A Second Endemic Land Mammal for the Hawaiian Islands: A New Genus and Species of Fossil Bat (Chiroptera: Vespertilionidae)

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A second endemic land mammal for the Hawaiian Islands: a new genus and species of fossil bat (Chiroptera: Vespertilionidae)

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ABSTRACT

Located over 3800 km from the nearest continent, the Hawaiian Islands have previously been thought to support only one endemic land mammal, the extant Hawaiian hoary bat (*Lasiurus cinereus semotus*), a taxon that apparently initially dispersed from mainland North America between 10,000 and 7000 years ago. Some uncertainty exists regarding the status of this taxon (i.e., whether or not populations representing more recent invasions of *L. cinereus* from North America are exchanging genes with the older lineage, and whether or not *semotus* represents a distinct species), but all researchers agree that hoary bats are the only endemic land mammals extant in the islands today. However, fossil evidence indicates that the Hawaiian Islands once supported another quite different endemic bat species that is now extinct. Skeletal remains of a new genus and species of vespertilionid bat are herein described from various Late Pleistocene and Holocene/Recent deposits on the five largest Hawaiian Islands. The new taxon is diagnosed by a mosaic of features including dental formula, molar morphology, skull shape, and metacarpal formula. This new taxon, which is smaller than Hawaiian hoary bat, was apparently present in the Hawaiian Islands by 320,000 years B.P. and survived until at least 1100 years ago and possibly much later. Accordingly, two species of bats coexisted on the Hawaiian Islands for several thousand years. As with numerous extinct endemic bird species, the extinction of the new bat taxon described here may have resulted either directly or indirectly from human colonization of the islands and the invasive nonnative species that came with human explorers and settlers.

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INTRODUCTION

The Hawaiian Islands are one of the most geographically isolated archipelagos in the world. Located over 3800 km from any continent, the Hawaiian Islands host a diverse and unusual flora and fauna including many endemic species (Ziegler, 2002). The islands formed as a result of volcanism associated with a hotspot under the Pacific tectonic plate, but although the hotspot has been active for many millions of years, the oldest of the current exposed "high islands" (those that have not been eroded over time to become low remnant islands and atolls) are only circa 6 million years old (Price and Clague, 2002; Sherrod et al., 2007). The Hawaiian Islands have never been connected to a continent, and all native plant and animal species are believed to have colonized the archipelago via long-distance dispersal by sea or air (e.g., on oceanic flotsam, drifting on air currents, by active flight, or by hitching a ride such as seeds or snails attached to birds; Russell et al., 2015, and references cited therein).

The terrestrial vertebrate fauna of the Hawaiian Islands is much less diverse than that found on any of the nearest continental regions and less isolated islands, probably due to the great extent of open ocean between the Hawaiian archipelago and any source areas for colonization. The terrestrial vertebrate fauna of the Hawaiian Islands is dominated by birds, many of which represent endemic adaptive radiations (Ziegler, 2002; Cowie and Holland, 2008; Lerner et al., 2011). The best known of these is the Hawaiian Honeycreepers, which comprise over 50 species (Cowie and Holland, 2008; Lerner et al., 2011). Many other endemic birds are or were also present in the islands, although a large number of these—perhaps as many as 70%—are now extinct (Boyer, 2008). Endemic reptiles and amphibians are completely absent from the Hawaiian Islands, although at least 20 species (e.g., *Iguana* and *Chameleo* lizards, *Eleutherodactylus* and *Rana* frogs) have been introduced by humans (Moulton and Pimm, 1986; Kraus et al., 1999). The mammalian fauna of the Hawaiian archipelago is also small (Ziegler, 2002). At least 17 species of nonnative mammals are established in the islands, including rats, mongooses, and a diverse array of domestic species (cats, dogs, goats, sheep, pigs, horses, cattle). Additionally, there are two extant mammals native to the Hawaiian Islands: the Hawaiian monk seal (*Monachus schauinslandi*) and the Hawaiian hoary bat (Atkinson, 1977; Olson and James, 1982b, 1984; Tomich, 1986; Athens et al., 2002; Ziegler, 2002). Monk seals are primarily aquatic, leaving the endemic terrestrial mammalian fauna particularly small—and limited to bats.

