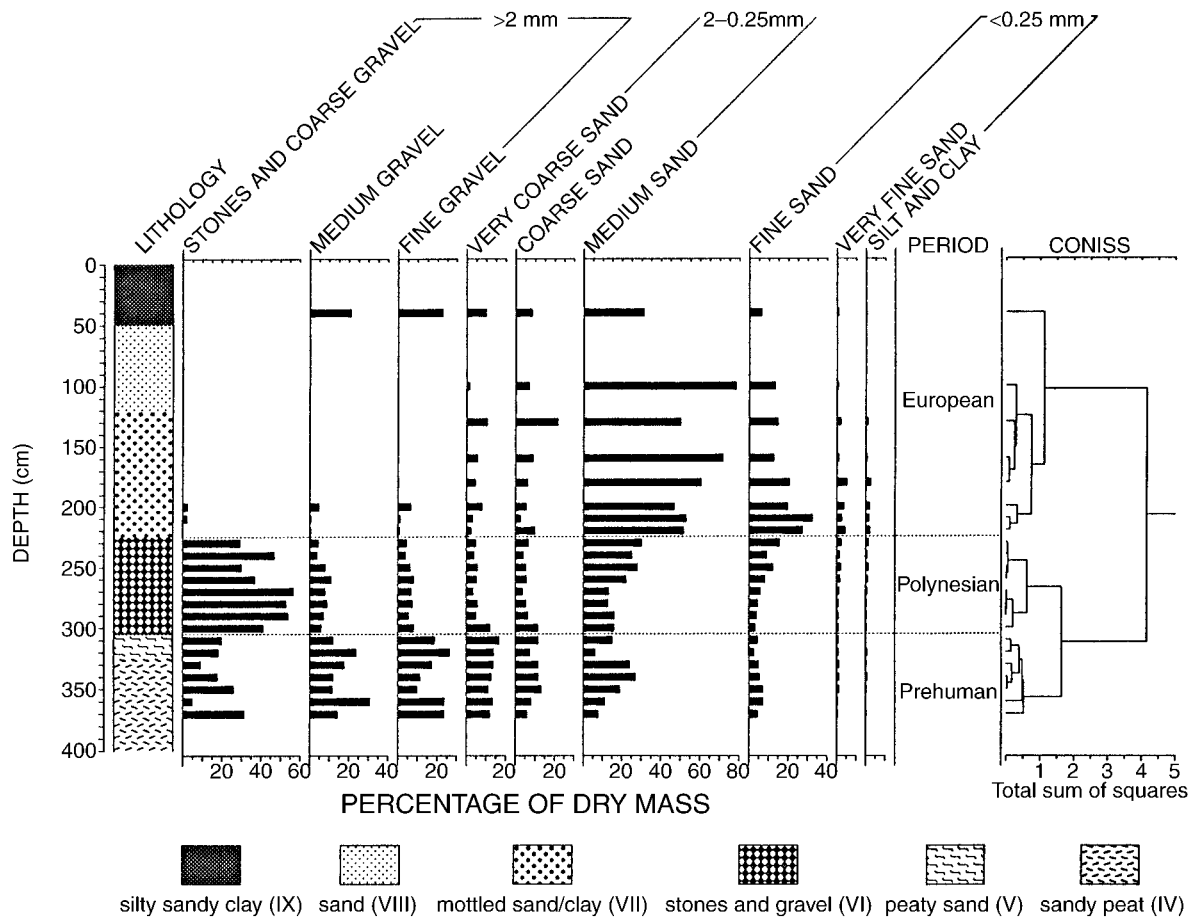


FIG. 5. Particle size analysis of the top 4 m of EP stratigraphy, grid LL49.

marine influence between about 6500 and 1100 yr BP in the form of marine and brackish-water taxa. Holocene marine incursion is of considerable interest in Hawaiian coastal ponds because of the long-standing controversy surrounding evidence for a 1.8 m a.s.l. high stand in the mid-Holocene in the Hawaiian Islands (Stearns 1978, Jones 1992). Although the geomorphology and hydrology of 'Uko'a Pond have not been studied in detail, it would appear from the USGS 1983 1:24 000 topographic map and a 1977 aerial photo (Athens et al. 1995:8) that the basin is separated from the sea on the northwest only by dune sands of ~3 m height, and that the south end of the basin is drained by a stream that integrates directly with the sea. Thus this pond has little geomorphological buffering from tsunamis, hurricanes, or higher sea stands.

The Māhā'ulepū Caves, on the other hand, have apparently been well protected from direct marine influence since about 6550 yr BP by the topographic and hydrological regime. Direct marine overwash would require a surge of ≥ 7.2 m a.s.l. in order to breach the wall of the sinkhole. Water can and does enter on the north side through the entrance, but this landward side of the feature was bounded by a large freshwater lake

(Kapunakea Pond) prior to drainage in the 20th century. Maps from the 19th and early 20th century (map collection, Grove Farm Homestead Museum) show that Kapunakea Pond was impounded by a large sandbar on the seaward side, with surface drainage into the ocean limited to a narrow channel. Such a channel must have existed here at least intermittently in the mid-Holocene, because the mullet (*Mugil cephalus*), a marine fish that frequents brackish and fresh water, was able to reach the sinkhole. Bones of this fish are among the most common vertebrate fossils in Unit IV. Abundant shells of estuarine molluscs (such as *Theodoxus* spp. and *Bittium* sp.) are further evidence of a tenuous marine connection, although the adults may frequent brackish to fresh coastal waters (Kay 1979).

Groundwater and surface-water flow are very strong here, effectively opposing incursion by the saltwater aquifer. For instance, Waiopili Stream adjacent to the entrance, although only ~125 m from the sea at this point, has a specific conductance of 183.6 ± 69.9 $\mu\text{mhos/cm}$ (mean $\pm 1\sigma$, $n = 3$, measured at high, intermediate, and low tide) and a pH of 7.1 ± 0.3 . This would correspond to a maximum salinity of ~87 mg/L. The adjacent ocean, by contrast, is generally

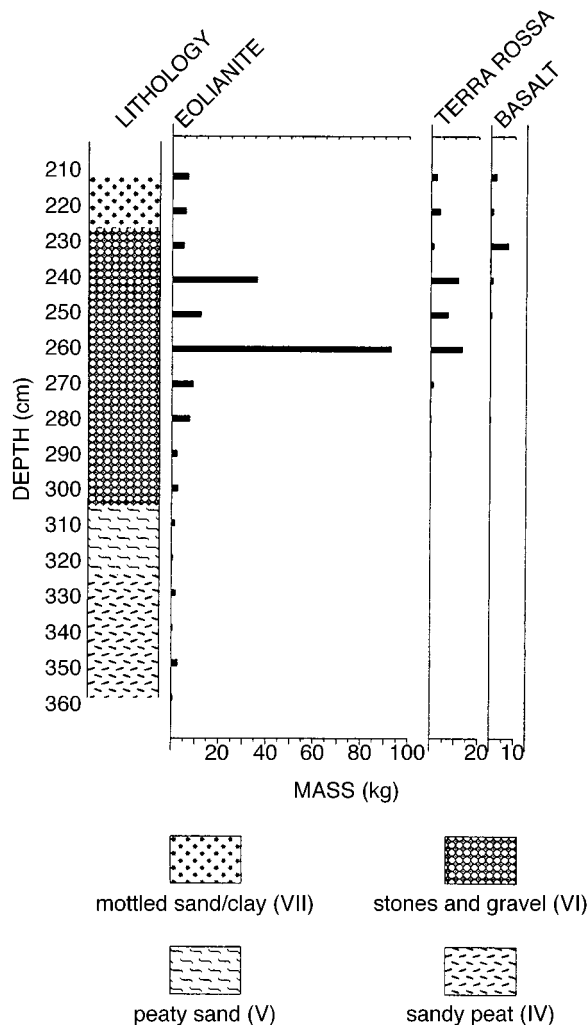


FIG. 6. Types of stones, by mass, in 10-cm increments of grid KK47. Only the segment 210–360 cm is shown, as few stones occur above and below these levels.

~50 000 $\mu\text{mhos/cm}$ (maximum salinity of ~30 g/L) and pH 8.0. The groundwater inside the cave system, measured at six points distributed over the surface of the water table, gives a specific conductance of $630.5 \pm 62.6 \mu\text{mhos/cm}$ (maximum salinity of ~305 mg/L) and a pH of 7.2 ± 0.5 . Thus, despite their proximity to the ocean, the waters of the cave system are heavily influenced by ground water derived from terrestrial sources. The adjacent Waiopili Spring is a powerful source of fresh water. Pumping of this source during the early 20th century for irrigation demonstrated the strength of groundwater flow in this area, as 3×10^6 gallons were pumped daily, with only slight lowering of Kapunakea Pond's level after two weeks of pumping (Alexander 1937:166).

The groundwater level today stands at ~20–30 cm a.s.l. inside the cave, with no detectable tidal influence. The highest levels occur in winter. The combination of freshwater buoyancy and perhaps some perching by an

aquard or aquaclude layer apparently maintains this high wedge of fresh water. At the sump in the southernmost reach of the south cave, the resurgent groundwater has a discernible seaward flow, and freshwater seepage into the ocean is detectable on the shore outside the cave at very low tide.

The most extensive shoreline dissolution features on the cave and sinkhole walls are ~0.5–1.5 m below present sea level (~2.3–3.3 m below datum; the datum is 1.82 m a.s.l.). Some woody deposits in solution pits formed in the cave wall are probably associated with a slightly lower sea stand that remained stable long enough for shoreline solution features to form. These materials date to about 5000 yr BP (dated macrofossils from KK46; see Table 1). Infilling has subsequently buried these shoreline features, perhaps as sea level rose to its maximum height and buoyed up the water table. The site's geomorphological and hydrological characteristics preclude precise measurement of the extent of this rise.

Molluscs and other invertebrates

Figure 8 shows the occurrence of selected invertebrates by stratigraphic unit in EP. A large land crab (*Geograpsus* sp.) of an undescribed, extinct species occurs in prehuman and Polynesian-aged sediments. The hapawai or hihawai, estuarine univalves *Theodoxus vespertinus* and *T. cariosus*, are abundant in prehuman sediments, relatively scarce in those of Polynesian times, and generally absent in sediments deposited since European contact. They are still found in several brackish-water estuaries along this coast of Kaua'i, but are not seen today in Waiopili Stream (D. Burney, *personal observation*).

Very large endemic terrestrial snails (*Carelia* sp., *Cyclamastra cyclostoma*) occur in early prehuman-aged sediments, but are very scarce to absent in later prehuman-aged sediments and those of the human period. This is also the pattern with *Endodonta* sp., a smaller endemic land snail. These three genera are apparently extinct on Kaua'i today (Christensen 1992).