BATS IN HAWAI'I: THE HAWAIIAN HOARY BAT: It has long been thought that the only extant terrestrial mammal endemic to the Hawaiian Islands is the Hawaiian hoary bat, *Lasiurus cinereus semotus* (Allen, 1890), a vespertilionine that is found on several and perhaps all of the eight main Hawaiian Islands (Jacobs, 1996; Russell et al., 2015; also see appendix 1 for notes on generic classification of hoary bats). This taxon has been treated as a subspecies of the mainland hoary bat *Lasiurus cinereus* by most authors (e.g., Tomich, 1986; Koopman, 1993, 1994; Jacobs, 1996; Simmons, 2005; Russell et al., 2015), although Baird et al. (2015) recently recommended recognizing it as distinct at the species level (see below). Hawaiian hoary bats are distinct morphologically from continental *L. cinereus*, being smaller in size yet having a proportionally larger gape and masseter muscles (Jacobs, 1996), and they use echolocation calls that are significantly higher in frequency (Barclay, 1986; Barclay et al., 1999). However, convincing evidence that Hawaiian populations represent a distinct species (rather than a subspecies of *L. cinereus*) has been lacking. Recently, Russell et el. (2015) analyzed mtDNA data from over 150 hoary bats (including 59 from the Hawaiian Islands) to determine the history of *Lasiurus* in Hawaiʻi and its relationship to continental *L. c. cinereus* and the related South American *L. c. villosissimus*. Surprisingly, they found that Hawaiian *Lasiurus* populations resulted from at least two relatively recent dispersal events from North American populations of *Lasiurus c. cinereus*, with the first colonization occurring no more than 10,000 years ago and the second perhaps 800 years ago (Russell et al., 2015). Cytochrome oxidase 1 (*CO1*) haplotypes of the older mitochondrial lineage (designated "Hawaii1") are ~3% different from those of the younger Hawaiian haplotypes ("Hawaii2"), which were found to be indistinguishable from those of North American *Lasiurus cinereus*. Indeed, one hoary bat *CO1* haplotype from Maui and Oʻahu was also found in Nebraska, Ontario, Saskatchewan, California, Michigan, and Georgia (Russell et al., 2015). Russell et al. (2015) collected and analyzed nuclear genetic data from Hawaiian bats (no North American samples were available) but did not find the same pattern of differentiation between groups in the nuclear loci. Compared with the mtDNA haplotype groups, between-population variation in the nuclear chymase (*CHY*) and recombination activating gene 2 (*RAG2*) loci was actually less than within-population variation in the Hawaiian Islands, although this difference was not statistically significant. Russell et al. (2015) noted that lack of congruent structure at the nuclear loci might result either from ongoing gene flow between the older and younger Hawaiian mitochondrial clades, or might be due to incomplete lineage sorting in the absence of gene flow. Given that distinguishing between these options was not possible with their data, Russell et al. chose to maintain the traditional taxonomy for the Hawaiian hoary bat, treating it as a single taxon distinct at the subspecies level from North American bats and retaining the name *Lasiurus cinereus semotus* for all Hawaiian populations pending additional studies of nuclear data and gene flow patterns.

In contrast, Baird et al. (2015) recommended sweeping changes in taxonomy of lasiurine bats—including those from Hawaiʻi—based on less evidence. On the basis of analyses of mitochondrial gene data sampled in only nine Hawaiian individuals plus additional mainland samples, these authors applied the name *semotus* to the older mtDNA lineage, raised *semotus* to species rank, concluded that the younger mtDNA lineage represents *cinereus*, and therefore claimed that two species of hoary bats coexist today in the Hawaiian Islands. Given the data available, we do not agree with any of the changes to the status of *Lasiurus cinereus semotus* proposed by Baird et al. (2015). First of all, the mitochondrial genome can be a very misleading guide to species limits if there is sex-biased dispersal within a species (Dávalos and Russell, 2014). Female philopatry and male-mediated dispersal bias, even at low levels (e.g., 1 female: 4 males), can result in a high "false positive" rate for species detection using mitochondrial haplotype variation and population structure alone (Dávalos and Russell, 2014). In the absence of nuclear genetic data, we agree with Russell et al. (2015) that male-mediated gene flow between the older and younger mtDNA groups of Hawaiian hoary bats cannot be ruled out. Concluding that the two Hawaiian haplotype groups represent two distinct species is premature, especially given that only ~2% cytochrome *b* (*cytb*) sequence divergence was detected between these groups by Baird et al. (2015: fig. 2). This percentage of *cytb* sequence divergence is quite low for between-species variation in bats, and is much more characteristic of within-species population variation patterns (Bradley and Baker; 2001; Baker and Bradley, 2006).