Figure 9 shows the number of smaller gastropods, including terrestrial, freshwater, and marine shells of species generally <1 cm in length, in 250-mL bulk sediment samples from grid LL49 of EP, 0.4–3.7 m below the surface (and datum). These samples contain 15 types identifiable to genus or species and no more than five unidentifiable individuals per level. Except for the *Endodonta* previously mentioned, no smaller snails disappear from the record before late Polynesian times. However, some types, including the presumably extinct snails *Orobophana juddii*, *Amastrella rugulosa*, *Leptachatina (Angulidens) cf. fossilis*, and one each of the two species of *Mirapupa* and *Cookeconcha* distinguished at the site, appear to decline in Polynesian times and are absent from European-aged sediments, except in the mixed zone at 2.3 m.

Other snails, such as another *Mirapupa*, two species of *Catinella*, *Tryonia cf. protea*, and *Tornatellides* sp.,

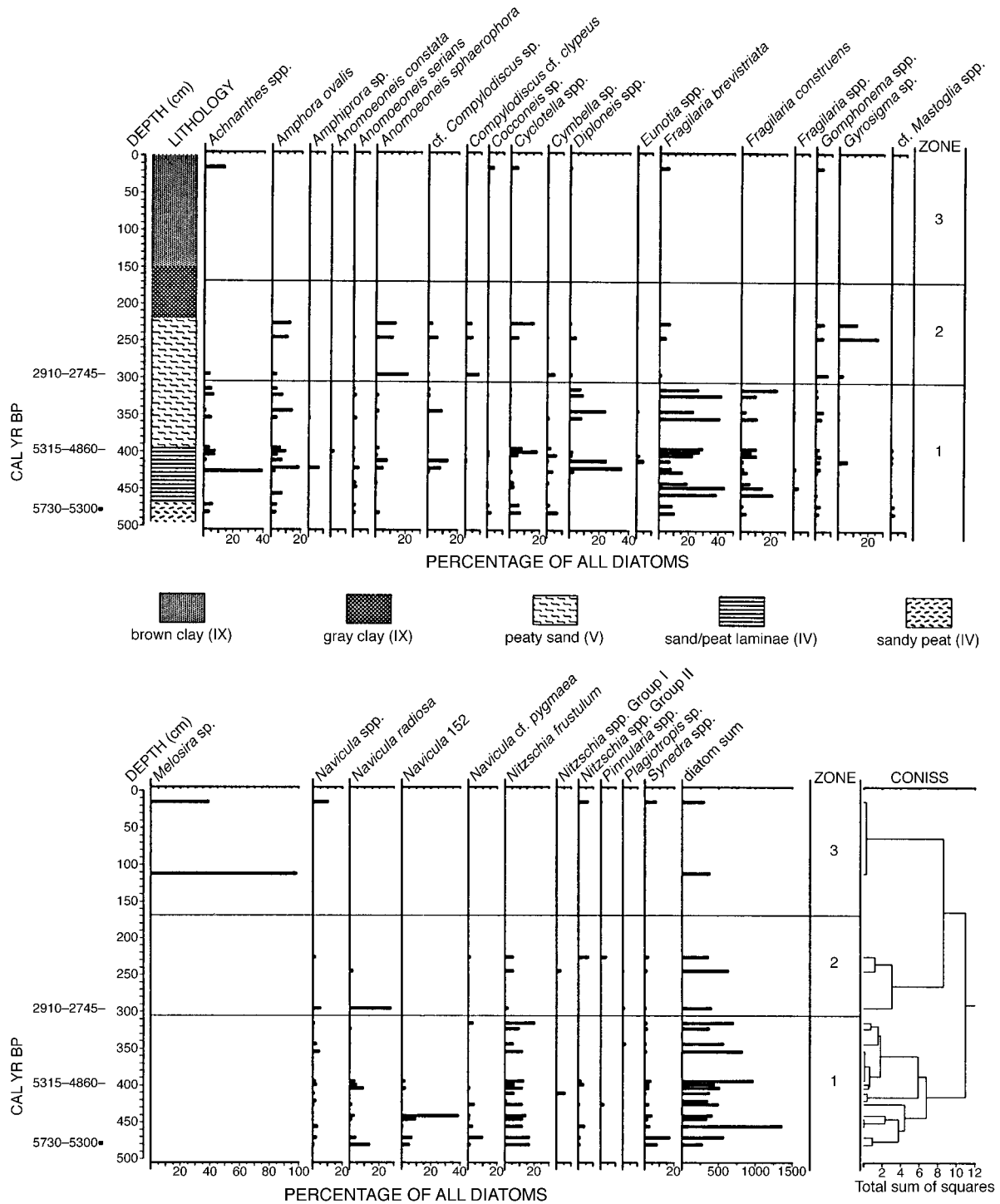


FIG. 7. Percentage diagram of all diatom taxa represented by $\geq 2\%$ in at least one level of core 3 in North Cave. Three ^{14}C dates are shown that were obtained directly from this sequence. Other levels are dated by reference to named stratigraphic units that trace to other parts of the site from which dates have been obtained (Table 1).

decline in the sediment sequence during the 19th century and are absent from Units VIII and IX, probably representing local extirpation. Unit VIII sediments, representing the late 19th and early 20th century, are

devoid of nearly all indigenous snails but two, *Lamellidea* sp. and the freshwater gastropod *Assiminea nitida*, that persist into the lower part of Unit IX.

Unit IX sediments are confirmed as late 20th century

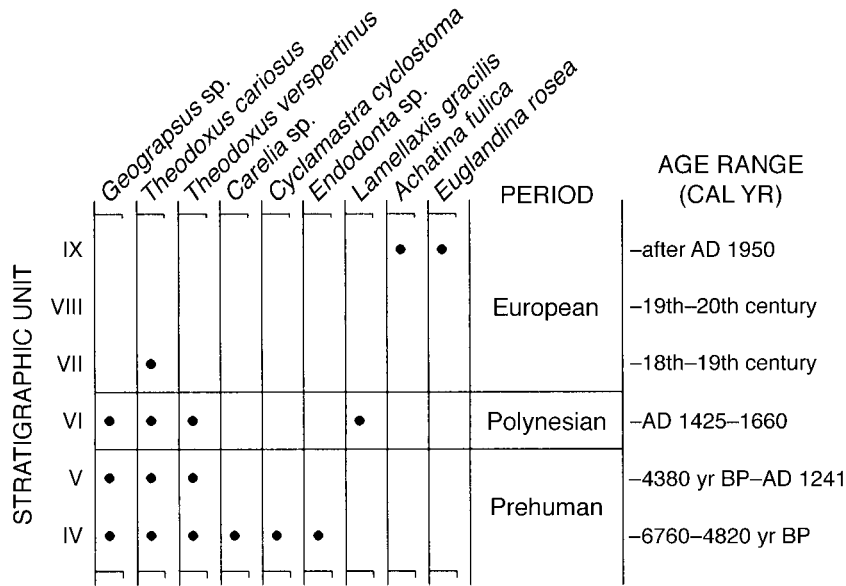


FIG. 8. Occurrence of shells of selected invertebrates by stratigraphic unit. Age ranges are the cumulative 2σ ranges for all calibrated dates from that unit (IV-VI) and best inferences for calibrated dates and index fossils of known date of introduction (VII-IX).

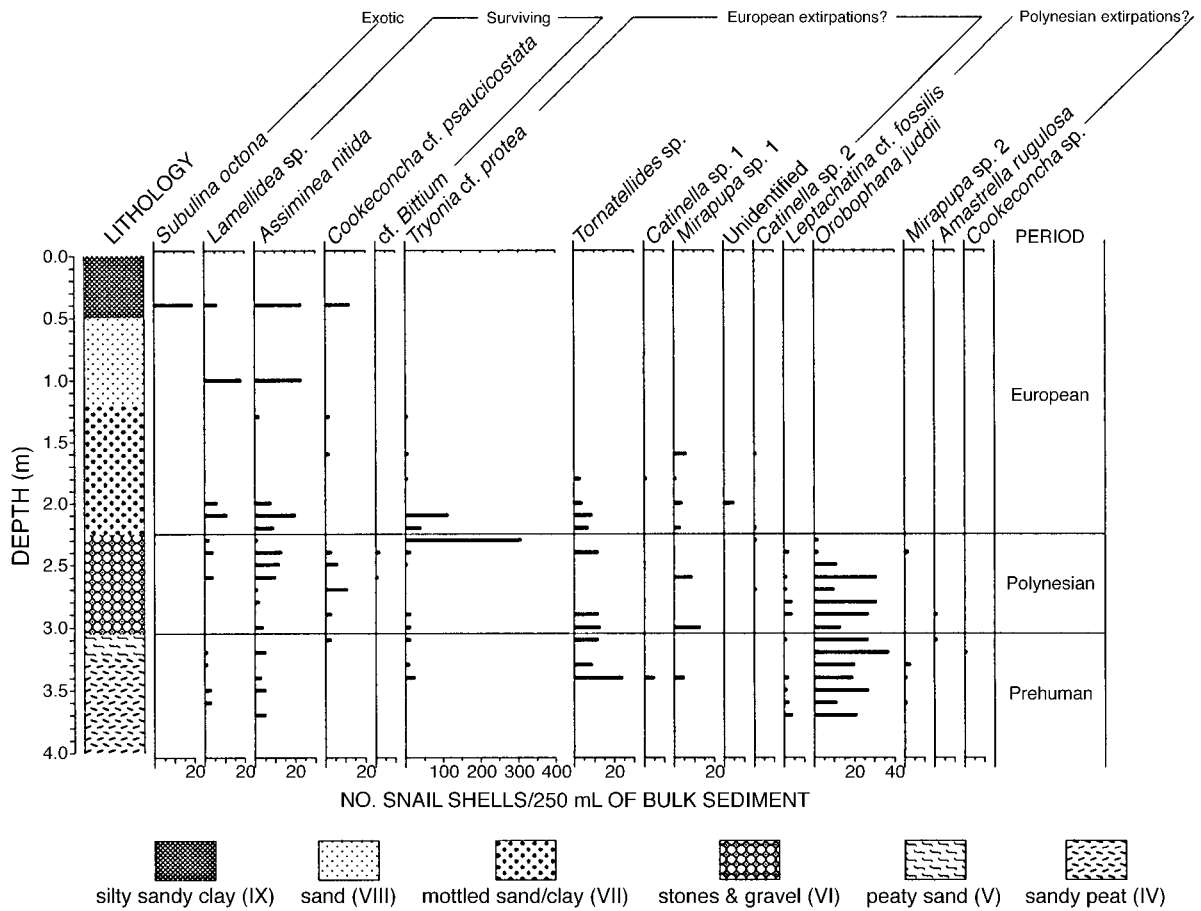


FIG. 9. Counts of the number of snail shells per 250-mL bulk sediment samples from EP, grid LL49, 40-370 cm.

by the presence of European-introduced snails: *Subulina octona*, an agricultural pest in the area, occurs throughout Unit IX and is abundant at 0.4 m. Another agricultural pest, the very large African herbivorous snail *Achatina fulica*, appears in Unit IX (Fig. 8), as does the large neotropical carnivorous snail *Euglandina rosea* (rosy wolfsnail) that first appears at ~50 cm and is common to the surface. *A. fulica* was introduced to the Hawaiian Islands in 1936, and *E. rosea* in 1957 (Kay 1983). The latter was imported in the hope of controlling other introduced snails, with little apparent success. One endemic terrestrial snail (*Cookeconcha* cf. *psauicostata*) is present in lowermost Unit IX, but it has not been found alive at the site.

These results are consistent with a pattern of disappearances at the site in which species fall into three "tiers" of extinction:

1) Some large species of terrestrial snails that were relatively scarce in the mid-Holocene seem to disappear from the record either just before or soon after human arrival (probably the latter, in our opinion). The small (<1 cm) snail *Endodonta* shows the same pattern of original scarcity and early disappearance. Whether these patterns represent prehuman decline due to climate change or other ecological shifts, or simply the Signor-Lipps Effect (the tendency of rare types to "disappear" in the fossil record in advance of their actual time of extinction; Signor and Lipps 1982), has not been ascertained.

2) Some medium-sized (0.25–1.0 cm) and small terrestrial snails decline and disappear from the site in the last 400 yr, after evidence for Polynesian activity, but before or at the time of first evidence for European influence at the site. This category includes three distinctive and formerly abundant medium-sized species: *Orobophana juddii*, *Amastrella rugulosa*, and *Leptachatina* cf. *fossilis*. It is conceivable that vegetation changes in the coastal area resulting from prehistoric human impacts, and/or depredation by the Pacific rat (*Rattus exulans*) or other Polynesian-introduced vertebrates (chickens and pigs) contributed to their decline.

3) All remaining endemic species of terrestrial snail except *Cookeconcha* cf. *psauicostata* disappear from the record during the 19th or early 20th century. These are replaced in submodern sediments by three introduced species of terrestrial snails, one of them a predator of other snails that could have played a role in the decline or extirpation of the last endemic terrestrial snail species still present at the site. Competition from the introduced and now abundant herbivorous snails *Subulina octona* and *Achatina fulica* may also have played a role. At present, these two species appear to represent almost the entire biomass of extant herbivorous molluscs at the site.

Terrestrial vertebrates

All units that were excavated (IV–IX) produced vertebrate remains. Units I–III, sampled only by small-

diameter cores, yielded insufficient material for this analysis. Unit X, storm debris from the 1990s, also contains vertebrates, but these were not analyzed.

Between 40 and 43 species of indigenous birds were identified from Units IV–VI (Table 2). This list is preliminary, as analyses of the undescribed species are not yet complete and four taxa remain undetermined. Three species of human-introduced birds were also recognized from the excavations. Other species (not listed in Table 2) were identified in surface bone collections, but these modern bones (many with soft tissue still attached) were not treated as part of the fossil assemblage. A wide range of fossil taxa and adaptive zones are contemporaneously represented, including pelagic seabirds, waders and shorebirds, waterfowl, raptors, and passerines with a wide variety of adaptations. See Table 2 for scientific names of extant birds identified here by the American Ornithologists' Union (AOU) (1998) checklist of common names.

The presence of Dark-rumped and Bonin Petrels, Wedge-tailed and Newell's Shearwaters, Great Frigatebirds, and boobies, including juvenile frigatebirds and petrels, suggests that the adjacent strand vegetation, dunes, and coastal trees may have been used by at least some of these species for nesting. Among waders and shorebirds, both residents and migrants are represented. Included in the former are the Black-crowned Night Heron, the Hawaiian Stilt, and an extinct species of flightless rail (*Porzana* sp.). Like other flightless island rails, this one was probably terrestrial and not necessarily associated with wetlands. Although flightless rails are often among the most common birds in prehuman bone deposits elsewhere in the Hawaiian Islands (Olson and James 1991), they are rare here. The now-endangered stilt, in contrast, is common in the Māhā'ulepū deposits, as is the Pacific Golden-Plover, a migrant shorebird still found seasonally on Kaua'i. It is primarily a bird of open country, not restricted to marshes or shores. A gull also occurs in the mid-Holocene deposits, apparently an unnamed endemic species of *Larus*. There are no resident gulls in the modern fauna, nor have any been found previously in fossil faunas, but Laughing Gulls and occasionally other species have been recorded as accidentals (Pratt et al. 1987). The Hawaiian Coot is also common as a fossil, and eggshells and juveniles confirm that it nested here in the mid-Holocene.

Anseriforms are particularly important in the fossil record of the archipelago, including many extinct species, some of them large terrestrial forms (Olson and James 1991). Bones of at least six types of waterfowl are present in the prehuman Māhā'ulepū sediments, including the extirpated, but re-introduced, Hawaiian Goose, or Nene. Surprisingly, the only anseriform that has escaped extinction on the island and that one might expect to find in a wetland deposit, the Hawaiian Duck, or Koloa (*Anas wyvilliana*), is rare or absent. Although the Hawaiian Duck is presently common in the area

TABLE 2. Avian taxa from the Māhā'ulepū Cave excavations, Hawaii.

Order and family	Species	Common name or description
Procellariiformes Procellariidae	<i>Pterodroma phaeopygia sandwichensis</i> <i>Pterodroma hypoleuca</i> ‡ <i>Puffinus pacificus</i> <i>Puffinus auricularis newelli</i>	Dark-rumped Petrel Bonin Petrel Wedge-tailed Shearwater Newell's Shearwater
Pelicaniformes Sulidae	<i>Sula</i> sp. <i>Fregata minor</i>	booby Great Frigatebird
Ciconiiformes Ardeidae	<i>Nycticorax nycticorax</i>	Black-crowned Night-Heron
Anseriformes Anatidae	<i>Branta</i> cf. <i>sandvicensis</i> ‡ <i>Branta</i> aff. <i>hylobadistes</i> ‡ aff. <i>Tadorna</i> sp.† <i>Anas</i> aff. <i>wyvilliana</i> § <i>Anas</i> cf. <i>laysanensis</i> ‡ aff. <i>Anas</i> sp.† <i>Chelychelynechen quassus</i> † <i>Buteo</i> cf. <i>solitarius</i> ‡	Hawaiian Goose or Nene large Nene-like goose undescribed long-legged duck, similar to shel- ducks Hawaiian Duck or Koloa Laysan Duck undescribed small-eyed duck turtle-jawed moa-nalo Hawaiian Hawk or Io
Falconiformes Accipitridae		
Galliformes Phasianidae	<i>Gallus gallus</i>	Red Junglefowl
Gruiformes Rallidae	<i>Porzana</i> sp.† <i>Fulica alai</i>	medium-sized rail Hawaiian Coot
Charadriiformes Charadriidae Recurvirostridae Scolopacidae Laridae	<i>Pluvialis fulva</i> <i>Himantopus mexicanus knudseni</i> Undetermined sp.§ <i>Larus</i> sp.† <i>Anous minutus</i> <i>Geopelia striata</i>	Pacific Golden-Plover Hawaiian Stilt large gull Black Noddy Zebra Dove (surface contaminant?)
Columbiformes Columbidae		
Strigiformes Strigidae	<i>Asio flammeus</i> <i>Grallistrix auceps</i> †	Short-eared Owl long-legged Kauai owl
Passeriformes Family incertae sedis Meliphagidae Monarchidae Turdidae Sturnidae Fringillidae	slender-billed species† very small species†§ <i>Moho braccatus</i> † <i>Chasiempis sandwichensis sclateri</i> <i>Myadestes myadestinus</i> † <i>Myadestes palmeri</i> <i>Acridotheres tristis</i> Genus undetermined† <i>Telespiza persecutrix</i> † <i>Loxioides bailleui</i> ‡ <i>Rhodacanthis</i> sp.† <i>Chloridops wahi</i> † <i>Xestospiza conica</i> † <i>Psittirostra psittacea</i> † <i>Hemignathus lucidus hanapepe</i> <i>Akialoa stejnegeri</i> [<i>Hemignathus ellisianus stejnegeri</i> , auct.]† <i>Akialoa</i> [<i>Hemignathus</i> auct.] <i>upupirostris</i> † <i>Loxops</i> [<i>Hemignathus</i> auct.] <i>parvus</i> <i>Loxops stejnegeri</i> [<i>Hemignathus kauaiensis</i> , auct.] <i>Himatione sanguinea</i>	Kaua'i Oo Kaua'i Elepaio Kamao Puaiohi or Small Kaua'i Thrush Common Myna (Unit IX only) finch resembles Laysan and Nihoa finches Palila resembles koa-finches medium-sized Kona finch fossil cone-billed finch Ou Kaua'i Nukupuu Kaua'i Akialoa hoopoe-billed fossil akialoa Anianiau Kaua'i Amakihi Apapane

Note: Scientific names follow Olson and James (1991) and James and Olson (1991), except that the genus *Akialoa* is recognized here.

† Species that are extinct or probably extinct.

‡ Species that survive elsewhere but no longer occur on Kaua'i (Hawaiian Goose recently reintroduced).

§ Taxa only tentatively identified as present in the assemblage.

and frequently seen on Waiopili Stream just outside the cave entrance, only a few bones from the site have been tentatively referred to *A. wyvilliana*.

Several other waterfowl from the site are currently under study: a small duck that closely resembles, and is probably conspecific with, the Laysan Duck (including many juveniles, indicating nesting nearby); an extinct flightless moa-nalo (*Chelychelynechen quasus*); a large, extinct Nene-like flightless goose (*Branta* aff. *hylobadistes*; Olson and James 1991); and a previously unknown anatid with long, slender legs, perhaps allied with the shelduck genus *Tadorna*. Strangest of all, a cranium and several other bones represent a small, stout-legged duck with a remarkably broadened and flattened skull and greatly reduced orbital cavities. These last two extinct anatids are newly documented faunal elements for the Hawaiian archipelago.

Raptor bones are abundant in Units IV and V, and are present but less well represented in Unit VI. Remains of the extinct long-legged, bird-catching owl *Grallistrix auceps* are frequently encountered, as are those of a hawk tentatively identified as the Hawaiian Hawk or Io, a species whose distribution has been restricted to the island of Hawai'i in historic times. The only other fossil record of Hawaiian Hawk (Olson and James 1997) on Kaua'i is a coracoid from the nearby Makawehi Dunes. Another raptor, the Hawaiian Short-eared Owl, or Pueo, does not occur below Unit VI.