Another issue of importance is the correct application of the name *semotus*. If there actually are two species of hoary bats extant in the Hawaiian Islands, it is not at all clear to which lineage (“Hawaii1” or “Hawaii2”) the name *semotus* should be applied. Baird et al. (2015: 15) claimed that “the most conservative approach to assigning names… is to assume that the more distinct clade is *semotus*, while the Hawaiian individuals with haplotypes more closely related to North American individuals belong to *cinereus*.” This statement reflects a lack of understanding of the rules of zoological nomenclature. It is identity of name-bearing type specimen(s) that determines the application of zoological names, not convenience nor the age of lineages (Ride, 1999). Lyon and Osgood (1909) designated a lectotype for *Atalapha semota* Allen, 1890 (= *Lasiurus cinereus semotus*), which is housed in the United States National Museum (USNM 15631). The type locality and the island of origin of this specimen within the Hawaiian archipelago unfortunately remain unknown (Lyon and Osgood, 1909). Representatives of both *Lasiurus* mtDNA haplotype groups co-occur on the islands of Maui, Kaua‘i, and O‘ahu (Russell et al., 2015; Baird et al., 2015), suggesting that both groups may occur in sympatry broadly across the islands. Only the big island of Hawai‘i seems to support a single haplotype group—the older one (the “Hawaii1” group of Russell et al., 2015). Some morphological differences have been suggested to exist between populations of hoary bats on the islands of Hawai‘i and Maui (U.S. Fish and Wildlife Service, 2011) that might reflect morphological differences between the haplotype groups, but these have yet to be formally analyzed or correlated with the mtDNA haplotypes. Without examination of the lectotype—and confirmation of its association with a particular haplotype group—there is no way to determine the correct application of the name *semotus* if there are two species of hoary bats in the Hawaiian Islands. If the lectotype belongs to the “Hawaii1” mtDNA lineage, then the name *semotus* would be available for the “Hawaii1” bats should they prove to be a distinct species or subspecies. If, however, the lectotype belongs to the “Hawaii2” lineage, which is apparently nearly identical to mainland *L. c. cinereus* populations, then a new name would be needed for the “Hawaii1” bats if they prove taxonomically distinct since in this case the name *semotus* would remain a junior synonym of *cinereus* applicable only to the “Hawaii2” bats.

In summary, although there *may* be two species of extant hoary bats in the Hawaiian Islands, this has yet to be demonstrated. We therefore maintain the traditional taxonomy for the Hawaiian hoary bat, treating it as a single taxon (*Lasiurus cinereus semotus*) pending future studies of nuclear genes and gene flow among various populations in the islands.

ADDITIONAL BATS IN HAWAI‘I: No museum specimens of bats from the Hawaiian Islands collected prior to 1861 seem to exist, but *Lasiurus cinereus semotus* is presumably the taxon for which the Hawaiian name *‘ōpe‘ape‘a* was being used at the time of European contact in 1778 (e.g., see Malo, 1951) as well as the bat historically noted in 1816 to be common on, at least, the island of O‘ahu (von Kotzebue, cited in Tomich, 1986). Two alien species of bats, *Tadarida brasiliensis* from North America and *Pipistrellus javanicus* from Japan, were apparently liberated on O‘ahu as potential mosquito-control agents in the 1890s, but these introductions evidently never led to successful establishment of nonnative populations of bats in the Hawaiian

Islands (Tomich, 1986). Accordingly, it was quite unexpected when one of us (F.G.H.) discovered bat skeletal remains in 1981 and 1982 that represented a species that was smaller than, and obviously distinct from, *Lasiurus cinereus semotus*. The initial specimens were collected while investigating lava tubes on Maui that turned out to preserve relatively abundant material of both bat species. Since that time, considerable additional skeletal material representing both of these species of bats has been recovered on Hawaiʻi, Kauaʻi, Maui, Molokaʻi, and Oʻahu (fig. 1; Ziegler et al., 2014). This material was collected from the exposed floors of additional lava tubes and from various sedimentary deposits both in and out of lava tubes. The smaller bat is unquestionably a member of the family Vespertilionidae and is similar in some respects (e.g., dentition) to species of *Lasiurus*, but it differs markedly in cranial shape. The mosaic of characters exhibited by this taxon likewise differs from all other previously described genera of vespertilionid bats. This bat is therefore formally described herein as a new genus and species. The environmental setting and related details are described for the important specimen collection sites for this new taxon. Brief comments on Hawaiian fossil remains referred to *Lasiurus cinereus semotus* are also presented.

METHODS AND MATERIALS

TERMINOLOGY: Two general classes of Hawaiian chiropteran material are considered here: obviously rather recent specimens of *Lasiurus cinereus semotus* (i.e., individuals either known or assumed from preservation of pelage or other soft parts to have lived within the past 100 years or so), and specimens of bats collected in Hawaiʻi solely as skeletal remains and for various reasons presumed to have died more than a century ago. Specimens of the former class are arbitrarily here termed "historic," and those of the latter "fossil" (even though many of them are not obviously permineralized). Specific age estimates, when known, are given as years before present (ybp). A portion of the fossil material from lava tubes, which generally is not permineralized and is often quite fragile, was hardened by brief immersion in an acetone solution of Alvar (polyvinyl acetal) or similar strengthening agent before removal from the substrate.

For cultural periods, we use "Polynesian" to indicate the approximate 1000 year span from the initial occupation of the Hawaiian Archipelago by Polynesians (probably by A.D. 800; Kirch, 1985) to the time of initial European arrival in 1778, and "postcontact" for the subsequent period.

Culturally sensitive and significant lava tubes are legally protected under Hawaiʻi or Federal laws, and information on their precise location is considered confidential. However, such data are archived with the appropriate land owner or agency involved. Accordingly, locality data given for lava tubes, including specific elevation above sea level and geographic coordinates, should be regarded as approximate. Depending on data available, these figures generally refer either to the position of the main or most frequently utilized entrance of the tube or to the point within the tube where a specimen was collected. When necessary, vertical distances in feet, and horizontal distances in miles, as stated in publications or collectors' records have been converted to metric measurements. The GIS coordinates and map datum are given if known.

SPECIMEN MEASUREMENTS: Lists of specimens examined for this study are provided in appendices 2 and 3. Dimensions of teeth and most skeletal elements were taken with dial calipers calibrated to 0.1 mm, using 3× or greater magnification for the dental measurements. All of the cranial measurements were taken in the manner illustrated by Handley (1959). Contra usual practice, forearm length was measured without including the carpals, which are not articulated with the radius in most of the fossils. Metacarpal lengths were taken as chord measurements of cleaned disarticulated bones with a flat millimeter rule, estimated to the nearest 0.5 mm. When both right and left members of a tooth row or bone pair were available for measurement, the figure listed is the mean value. Specimens were identified as "subadult" if the distal metacarpal epiphyses were not fused to the shaft, and measurements of clearly subadult individuals were not included in any of our analyses.

Abbreviations for morphological terms and measurements used in the description are as follows:

BCB	Braincase breadth measured as the greatest distance across parietal portion of the braincase superior to the auditory bullae
BCD	Braincase depth measured from the basicranial plane medial to auditory bullae to dorsalmost point along sagittal suture or crest
C–M3	Length of the upper toothrow measured from the anterior edge of canine to the posterior edge of the last molar (M3)
C–m3	Length of the lower toothrow measured from the anterior edge of canine to the posterior edge of the last molar (m3)
CRL	Cranial length measured from the posteriormost point of the lambdoidal crest to the anteriormost extent of premaxillae, excluding incisors and canines
FAL	Forearm length measured as the greatest length of the radius excluding carpals
FAN	Mediolateral distance across trochlear notch of radius
FAS	Mediolateral shaft width of radius, taken 5 mm distal to distal rim of trochlear notch
FDW	Mediolateral distance across condyles of distal femur
FEL	Greatest length of femur
FIL	Greatest length of fibula
FPW	Mediolateral distance across greater and lesser trochanters of proximal femur
HDW	Mediolateral distance across medial and lateral epicondyles of distal humerus
HUL	Greatest length of humerus, not including medial epicondylar spine
HPW	Greatest width across greater and lesser tuberosities of proximal humerus
IOW	Least width across interorbital constriction of frontal bones
M1–3	Combined crown length of upper three molars
m1–3	Combined crown length of lower three molars
m2–3	Combined crown length of lower posterior two molars
MAD	Depth of mandibular ramus immediately posterior to m3
MAH	Least distance between superiormost extent of mandibular coronoid process and ventral border of dentary
MAL	Distance between posterior surface of mandibular condyle and anteriormost extent of dentary, excluding incisors
Mc	Metacarpal
OR	Observed range of sample measurement