Remains of 18 or 19 species of endemic passerine birds and one introduced passerine (the Indian Myna, in the uppermost Unit IX only), were found in the excavations. The list of endemic passerines for the site includes many that are historically extinct or believed to be extinct (e.g., Kauai Oo, Kamao, Ou, and Kauai Akialoa). The extant Kauai Amakihi, Anianiau, and Puaiohi are also present. The species list from Māhā'ulepū Cave includes all but two of the passerines (*Oreomystis bairdi*, the Kauai Creeper or Akikiki, and *Ciridops tenax*, an extinct drepanidine) reported from owl pellet deposits in the nearby Makawehi Dunes (Olson and James 1982b, James and Olson 1991), plus four or five species that are new for the island.

Among new records for the island is the endangered Palila, historically known only from the island of Hawai'i. It has been previously reported in the fossil record as far west as O'ahu (Olson and James 1982b, James and Olson 1991). The koa-finches (*Rhodacanthis*) show a similar pattern of historical and fossil distribution. Fossils of an undescribed species of koa-finch from Māhā'ulepū extend the distribution of this extinct genus of drepanidines to Kaua'i. Two other new records for the island, a finch (Fringillidae, genus undetermined) and a slender-billed species (family and genus undetermined), are also new to science; their possible relationships to other Hawaiian birds are currently under study. Some of the passerine long bones in the deposit seem too small to belong to any of the other species listed, and these may represent another yet un-

described species (family and genus undetermined, listed in Table 2 as "very small species").

At least one non-avian vertebrate is also represented in Units IV–VI: the indigenous hoary bat (*Lasiurus cinereus*). A smaller, undescribed bat was also found, and is presently under study (Alan Ziegler, *unpublished data*).

Birds represented by MNI (minimum number of individuals, as inferred from comparison of bone elements) of three or more are shown in Fig. 10. Rarer taxa have been excluded from this analysis in order to minimize the Signor-Lipps Effect (Signor and Lipps 1982). In the upper units, vertebrate remains show marked changes, with many disappearances among the birds and the appearance of several introduced mammals, birds, and amphibians. Of the 19 species of indigenous birds in Units IV and V that meet the MNI criterion, 14 are present in Unit VI, but only one is in Unit VII (i.e., about the time of European contact), and none after that. The species that disappears last from the sediments is an extant species, the endangered Hawaiian Stilt.

Although the large number of "survivals" into Polynesian times are unexpected, some of these may represent sediment mixing, particularly redeposition from lower units by the inferred tsunami event of Unit VI. Also, presence within Unit VI does not demonstrate survival throughout the Polynesian period. Many of these species probably were absent from the site by the beginning of the European period, as suggested by their absence in Unit VII. Direct ¹⁴C dating of apparent late occurrences of extinct taxa would be required to properly address late survival. This work is being undertaken for some of the larger species. The stratigraphic evidence raises the possibility that the overall pattern observed is similar to that previously noted for land snails: a three-tiered extinction event, with some species lost very early in Polynesian times, others declining as the human population increased, and the last disappearances occurring after European contact. In the case of both the snails and the birds, however, it should be kept in mind that these patterns are inferred from a single site, and some species are known to have survived elsewhere. In the case of species that disappear from the stratigraphy but are surviving today, it is probable that they were common at the site before, and subsequently became so rare locally that the chances of preservation in the fossil record were severely diminished.

One prehistorically introduced vertebrate, the Pacific rat (*Rattus exulans*), appears in Unit V (possibly IV) and persists through VIII. Three other prehistoric introductions appear in Unit VI and persist through IX (chicken and pig) or VIII (dog). Five European introductions appear in sediments from postcontact time, beginning with the goat or sheep in Unit VII, then horses and cows in Unit VIII, and finally larger European-derived rats and both cane toads and bullfrogs

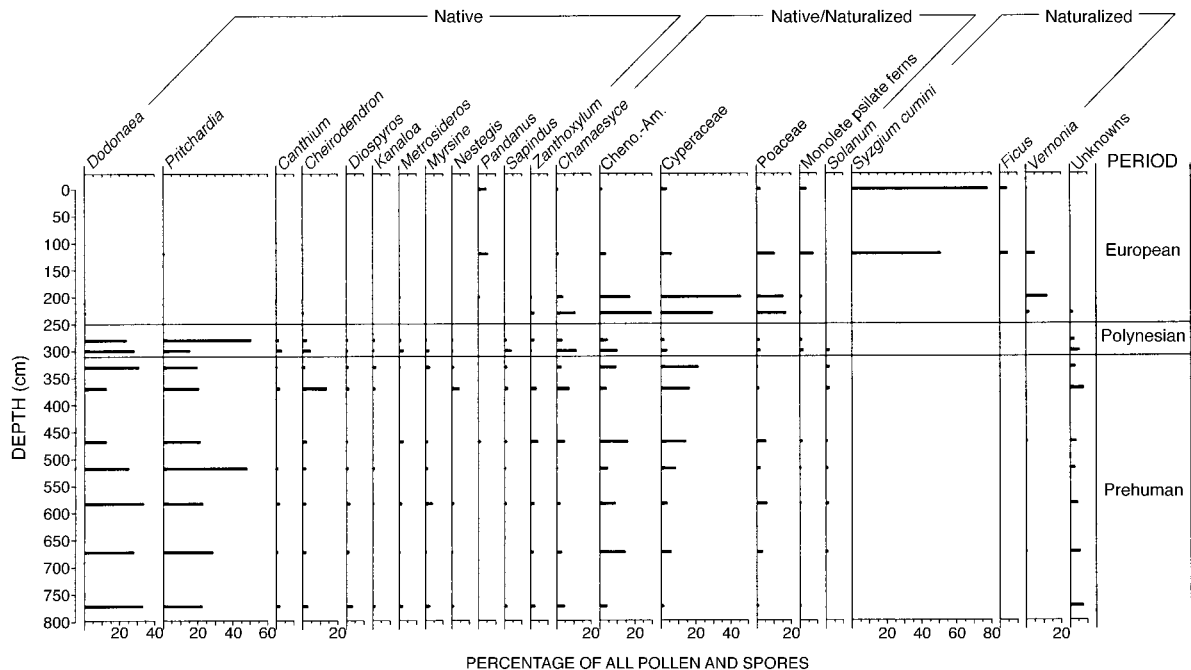


FIG. 11. Percentage diagram of all pollen and spore taxa represented by $\geq 2\%$ in at least one level analyzed. Samples from 0–3.7 m were taken from BAC-EP, grid LL49, which extends from the top of Unit IV to the surface (Unit IX). Samples from 4.6–7.8 m were taken from Core 6, extending the analysis to the base of Unit IV. See Fig. 4 for lithology and stratigraphic correlation. Taxonomic groupings are: “Native,” indigenous and endemic species; “Native/Naturalized,” taxa that include both native and introduced species; and “Naturalized,” taxa introduced since European contact.

tion presents evidence, from the abundant seeds of this genus found in the sediments, that a species of the “*P. remota* complex” (Wagner et al. 1999b) was present at the site in prehistoric times. Well-represented indigenous tree taxa include *Canthium*, *Cheirodendron*, *Diospyros*, *Metrosideros*, *Nestegis*, *Sapindus*, and *Zanthoxylum*. Like *Dodonaea* and *Pritchardia*, most of these are absent from the sediments by the beginning of European time. *Zanthoxylum* is an exception, as its pollen and the seeds of two species (*Z. dipetalum* and *Z. hawaiiense/kauaense*) persist in sediments until the beginning of the European period (Unit VII). Two other taxa that contribute many seeds to the prehuman sediments, *Cordia* and *Santalum* (see next section), are represented in prehuman pollen spectra only as traces, suggesting that they are weak pollen producers. *Pandanus* pollen appears as a trace in prehuman times, is represented by fruit in the Polynesian levels, and shows its highest pollen percentages in the 19th and 20th century.

Native shrubs or small trees of the prehuman period that disappear about the time of European contact include *Kanaloa* and *Myrsine*. A cosmopolitan genus of variable life form, *Chamaesyce*, shows a different pattern, with persistence up to the present. It is not known, however, whether these pollen grains represent native or introduced species in the upper part of the profile, as both are present in the vicinity today.

The problem of distinguishing pollen of indigenous

vs. naturalized members extends to other taxa, including *Solanum*. However, *Solanum* grains in this profile are all from sediments that predate the European introductions, and so must represent the native species. The problem is less tractable for Chenopodiaceae-Amaranthaceae (cheno-ams), Cyperaceae, Poaceae, and monolete psilate fern spores, because distinguishing these to genus is difficult and sometimes impossible, and many indigenous and naturalized species are known from Kaua'i. However, these four families show moderate to high percentages in prehuman and Polynesian times. Monolete spores (as well as trace amounts of several kinds of trilete spores) reach their highest values in the entire profile in the late 19th and 20th centuries. Cheno-ams, sedges, and grasses each reach $\geq 20\%$ in the 19th century, probably reflecting deforestation followed by overgrazing. Their large presence in prehuman times is not surprising, because strand, estuarine, and open woodland communities are inferred from plant macrofossils and animal remains to have been nearby.

Pollen of the European-introduced composite herb *Vernonia* is also common in 19th century sediments. By the late 19th century, pollen of *Syzygium* becomes abundant, almost certainly all from the European-introduced Asian species *S. cumini* (Java plum), which dominates both the recent pollen spectra and the vegetation inside the sinkhole today. The other tree that occurs in the sinkhole, the Chinese banyan (*Ficus mi-*

TABLE 3. Identified plant macrofossils from Māhā'ulepū Cave sediments.

Species by unit	Family
Units IV and V	
<i>Cordia subcordata</i>	Boraginaceae
<i>Exocarpos</i> cf. <i>luteolus</i>	Santalaceae
<i>Jacquemontia ovalifolia</i>	Convolvulaceae
aff. <i>Kanaloa</i>	Fabaceae
<i>Kokia kauaiensis</i>	Malvaceae
<i>Melicope</i> cf. <i>anisata/palli</i>	Rutaceae
<i>Melicope</i> cf. <i>ovata</i>	Rutaceae
<i>Metrosideros polymorpha</i>	Myrtaceae
<i>Ochrosia kauaiensis</i>	Apocynaceae
<i>Pandanus tectorius</i>	Pandanaceae
<i>Pritchardia</i> cf. "remota complex"	Arecaceae
<i>Psychotria</i> cf. <i>greenwelliae</i>	Rubiaceae
<i>Pteralyxia kauaiensis</i>	Apocynaceae
<i>Rauvolfia sandwicensis</i>	Apocynaceae
<i>Santalum freycinetianum</i>	Santalaceae
<i>Santalum</i> sp.	Santalaceae
<i>Sapindus oahuense</i>	Sapindaceae
<i>Scaevola taccada</i>	Goodeniaceae
<i>Wikstroemia uva-ursi</i>	Thymelaeaceae
<i>Zanthoxylum dipetalum</i>	Rutaceae
<i>Zanthoxylum hawaiiense/kauaense</i>	Rutaceae
Units VI–VIII only	
<i>Aleurites moluccana</i>	Euphorbiaceae
<i>Cocos nucifera</i>	Arecaceae
<i>Dioscorea bulbifera</i> †	Dioscoreaceae
<i>Lagenaria siceraria</i>	Cucurbitaceae
<i>Touchardia latifolia</i> ‡	Urticaceae
Unit IX only	
<i>Leucaena leucocephala</i>	Fabaceae
<i>Prosopis pallida</i>	Fabaceae
<i>Syzygium cumini</i>	Myrtaceae

Note: All plant macrofossils are seeds or fruits, except where indicated otherwise by footnotes.