PAB	Distance across palate between lateral M3 faces
RAB	Distance between anterior openings of infraorbital canal of rostrum
SGW	Anteroposterior width of glenoid fossa of scapula
TIL	Length of tibia
TPW	Mediolateral distance across medial and lateral condyles of proximal tibia
ZYB	Greatest distance across lateral surfaces of zygomatic arches

Institutional Abbreviations: Specimens examined, including material from the Hawaiian Islands and comparative material representing other vespertilionid genera and species from around the world, are listed in appendices 2 and 3. Abbreviations used for institutions as well as prefixes of catalog numbers for the specimens examined are as follows:

AMNH	American Museum of Natural History, New York
BBM, BBM-X, BPBM	Bishop Museum, Honolulu, Hawai‘i, catalog number prefixes
BMAS	Bishop Museum Archaeological Sites prefix
CSH	Cultural Surveys Hawai‘i
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, catalog number prefix
SIHP	Hawai‘i State Inventory of Historic Places Sites prefix
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., catalog number prefix

SYSTEMATICS

Family Vespertilionidae Gray, 1821

Synemporion keana, gen. and sp. nov.

Lava-tube Bat
Figures 2–8, tables 1–3

Holotype: BPBM 159269, a nearly complete skeleton of an adult individual including skull, both dentaries, and partial body skeleton with both scapulae, humeri, ulnae, radii, and femora; right tibia and partial innominate with 2 fused sacral vertebrae; 8 metacarpals; 2 manual phalanges; 1 pedal phalanx; atlas; 2 thoracic vertebrae; and 1 rib. This individual was collected on 16 September 1982 by Francis G. Howarth and Fred D. Stone, Field No. 22 of F.G. Howarth.

Paratypes: Specimens representing at least 110 individuals from 5 Hawaiian Islands, as listed in appendix 2, including 33 partial to nearly complete skulls, 9 dentaries, 34 associated partial post cranial skeletons, and 60 individual post cranial bones.

Type Locality: Hawaiian Islands, Maui Island, ‘Ulupalakua Ranch, Māhiehie Cave, 500 m, 20.63°N; 156.39°W (WGS 84 datum).

Geographic and Geologic Range: Hawaiian Islands, at least the five largest islands, from ca. Middle Pleistocene to Late Holocene (but apparently not into post-1778 historic period), with details as follows. Kaua‘i: infill of sinkhole of Late Pleistocene lithified calcareous dune deposits, and in Early Holocene eolian surface calcareous sand-dune deposits; O‘ahu: in

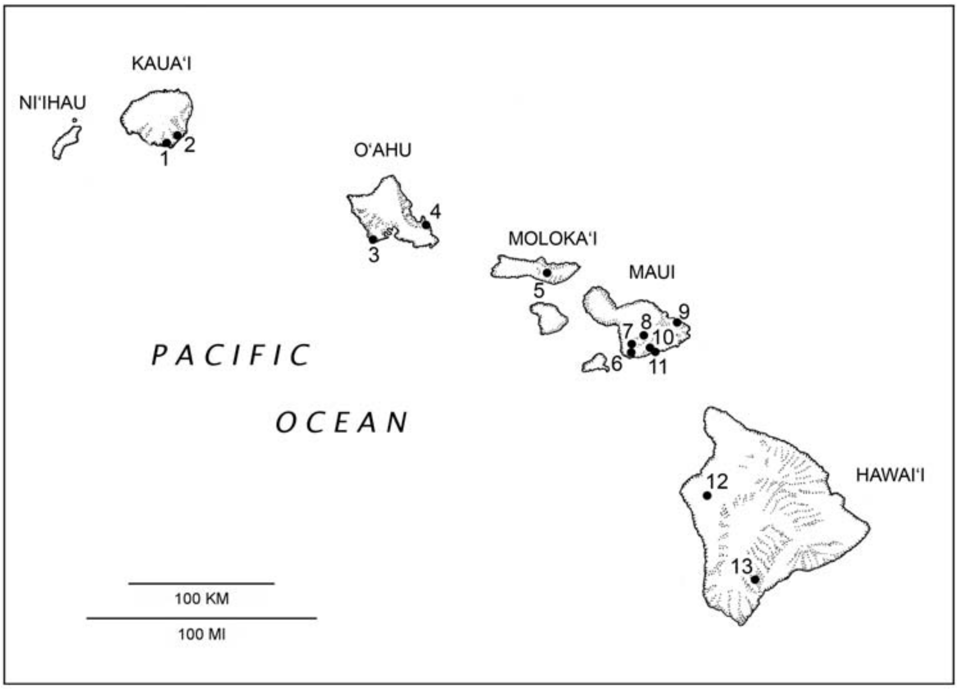

FIGURE 1. Map of the main Hawaiian Islands showing relative locations of the principle collecting sites of fossil *Synemporion keana*. See appendix 2 for list of specimens from each site and appendix 4 for detailed descriptions of each site. (**1**) Makawehi Point dunes; (**2**) Māhāʻulepū Limestone Sinkhole; (**3**) limestone sinkholes near Barbers Point; (**4**) Ulupaʻu Head lake deposit; (**5**) Lua Lolo Piping Cave; (**6**) Puʻu Naio Cave; (**7**) Māhiehie Cave; (**8**) Puʻu Mākua Cave; (**9**) Kaʻeleku Caverns; (**10**) Crystal Cave; (**11**) Kahāwaihapapa Cave; (**12**) ʻŪmiʻi Manu Cave; (**13**) Kahuku Ranch Cave.

Middle Pleistocene pond deposits of volcanic tuff-cone crater, as well as in later-Pleistocene-to-Holocene composite soil deposits (primarily sedimentary) within limestone sinkholes in emergent Late Pleistocene coral-algal reefs; Molokaʻi: in presumably Polynesian or early post-contact alluvial sediment on floor of a dynamically active piping cave; Maui: on exposed floor, embedded in mineralized crusts on walls and in alluvial sediments of Late Pleistocene or Holocene lava tubes; Hawaiʻi: on exposed floor or in alluvial deposits of Late Pleistocene and Holocene lava tubes; approximate locations of these sites are shown in figure 1, and detailed information on all sites is provided in appendix 4.

Etymology: The genus name *Synemporion* root from Greek common noun *synemporos,* "fellow traveler or companion," with addition of the suffix *-ion* to form a neuter diminutive, in allusion to the new bat's former co-occupation of the tectonically mobile Hawaiian Islands with the larger *Lasiurus cinereus semotus.* The specific name is a noun in apposition, formed from Hawaiian: the demonstrative *ke,* plus *ana,* "cave" or "lava tube," referring to the subterranean provenience of the holotype and a majority of the paratypes.

Diagnosis: A small vespertilionid with a dental formula of I1/3, C1/1, P1–2/2, M3/3 = 30–32. Distinguished from other vespertilionid genera with broadly similar dental formulae (*Scotoecus, Scotozous, Chalinolobus, Lasiurus, Nycticeius, Rhogeesa, Scotomanes, Scotophilus,*