† Tuber.

‡ Distinctive braided fibers.

crocarpa), is also present in recent spectra, along with traces of the introduced leguminous trees *Prosopis* and *Leucaena*, which presently dominate the landscape surrounding the site.

Plant macrofossils

The Māhā'ulepū sediments are extremely rich in plant remains, particularly Units IV and V from the mid-Holocene. Only seeds and fruits larger than 1 mm have been studied so far, and 29 types of seeds or other plant macrofossils have been tentatively identified to genus or species (Table 3). Most of these have been confirmed from pollen evidence (Fig. 11). Large samples of well-preserved wood and leaves have also been collected, but these have not yet been studied.

Some plants typical of the strand vegetation growing on the seaward side of the cave system today were also components of the surrounding vegetation in the prehuman Holocene, including naupaka (*Scaevola taccada*) and pa'uohi'iaka (*Jacquemontia ovalifolia*). The high frequency of grass pollen in the prehuman sediments may also reflect strand and dune vegetation types, because indigenous grasses frequent these habitats.

Indigenous plants typical of dry-to-mesic habitats at low elevations are well represented as seeds and/or pollen, among them 'akia (*Wikstroemia uva-ursi*), 'a'ali'i (*Dodonaea viscosa*), soapberry (*Sapindus oahuense*), hao (*Rauvolfia sandwicensis*), and sandalwood (*Santalum freycinetianum* and *Santalum* sp.). This is the type of vegetation that one might have predicted for the site in prehuman times, based on the amount of rainfall typical of this leeward site (~1000 mm; Giambelluca and Schroeder 1998).

Two seed pods that are currently under study are very similar to *Kanaloa kahoolawensis*, a mimosoid shrub described recently (Lorence and Wood 1994) from two live specimens on a sea stack near the island of Kaho'olawe. Comparison of the pollen from this rare plant showed that it was essentially identical to a pollen type that has been identified from cores on O'ahu (Athens et al. 1992, Hotchkiss and Juvik 1999) and excavations on Maui (James and Burney 1997). *Kanaloa*-type pollen was also found in Units IV, V, and VI of Māhā'ulepū. This is the only plant extinction documented from the site, although it is possible that some of the unknown pollen types represent taxa not previously recorded for Kaua'i.

Macrofossils of many plants restricted to higher elevations today were also found at Māhā'ulepū. Presently, the rare endemic shrub *Exocarpos luteolus*, for instance, is found on widely scattered dry ridges, but not below 600 m. Taxa identified from seeds also show the prehuman presence of species now restricted to mesic and wet forest, many of them quite rare today and generally restricted to windward sites at high elevations, where rainfall is more than twice as high. An example is *Kokia kauaiensis*, a very rare tree known only from remote mesic valleys of western Kaua'i at elevations of 350–660 m, and from a separate, small population in eastern Kaua'i (Wagner et al. 1999b). *Ochrosia kauaiensis* and *Pteralyxia kauaiensis* are two endemic tree species now rare and restricted to a few mesic to wet slopes and ridges. Some tree seeds that have been identified belong to species that are generally scarce today, although they are found in a wide variety of upland (but not coastal) environments, from dry to wet, throughout the Hawaiian Islands, e.g., *Zanthoxylum dipetalum* and *Zanthoxylum hawaiiense*. Seeds of the latter are among the most frequently encountered in the mid-Holocene sediments. The seeds of *Z. kauaense* are apparently identical to those of *Z. hawaiiense*, and it is not certain which species is represented in the Māhā'ulepū fossil record, or indeed whether this Kaua'i form constitutes a separate species from the more widely distributed *Z. hawaiiense*, which is also known from Kaua'i (Wagner et al. 1999b).

Evidence from both seeds and pollen indicates that one of the most common trees at the site in the prehuman Holocene was the loulou palm (*Pritchardia*). The abundant and well-preserved seeds from Units IV and V are a small, subglobose type similar to those of the

species referred to in Wagner et al. (1999b) as the “*P. remota* complex.” Pollen studies of coastal sites on O‘ahu (summarized in Athens 1997) also indicate that *Pritchardia* was an important component of lowland vegetation there. Palms may be overrepresented in pollen spectra because they are abundant pollen producers, whereas many dicotyledonous species are insect-pollinated and therefore are only weakly represented in fossil spectra (Burney 1988, Hotchkiss 1998). The abundance of *Pritchardia* seeds at Māhā‘ulepū, however, confirms its importance in the community. Most *Pritchardia* occurrences today are at mid- to high-elevation, mesic to wet sites, but this may be a function (as in the case of many of the species previously discussed) of the pattern of human disturbance in the Hawaiian Islands, in which the drier lowlands have been almost completely degraded by human activity and native trees survive primarily on steep mountains and in the very wet upper stretches of windward valleys.

Another important discovery from the plant macrofossil record is the abundant evidence for the prehuman presence of kou (*Cordia subcordata*). Although at least one early botanist believed this tree to be indigenous (Sinclair 1885), and it is regarded as native to some South Pacific and Indian Ocean islands (Wagner et al. 1990), most authors have considered it to be a Polynesian introduction in the Hawaiian Islands. Its well-preserved fruits are the most conspicuous plant macrofossil of Units IV and V. Eight AMS (accelerator mass spectrometer) dates on kou fruits range in age from 5300 to 5945 cal yr BP at 2σ (Table 1). Although this now-rare tree was utilized by Polynesians for wood carving and as a source of food, it must have reached Kaua‘i well ahead of people.

Another plant, highly regarded by the Polynesians and also formerly thought to have been introduced by them, is hala or screw pine (*Pandanus tectorius*). Its pollen and fruits occur sparsely in prehuman sediments at Māhā‘ulepū, but the fruit are more prevalent in the Polynesian-aged sediments of Unit VI, and pollen reaches its highest values in the last two centuries. The discovery of *Pandanus* fruits in a lava flow >500 000 yr old on the north coast of Kaua‘i (J. TenBruggencate, *personal communication*) confirms its prehuman presence on the island.

Macrofossils of four taxa utilized, and presumably introduced, by Polynesians are absent from the prehuman sediments, but occur in Unit VI and above. Most common of these are the kukui (*Aleurites moluccana*) and the bottle gourd (*Lagenaria siceraria*), the latter represented by many seeds, exocarps, and stems. A few of the larger pieces of gourd from below the water table in Unit VI displayed painted designs. Also present in this unit were pieces of coconut endocarp (*Cocos nucifera*) of the small niu hiwa type (so-called “bitter coconut”) used prehistorically for ceremonies, medicine, and cooking. A tuber of the bitter yam (*Dioscorea bulbifera*) was also found in this unit.

Unit VI has also yielded at least two kinds of plant fiber, woven into cords. The coarser type appears to be derived from coconut, but a smooth fiber used in some of the cords found is almost certainly olona (*Touchardia latifolia*).

Unit IX abundantly contains three kinds of plant macrofossil: (1) seeds of koa haole (*Leucaena leucocephala*), a leguminous tree now dominant on the surrounding landscape, introduced to the Hawaiian Islands prior to 1837 (Wagner et al. 1999b); (2) seeds and distinctive thorns of kiawe or algoroba (*Prosopis pallida*), introduced in about 1828 (Cuddihy and Stone 1990); and (3) seeds of Java plum (*Syzygium cumini*), introduced in 1871 (Cuddihy and Stone 1990) and currently represented at the site by several large trees growing inside the sinkhole.

Human evidence

Only the broad outlines of archaeological and historical findings concerning the Māhā‘ulepū Caves will be given here. More information, including stratigraphic profiles, description of layers and features, and inventories of artifacts, is contained in Kikuchi and Burney (1998). Additional details, including photographs and descriptions of artifacts and reconstruction of human activities at the site, will appear in forthcoming publications. For the present purpose of overall site reconstruction, information will be summarized by stratigraphic unit.

No human artifacts or other direct evidence for a human presence have been found in Units I–V. As previously noted, Units IV and V in EP do contain a few bones of the Polynesian-introduced *Rattus exulans*, as well as small fragments of kukui nut shell and marine-derived food items (e.g., sea urchin spines), but these were found beneath large stones from Unit VI that may have displaced younger material downward. Small objects may also detach from the walls of an excavation and contaminate lower layers, especially below the water table.

Dates on the sediments and fossils of Unit V (Table 1) show that this material is of mixed ages, with ^{14}C dates from 3760 to 822 yr BP. As described in the Appendix, it would appear that sedimentation was very slow after about 3000 yr BP, and that the postulated tsunami event that deposited Unit VI planed off some but not all the material accumulated between around 3000 to 500 yr BP. In the North Cave, the approximate center of the unit dated to 2705 ± 55 yr BP in Core 3. This is well away from the area of direct overwash along the east wall of the sinkhole. Additional support for sediment removal between Units V and VI comes from the presence of mixed organic sediments in the humic sand matrix of Unit VI sediments deposited as a turbidite fan in the South Cave, probably carried there as the tsunami waters drained seaward via the sump at the extreme south of this passage.

Evidence for people in the cave prior to Unit VI is

thus ambiguous. The disappearance of several species of endemic snails in Unit V, and the possible decline of flightless birds about this time, would hint that early human impacts might have occurred. Other than the Pacific rat, the first securely dated evidence for humans in the site comes from three associated fragments of exocarp from the introduced bottle gourd at the base of Unit VI. These were found 285–295 cm bs in grid JJ46 of EP and dated to 410 ± 40 yr BP (cal yr AD 1425–1520 and 1575–1625). From the top of the same unit, a kukui nut from 235–245 cm bs in grid KK46 dates to 380 ± 50 yr BP (cal yr AD 1430–1645). These and the other dates from Unit VI (Table 1) confirm that the artifacts from this layer are from relatively late in prehistoric Polynesian times. Whether this indicates relatively late settlement along the drier leeward coast of Kaua'i, or is merely negative evidence, cannot be determined from the excavations conducted so far.

The human artifacts and midden materials deposited in Unit VI, all of which were recovered from EP, were apparently swept into the sinkhole by marine overwash during the tsunami. The perfect preservation of wooden objects, cordage, and painted gourds suggests rapid burial in wet, anoxic sediments. Unless the water table has risen a full meter in the last four centuries, or an equivalent amount of subsidence has occurred in this time, both unlikely scenarios, then all Unit VI archaeological materials were deposited subaqueously.

This artifact assemblage suggests that a coastal fishing camp may have been located nearby, as the collection is dominated by fishhooks, coral and sea urchin spine abraders, and marine-derived midden material. The latter includes fish bones and many shells of edible molluscs and echinoderms apparently preferred by Polynesians. Because of the subphreatic nature of the deposit, no features or spatial arrangements were apparent in the artifacts. Essentially, the artifacts were mixed with a jumble of stones that were rolled in from above by the marine overwash episode and deposited in the sinkhole lake. A few bones of extinct birds have been found in this layer, but it is not clear whether they are temporally associated with Polynesian activity or redeposited from the dunes above by the overwash (see section on *Terrestrial vertebrates*). Many of these bones are broken and abraded.

At the bottom of Unit VII in EP are cultural materials indicating the early phase of European contact, including remains of goats or sheep and small fragments of iron. Despite this evidence for European influence and the younger radiocarbon dates (Table 1), no large changes in diet or artifact assemblage are apparent in Unit VII. This layer is likely to represent 18th and early 19th century Hawaiian culture. By this time, or perhaps slightly later, some use of the South Cave by humans becomes apparent in the form of evidence for fishhook manufacture, cooking, and possibly ritual activity. Dating of this material is problematic, owing to the limitations on ^{14}C -dating of materials <200 yr old, but

most of this material probably belongs to Unit VIII or late Unit VII. Fire pits, postholes (probably for a small platform to allow people to sit above the wet, sandy substrate), and stone, shell, and bone debitage suggest at least seasonal use of the South Cave, perhaps during summer, when the water table is several cm lower (D. Burney, *personal observation*). At any rate, periodic flooding of the substrate appears to have buried the artifacts and prevented any sort of settled use of the site. A small stream along the west wall in the front of the South Cave cut through the deposits and has redeposited materials of mixed age, ranging over the last two centuries (Table 1).

Dune migration in the late 19th and early 20th century effectively buried the cultural deposits of EP to well above the present water table. Photographic and sedimentological evidence, as well as historical accounts (Alexander 1937, Krause 1984), suggest that the surrounding landscape was heavily overgrazed in this period. In the mid-to-late 20th century, all of the cave floor except the highest parts of the South Cave were subsequently buried in silty clay, Unit IX, probably as a result of quarrying, agriculture, and rechannelization.

SUMMARY OF BIOSTRATIGRAPHIC RECORD

Key events at Māhā'ulepū (Table 4) began with the formation of the eolianite material that comprises the cave and sinkhole walls from dune sands that probably accumulated during a previous high stand of the sea during a Pleistocene interglacial (Unit I). By around 9500 cal yr BP, a cave had formed that was accumulating sediments on its floor (Unit II). As sea level rose again to within a few meters of its present height, a sea incursion left behind marine bivalves (Unit III) and parts of the cave roof collapsed, forming a large doline, or sinkhole. A lake formed in this sinkhole. The diatom flora in its highly organic sediments (Unit IV) indicates that the water was fresh to slightly brackish. Throughout most of the rest of the Holocene, this lake accumulated a rich record of the endemic land snails (at least 14 species), birds (40–43 species), and the macrofossils and pollen of a flora that included a mixture of taxa presently associated with environments from xeric to very wet and a wide range of elevations.

The first evidence for Polynesians at the site, remains of the Pacific rat dated to cal yr AD 1039–1241, occurs in a layer (Unit V) from which some of the endemic snail species, particularly the larger ones, are absent. Many now-extinct birds are still represented, but they and many other endemic snail species become scarcer in the layer above, which also contains sedimentary evidence interpreted here as a tsunami deposit (Unit VI). During this interval (cal yr AD 1430–1665), artifactual and midden evidence indicates that prehistoric Polynesians lived nearby. Bones of dogs, chickens, and pigs are common. Despite the recovery of extensive dietary remains, however, no direct evidence was found that these people were utilizing now-extinct birds as

TABLE 4. Chronology of key stratigraphic events at Māhā'ulepū, Kaua'i.

Date	Event (stratigraphic unit given in parentheses)
A previous interglacial	Rising sea produces dune deposits; diagenetic processes solidify calcareous sands as eolianite (I).
Late Pleistocene ca. 9500 cal yr BP ca. 7000 cal yr BP	Cave passages form in eolianite deposits. Cave present, floor relatively dry (II). Marine incursion at site (III); parts of cave roof collapse.
Mid-to-late Holocene	Sinkhole paleolake occupies site. Fossils of diverse community of birds, land snails, and plants are deposited (IV).
AD 1039–1241	First evidence for Polynesians at the site. Some endemic snails absent from upper part of this layer (V); others decline over subsequent centuries and disappear from record before first evidence for Europeans. Fossils of some extinct birds still present.
AD 1430–1665	Sometime during this interval, a marine overwash event (probably a tsunami) leaves a deposit of boulders and cobbles in the sinkhole (VI). Some native vegetation still present in the vicinity.
Late 18th century	Sedimentation of thin sand and clay lenses (VII). First evidence for European livestock. Surviving terrestrial snail species in decline. Many previously well-represented plant species are absent, others are increasingly scarce.
19th, early 20th century	Feral livestock proliferate. Vegetation removal results in dune reactivation, with thick sand unit deposited on portions of the site (VIII). Trees introduced by Europeans become established in vicinity.
1950s	Drainage of Kapunakea Pond, agricultural development, and quarrying activities accelerate deposition of silty clay on the site (IX). A neotropical carnivorous snail, <i>Euglandina rosea</i> , is introduced to the island. All snails deposited after this time are exotic species.
1992	Hurricane Iniki hits Kaua'i; the site receives storm overwash (X).

food items, suggesting that they were either quite scarce by around 1500 AD, or were not preferred food items. The last fossil occurrences of some of these birds are in this layer. Pollen and macrofossils of many native plant species are still present.

In the late 18th century, thin sand and clay lenses accumulated on the site (Unit VII); they contain the first fossils of European-introduced livestock. The remaining native terrestrial snail species decline after European arrival. Many previously well-represented plant species are absent and others become increasingly scarce. During the 19th century, abundant bones of cows, horses, and other European livestock confirm historical accounts that feral livestock had proliferated along this coast. Photographic evidence suggests that vegetation was suppressed. Pollen data confirm the open and disturbed character of the vegetation at this time, and document the appearance of trees and other plants introduced by Europeans. Dune reactivation resulted in the deposition of a thick sand layer (Unit VIII) over portions of the site. By the mid-20th century, the drainage of Kapunakea Pond outside the cave, coupled with agricultural development and quarrying activity

nearby, led to the highest sedimentation rates recorded at the site. This silty clay (Unit IX) documents the appearance at the site of additional introductions, including the neotropical carnivorous snail *Euglandina rosea*. The last endemic land snail species disappears concurrent with its arrival. Since then, only exotic snails occur in the sediments, alongside other exotic species and the litter of modern life. During Hurricane Iniki in September 1992, a storm surge left behind a distinct sedimentary signal (Unit X) of the most severe hurricane event of Kaua'i's historical period.

DISCUSSION

An extraordinary biota lived on Kaua'i's south coast in the Holocene prior to human arrival. Especially striking is the apparent juxtaposition of plant species not found together today. Only one still-prevalent vegetation community occupied portions of the site, that of the strand plants on the adjacent beach. The other plant associations inferred for the site are unusual, probably lacking a close modern analog (for a discussion of the problem of non-analog communities in prehistoric Hawai'i, see Hotchkiss [1998]). What might be regarded

as xeric, mesic, and wet forest species seem to have coexisted here in the mid-Holocene.

We suggest that the interpretation of such plant taxa as *Zanthoxylum*, *Kokia*, and *Pritchardia* as types indicative of wetter conditions than presently found at the site is unwarranted. Many plants may be restricted to high elevations and wet sites today simply because these remote locations have, by nature of their difficult topography and climate, resisted most human impacts more effectively than the coastal lowlands. The latter are nearly always the first habitats to succumb to anthropogenic devastation on any island, and this pattern is well documented for the Hawaiian Islands (Cuddihy and Stone 1990). An alternate explanation, not mutually exclusive, is that the outcropping fresh water in the bottom of Māhā'ulepū Valley created a groundwater forest at the site, favoring wet-adapted plants. The coeval presence of dry-adapted and mesic plants on the site would cast doubt on such a purely edaphic explanation, however. Perhaps such groundwater forest formations, containing many species associated only with high elevations today, were typical of low-lying portions of the dry leeward coasts of the Hawaiian Islands in prehuman times, but the authors are unaware of any intact examples.

An alternate explanation would be that the site, which receives ~1000 mm of rainfall annually today, was much wetter in the mid-Holocene. Burney et al. (1995) present pollen and sedimentological evidence that a high-elevation area on Maui was wetter than present between around 5700 to 2200 yr BP, probably as a result of a higher altitude for the upper boundary of the mid-Pacific trade wind inversion layer at that time. This suggests that the North Pacific subtropical anticyclone may have been stronger than in present summer conditions. One result would be increased high-elevation rainfall, but the situation in mid-elevations and coastal lowlands is less clear (Hotchkiss 1998). Athens (1997) summarizes several lowland pollen studies from O'ahu that would suggest less rain, rather than more rain than at present, fell in the mid-Holocene in the Hawaiian lowlands.

Thus the presence of mesic and wet forest trees at the site in the mid-Holocene is not likely to be simply a function of higher rainfall. Neither is it likely to be fully explained by a higher water table as a result of a higher sea stand at the time. A much higher sea stand would have flooded the site with salt water, producing a distinct signal from the diatom record that was not observed. Instead, the pollen data show that vegetation change was underway soon after the first evidence for prehistoric humans, and that the diverse vegetation persisted up until that time without much apparent change.

Little more can be said about the extent, timing, and direct causes of the changes wrought in the earliest period of Hawaiian settlement, based on this study, because of the disturbance and partial removal of sediments ranging from roughly three millennia ago to

about AD 1500. Nevertheless, the record shows that large biotic changes apparently occurred between around 3000 and 400 cal yr BP, during or just before the human period. The snail data suggest that some changes derived from Polynesian impacts, but others followed the arrival of Europeans. It also may be significant that the extensive midden deposits from the site, including those of pre-European times, contain few bones of now-extinct birds (and some of these are highly abraded, as if redeposited), and only a few more of extant seabirds such as Newell's Shearwater. Instead, >99% of the recovered midden material spanning the last four centuries of Hawaiian diet is composed of marine organisms, domestic animals, and cultivated plants (Kikuchi and Burney 1998). This would suggest that either: (1) late prehistoric Hawaiians had little interest in utilizing indigenous terrestrial animals, or (2) most of these species were rare or extinct by roughly AD 1500.