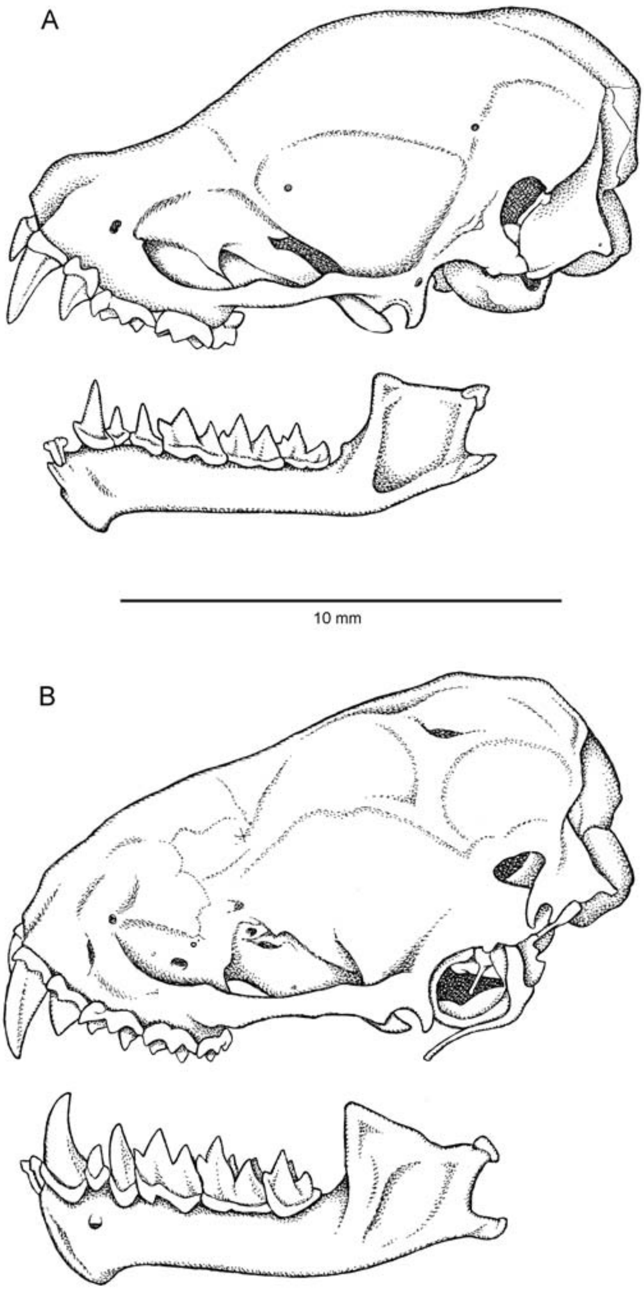

FIGURE 2. Lateral views of the skull and left dentary of **A,** the holotype of *Synemporion keana* (BPBM 159269) compared with **B,** *Lasiurus cinereus semotus* (BPBM 184506). Note the difference in the rostral profile between the two species, including the more robust lower jaw dentition in *Lasiurus* compared with *Synemporion*.