Which of these hypotheses is correct cannot be determined from the evidence analyzed from this site, but other studies, particularly that of James et al. (1987), provide some clarification. Their lava tube site on Maui yielded a fairly continuous sedimentary record of the Holocene, including bird bones spanning the entire period of Polynesian settlement. Careful dating there shows only a slight (2σ) temporal overlap between the first evidence for humans at the site (bones of *Rattus exulans*), and the last evidence for the large flightless moa-nalo *Thambetothen chauliodous*. It is reasonable to suppose (but the evidence is inconclusive) that such presumably vulnerable and delectable species might have succumbed rapidly to overhunting, but that smaller birds, snails, and plants would have declined more slowly in the wake of an array of potentially synergistic impacts, including introduced species, deforestation, disease, and overharvesting (Olson and James 1982a, 1984, Olson 1989, Burney 1993, 1997, James 1995).

A pattern of extinctions and extirpations in the wake of a multiplicity of human impacts on islands is well documented for birds throughout the tropical Pacific (Steadman 1995). The type of "climate vs. humans" debate that has characterized analysis of causes for the North American extinctions at the end of the Pleistocene has attracted less interest on oceanic islands because of the generally poor fit between the timing of these island extinctions and the strongest climatic shifts documented (Martin 1984, Burney 1993).

The case of islands first colonized by humans in historic times is particularly suggestive regarding the complexities of the human role in island transformations. In the Mascarenes and Galápagos Islands, for instance, written documentation of the fate of these pristine island biotas leaves little doubt that the effects of human-caused biological invasions, overhunting, and habitat modification worked in concert to provoke biotic collapse. If these historic extinctions can be viewed as a "Rosetta Stone" for interpreting prehis-

toric extinctions, as Diamond (1984) maintains, then it is likely that the global pattern of late prehistoric extinctions reflects several human-derived causes that have acted with powerful synergy.

What is made abundantly clear by the extraordinary preservation at Māhā'ulepū is the breadth and depth of the losses. Of the 40–43 indigenous bird species documented for the site, only a few seabirds, migrant shorebirds, waterfowl, and one raptor (the Pueo, which we suspect is not truly a native species) are still found in the immediate vicinity today. All of the passerine birds are absent from the lowlands and only a few survive in the mountains, and most waterfowl and raptors are extinct or extirpated from Kaua'i. All of the 14 identified taxa of endemic land snails are absent from the vicinity today, and nearly all are presumed extinct. Most of the trees that were common before human arrival are now rare, many are restricted to a few isolated mountains or upper valleys on Kaua'i, and some may be extinct. In contrast, the 20th century sediments at the site contain a depauperate assemblage of cosmopolitan weeds, introduced snails, rats, toads, and domestic animal species, most of these introduced by Europeans over the last two centuries. Māhā'ulepū documents the purloined riches of a truly lost world.

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APPENDIX

SEDIMENTOLOGY AND GEOCHRONOLOGY OF THE MĀHĀ'ULEPŪ CAVE SYSTEM

The basal limestone, Unit I, was reached in the North Cave (Cores 7, 8), the center of the sinkhole (Core 6), its southeastern edge (EP), and the rear portion of the South Cave (Cores 9, 10). This is apparently the limestone floor of the cave and sinkhole, a part of the original eolianite matrix. The floor seems to have been polished by flowing water near the entrance, where it is mantled by gravel consisting of pebbles and fragments of limestone. In this vicinity, the floor is ~2 m below datum, high relative to the rest of the North Cave floor (e.g., Cores 3 and 5, where the floor was detected at ~7.3 m below datum by probing). This floor dips toward the south.

The maximum depth of the limestone floor detected was at Core 6 in the center of the sinkhole. There, true depth is obscured by boulders several meters in diameter from the collapsed ceiling, but it is ≥ 9.3 m below the present surface (bs), or ~10.1 m below datum (bd). At the southeastern edge of the sinkhole, in EP grid II45, the floor appears to be at 6.3 m bd, but we could not ascertain whether this is the actual floor or merely ceiling material mantling the floor. Evidence from dating Units II and III suggests the latter.

Large pieces of roof collapse are exposed on the surface at the junction of the sinkhole and South Cave (SC). Core 11 reached eolianite at ~140 cm. Whether or not the boulders extend to the basal limestone (Unit I) here was not determined, because sand collapse prevented extensive excavation. However, excavations at SC suggest that the actual floor may be no more than ~4 m bd. Continuing southward, the limestone floor slopes upward to a depth of ~2.0 m bd at the locations of Cores 9 and 10, where the floor has a smooth, water-polished surface.

Unit II is a silty clay with angular limestone gravel and large breakdown boulders, apparently from the ceiling collapse. This unit is well developed in the center of the sinkhole. Core 6 yielded ~1 m of this type of sediment, and probing with a flexible steel rod confirmed that the sediments are squeezed between the interstices of breakdown blocks. The fine sediments lack index fossils, except for highly oxidized grains of *Pritchardia* and other indigenous pollen types. This unit appears to be of subaerial origin. The reddish color of the silt and clay grains suggests deposition on a dry cave floor prior to flooding. It is likely that the heavy breakdown intruded into this layer by virtue of its greater density. Two radiocarbon dates on sediment (Table 1) were obtained from this unit, coeval at 1σ : 8490 ± 80 and 8520 ± 80 yr BP (combined calibrated range at 2σ : 9580–9320 cal yr BP). These are vertically separated by 43 cm, and the layer is disturbed by boulders probably derived from roof collapse. The contemporaneous dates are also consistent with the possibility that the entire unit was deposited rapidly through erosion off the ground surface above during collapse, as observed in a similar collapsed-cave feature in Madagascar (Burney et al. 1997).

A trace of this unit was collected at the base of EP. At this location, it was overlain by Unit III, which has not been

detected in other parts of the cave. Unit III consists of un-abraded marine shells, still nacreous and retaining pigmentation, of types associated with estuarine environments (*Mytilus* sp. and *Isoognomum* sp.). An AMS date on an acid-etched *Mytilus* shell was 6550 ± 90 yr BP (7190–6660 cal yr BP). This implies that the early Holocene cave floor was flooded by the rising sea at this time, during or after the episode of major ceiling collapse. Shells were recovered from a small, sheltered pocket in the sinkhole wall in EP grid II45 at a depth of 600–630 cm below datum. This is 418–448 cm below present sea level. Above this level, no evidence appears in the record for direct marine incursion (except via probable tsunami overwash in Unit VI). It is possible that the stage of cave collapse that turned the largest chamber of the cave into an open sinkhole sometime between 8.5 and 6.5 kyr BP also may have modified the seaward side of the cave (e.g., the rear portion of the South Cave) in such a way as to block the further direct ingress of the rising mid-Holocene sea. The presence of huge breakdown blocks and a thick lens of sand in the southern and southeastern portions of the rear of South Cave also suggest that an opening to the rising sea may have been blocked there.

Unit IV is a thick and distinct layer throughout the North Cave and sinkhole. Because it is a richly fossiliferous layer containing bones, terrestrial snail shells, seeds, wood, pollen, diatoms, and many other biological materials, much of the radiocarbon dating effort has been concentrated on this layer, with dates ranging from 5860 ± 50 yr BP (6760–6545 cal yr BP) near the base of the unit at 832–836 cm bs (912–916 cm bd) in Core 6, to 4310 ± 60 yr BP (5035–5005, 4990–4820 cal yr BP) in EP grid LL49, 365–375 cm bd, and 4680 ± 50 yr BP (5580–5515, 5490–5305 cal yr BP) in EP grid KK46, 100 cm higher in the column. Dating evidence from KK46 (Table 1) shows that the extensive overhang on the southeastern corner of EP has protected Unit IV here from the erosion features and coarse-clastic deposition that unconformably overlie Units IV and V elsewhere in the cave, including the adjacent outer parts of EP. Unit IV is also represented in the longest core from North Cave. The top of the unit in Core 3 dates to 4470 ± 70 yr BP (5315–4860 cal yr BP) at 398–399 cm bs (428–429 cm bd). Below this level, down to 477–481 cm bs (507–511 cm bd) where a date of 4780 ± 110 yr BP (5730–5300 cal yr BP) was obtained, the unit is markedly laminated, with alternating thin bands of humic sand, sandy peat, algal mud, and molluscan gravel. Because this unit has not been excavated in North Cave, it is impossible to determine from the small-diameter sample from Core 3 whether these are lenses only, or possibly more extensive thin layers, perhaps resulting from the quiet sedimentation environment of the portion of the lake that was inside this sheltered alcove of the North Cave passage.

Unit IV in the sinkhole is also complex and variable in composition, especially near the top. Its prevalent matrix throughout is a sandy peat, with thin bands of molluscan gravel (derived from terrestrial snails), eolian humic sand,

and sapropel (algal gyttja). Extensive excavation in EP shows that these bands are often lenses that pinch out over distances of ≤ 1 m, apparently representing episodic infillings of small hollows in the sandy peat matrix. Color is variable, with the sand lenses and molluscan gravels being generally white, beige, or light yellow, and the prevalent sandy peat generally black (N 2/0). Many of the fossils in this unit are preserved in excellent condition, including delicate parts of land crabs (*Geograpsus* sp.), articulated fish skeletons with scales, intact bird skulls, and even a few feathers. The unit has almost certainly been under water constantly since the time of deposition. The contorted nature of the lenses and laminae near the top of the unit in EP are probably a result of the settling of the large rocks deposited in Unit VI. Unit IV pinches out in South Cave. The vicinity of the drip line (Cores 11 and 12) has a sandy and rocky overburden that prevents determination of the exact location of the peat layer's truncation.

In the mid-Holocene (roughly 6000–4000 yr BP), a body of water apparently stood in the sinkhole and North Cave areas, probably linked on the north end to the larger Kapunakea Pond on the outside, and draining slowly seaward over the shallow rocky floor of South Cave through the sump still active (and draining southward) at the extreme southern terminus of South Cave (Fig. 1). At the center of the sinkhole, this sandy peat accumulated at the rate of ~ 500 yr/m or 2 mm/yr.

Unit V is problematic, due to the disturbance of the layer in the sinkhole by the extreme depositional event (tsunami overwash) of Unit VI. Unit V, consisting primarily of peaty sand with lenses or laminae of humic sandy clay, sandy peat, algal mud, and molluscan gravel, is most distinct in North Cave, where it extends from 400 to 220 cm bs (430–250 cm bd). A date from the middle of this unit at 296–297 cm bs in Core 3 was 2705 ± 55 yr BP (2910–2745 cal yr BP). This unit extends from 360 to 240 cm bs (435–320 cm bd) in Core 6 at the center of the sinkhole, and a date from the base of this unit at 356–358 cm bs yielded an age of 3760 ± 70 (4380–3915 cal yr BP).

In EP, Unit V is extremely convoluted by rocks intruding from Unit VI, but ranges roughly from 305 to 325 cm, extending as much as 1 m higher underneath the overhang along the wall in KK46 and adjacent grids. In LL49, a square not protected by an overhang, a sediment date from 305–315 cm yielded an age of 3670 ± 60 yr BP (4155–3845 cal yr BP).

Unit V is rich in bird and fish bones and snail shells. Although a few of the larger and rarer terrestrial snails found in Unit IV are absent, many extinct taxa are present; no definite evidence of human presence has been found in this unit except for small pieces of kukui (*Aleurites moluccana*) nut and marine shell, and a few bones and teeth of *Rattus exulans* (see *Terrestrial vertebrates*). These may have been displaced downward into older sediment by rockfall. An AMS gelatin date on a right pelvis of *R. exulans* from Unit V at 305–315 cm bd in EP grid LL49 yielded an age of 822 ± 60 yr BP (AD 1039–1291). This is the youngest date obtained from this unit; a date on a sediment sample from the same depth in LL49 of EP was 3670 ± 60 yr BP. The latter date is comparable to that obtained from insoluble residue filtered from the gelatin fraction of the rat bone, probably sediment-derived organic acids, of 3038 ± 60 yr BP. The second-youngest date from this unit was on the gelatin fraction of a femur of the extinct Long-legged Owl, *Grallistrix auceps*: 2328 ± 60 yr BP (2485–2299, 2265–2178, and 2168–2157 cal yr BP). A pedal phalanx of the hawk *Buteo* cf. *solitarius* dated to 3416 ± 60 yr BP (3830–3475 cal yr BP). These were protected from subsequent depositional events inside a sheltered pocket in the wall of EP grid KK46 at 245–255 cm bd.

A major unconformity separates Unit V from Unit VI except in the vicinity of EP, where the bottom of VI and the top of V have been mixed by large boulders, some > 100 kg.

Unit VI is unlike anything else in the entire stratigraphic column. Particle size analysis of bulk samples from KK47 reveals a distinctive signature for this layer (Fig. 5). Likewise, classification of stones (Fig. 6) also shows a strong contrast with all other units, with a significant component of allochthonous stones, notably terra rossa (lithified red soil) and a dense black vesicular basalt in this unit only. Both rock types are common on the beach and on the slope seaward of the cave. The coarse fractions of all other units are made up primarily of autochthonous materials, including molluscan gravel and partially redissolved eolianite and flowstone in Units IV and V, and micro-aggregated clay in Unit IX.

The unusual nature of this deposit is also apparent in the dating of plant macrofossils distributed through a 50-cm vertical profile of the layer in EP. All four dates are essentially identical after calibration at 2σ (the combined range is cal yr AD 1425–1660; see Table 1). These are on anthropogenic materials: plant macrofossils from kukui or candle-nut, and bottle gourd (*Lagenaria siceraria*), both Polynesian introductions.

The layer itself is laterally variable. At EP, adjacent to the lowest part of the sinkhole rim on the seaward side, it is ~ 80 cm thick (305–225 cm bs). There the layer is composed of boulders, cobbles, gravel, and sand. These rocks, being highly fractured, mostly angular, and lacking an in situ patina, are consistent with an interpretation of the layer as the result of a single high-energy event. Other components of the unit include marine elements such as coral fragments, abraded mollusc shells, and coarse beach sand. Artifacts of pre-contact types (i.e., no European-derived materials) are present, including many wooden objects (tattoo needles, fragments of canoes and paddles, carved sticks). Large fragments of bottle gourds, some nearly complete, are pressed beneath big stones. All of these lines of evidence are consistent with interpretation of this as a marine overwash deposit from a single high-energy event that occurred ~ 400 yr ago.

Further evidence for this interpretation comes from Unit VI elsewhere in the deposit. The layer extends to the center of the sinkhole at ~ 180 –240 cm bs (250–320 cm bd) in Cores 4 and 6 as a deposit of angular gravel and sand. Beyond, in South Cave, Cores 1, 9, 10, 11, and 12 and the deepest portion of the SC excavation trace a turbidite fan thinning and fining southward into the rear of the cave. In North Cave, all the cores record a thin band of angular gravel and wood fragments. Cores near the west wall of the sinkhole (Cores 14 and 15) were stopped by the densely packed gravel and cobbles at the top of Unit VI.

For marine overwash to breach the east wall, a surge of ≥ 7.2 m a.s.l. would be required. Tremendous sustained energy (in the form of a wave or waves of much greater height than this) would be required to lift large allochthonous boulders from the adjacent beach and drop them over the wall into the vicinity of EP. A tsunami seems the most likely source of the necessary energy. This interpretation is supported by historical accounts of tsunamis on Kaua'i up to ~ 16 m in height. Waves of such magnitude, probably propagating from the Aleutians, have been recorded only on the north coast of the island in historical times (Curtis 1998). The Māhā'ulepū region, on the other hand, would catch the full force of tsunamis or storm surges propagating from the southeast in particular. Tsunamis originating from this direction from both the W coast of South America and also the vicinity of the island of Hawai'i have been recorded in the archipelago (Curtis 1998). A hurricane seems a less likely agent, as the historically recorded hurricane of greatest magnitude on this coast produced a very different type of deposit in the cave, consisting of plant debris and dune sands (see description of Unit X).

Unit VII is primarily "salt-and-pepper" humic sand (i.e., a matrix of white calcareous sand with darker mafic grains

and fine organic detritus), with mottles and lenses of clay of various colors, reddish-brown to dark gray. In EP, numerous color and texture changes are apparent in this layer, but these do not trace to the center of the sinkhole or beyond. Unit VII of Cores 4, 6, 14, and 15 is primarily a uniform humic sand of the "salt-and-pepper" type. At 225 cm in EP, a very dark grayish brown humic sand (2.5Y 3/2) containing goat or sheep teeth, evidence for European contact, yielded a plant macrofossil date of 90 ± 40 (cal yr AD 1675–1765, 1800–1940, 1945–1955). Sediments are banded above this level in EP, with reddish-brown 5YR 4/4 laminae with more clay, and darker humic zones with much charcoal, marine shells of types preferred by Polynesians for food, and bones of chicken and pig. A few fragments of iron also come from this layer.

This unit is also present in South Cave in a channel fill deposit along the wall. A resurgent stream flows under the edge of the wall here, emerging near the core 9 location and flowing out to the sump at the extreme south end of the cave. This fill is a brownish-gray sandy clay, becoming sandier and lighter in color away from the wall. A piece of gourd from this artifact-rich component of SC Unit VII, collected 325–335 cm bd directly on top of stones probably associated with Unit VI, dated to 180 ± 50 yr BP (cal yr AD 1645–1950). Unit VII is virtually absent in North Cave, although a thin band of black clay (N 2/0) in Cores 2, 3, and 5 that appears between Units VI and IX is probably the same black clay as the thin band on top of Unit VII in the sinkhole center recorded in Cores 4 and 6.

Unit VIII is sterile sand in EP at 50–120 cm bd, fully above the water table. This appears to be a thick dome of sand derived from dune migration on the landscape surrounding the cave, resulting in collapse over the east wall. This unit is not present in the sinkhole center or in North Cave. A coeval sand unit occurs as a thick lens in the front of South Cave, perhaps also derived from dune deflation coupled with periodic flooding, as indicated by thin, undulating discontinuous laminae of darker silty sand in the top of this unit in the SC excavations and Cores 1, 9, and 10. In EP, the unit is virtually devoid of biological and cultural materials other than live and dead tree roots, a horse skeleton, and a small piece of coarse cloth. The unit is far more interesting in SC, where it contains numerous anthropogenic features, including post-holes, fire pits, and midden materials. The presence of iron and other introduced materials is consistent with the five radiocarbon dates from this layer, indicating that Unit VIII derives from the 19th and early 20th century. The cause of dune reactivation at this time is apparent from a photograph (negative #46191) obtained from the Bishop Museum Archives

and likely to date from the late 19th century. It shows the landscape north of the cave, including the entrance and Kapunakea Pond. The area is virtually devoid of vegetation, exhibiting signs of extreme overgrazing by livestock.

Unit IX is present in all the cores and excavations, and is missing only from the high sandy areas in the back of the southeastern portion of South Cave. The unit is a dark brown loam-like sandy silty clay (7.5 YR3/2) that is too recent for conventional radiocarbon dating and dendrocalibration. A kuku nut from SC, grid N35, 142–146 cm bd, dated to 10 ± 40 yr BP. The age of this unit can also be inferred by the presence of European-introduced snails (*Subulina octona*) all the way to the base of the unit. In North Cave, the rosy wolfsnail (*Euglandina rosea*) was found at 50 cm in a test pit adjacent to Core 3. It was introduced to Kaua'i in 1957 (Kay 1983). This unit extends below the water table in North Cave and the sinkhole center, confirming accounts of elderly persons living in the area (e.g., L. Kapaka-Arboleda 1997, *personal communication*) that the low parts of the sinkhole and North Cave held shallow water at least seasonally until recent decades. The clay is gleyed to very dark gray color (10YR 3/1) below the water table, and contains indigenous freshwater snails. An attempt to radiocarbon-date the lowermost part of this unit failed: the date of 2145 ± 55 yr BP on the organic fraction of the sediment is too old by more than an order of magnitude. Subsequent discussion in 1996 with elderly resident Adena Gillin (now deceased) revealed the source of the discrepancy. In the 1950s, her husband Elbert Gillin, an engineer for the Grove Farm Company, channeled the Waiopili Stream outside the entrance and thus drained off the Kapunakea Pond. This, perhaps coupled with erosion from the cane fields and rock quarry in the watershed, has resulted in the over-bank redeposition of old pond sediments and marshy soils through the entrance and into the cave in the late 20th century.

Unit X consists of woody debris and dune sands deposited by Hurricane Iniki in 1992. This material was deposited after we started to work in the cave (following the collection of Cores 1–3 on a survey trip in the weeks just before the hurricane). It consists of a thin mantle of sand in North Cave in the vicinity of Cores 2, 3, 7, and 8, and plant debris in discontinuous patches of abraded wood and leaves along the east wall from the entrance all the way to the sump in the extreme south of South Cave. Adjacent to Core 3, a shallow test pit revealed a similar sand lamina at ~15 cm bs, perhaps storm overwash from Hurricane 'Iwa in 1982. These deposits are quite distinct in appearance from the stony debris of Unit VI, but more similar to the sand lenses described for Units IV and V, which might also be storm deposits.