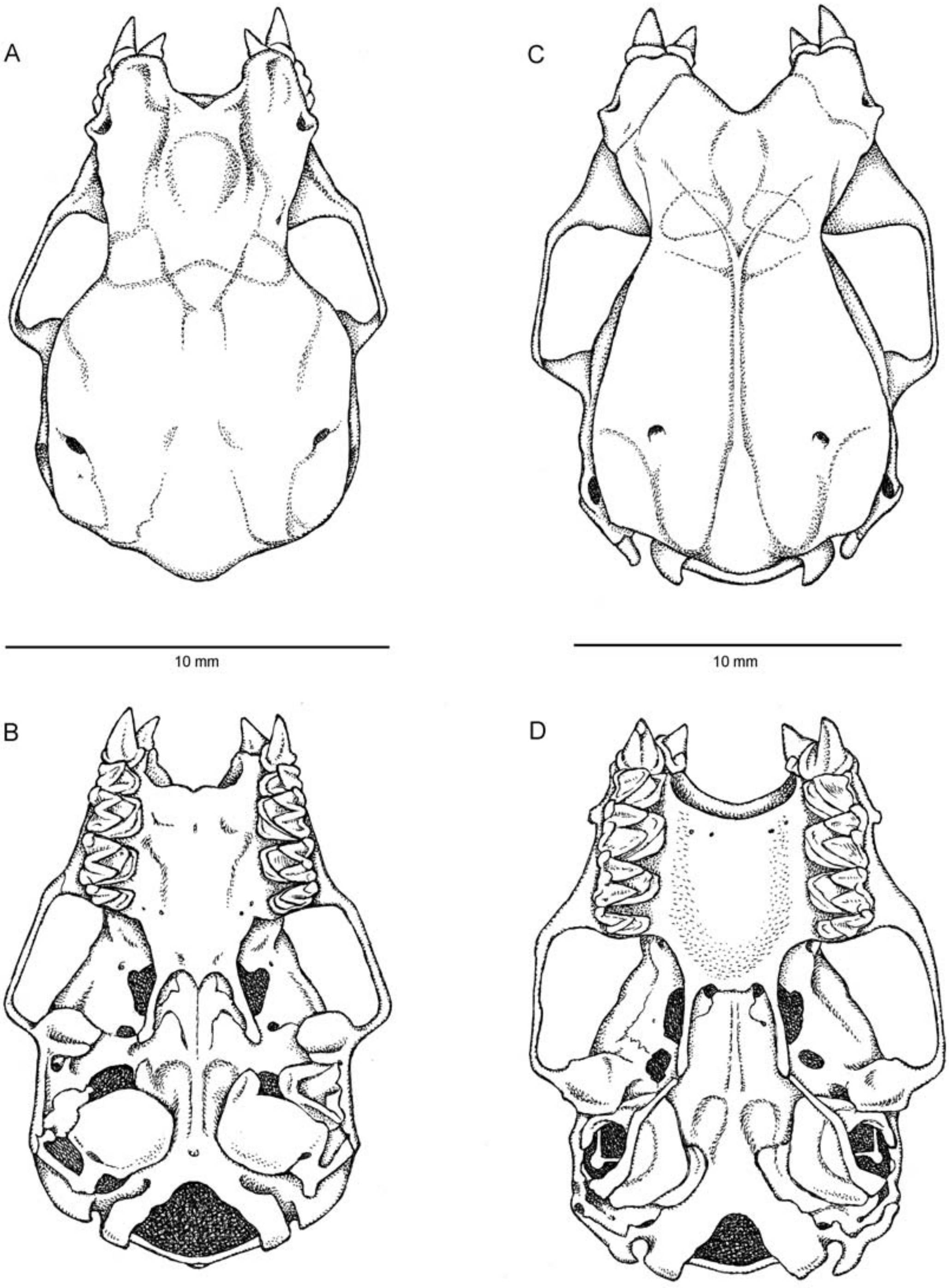

FIGURE 3. **A,** Dorsal view and **B,** ventral views of the skull of the holotype of *Synemporion keana* (BPBM 159269) compared with **C,** dorsal and **D,** ventral views of the skull of *Lasiurus cinereus semotus* (BPBM 184506). Note that the rostrum of *Synemporion* is narrower than that of *Lasiurus*, and that *Synemporion* also lacks a sagittal crest.

TABLE 1. Comparative craniodental measurements of Hawaiian bats. All measurements are in mm and were taken as described in the Methods and Materials section. Hypodigm measurements presented as "mean(range)N." Specimens measured are listed in appendix 3; subadult individuals were excluded from the summaries presented here. The *Synemporion keana* hypodigm measurements include those of the holotype.

	Synemporion keana		*Lasiurus cinereus semotus*	
	Holotype	Hypodigm	Fossil	Historic
CRL	13.6	13.7 (12.9–14.1) 17	15.1 (15.1) 1	15.3 (14.6–15.9) 14
ZYB	9.4	9.1 (8.7–9.5) 15	–	11.5 (11.0–12.4) 16
IOB	4.4	4.3 (4.1–4.6) 19	5.1 (5.1–5.2) 3	4.9 (4.7–5.1) 19
BCB	7.7	7.8 (7.4–8.1) 18	8.7 (8.7) 1	8.7 (8.2–9.0) 16
PAB	5.8	5.8 (5.6–6.2) 12	8.3 (8.0–8.6) 3	7.6 (7.0–8.3) 18
RAB	4.8	4.8 (4.6–5.0) 23	7.5 (6.4–8.5) 4	6.8 (6.4–7.2) 19
C–M3	4.8	4.7 (4.4–4.9) 16	5.9 (5.7–6.3) 3	5.8 (5.4–6.2) 21
M1–3	3.1	3.0 (2.7–3.3) 22	3.8 (3.6–4.1) 4	3.6 (3.4–3.8) 21
MAL	9.6	9.8 (9.5–10.3) 23	12.4 (11.4–13.5) 11	11.9 (11.2–12.6) 21
MAH	2.8	2.9 (2.5–3.2) 26	4.4 (3.7–5.2) 14	4.0 (3.7–4.7) 21
c–m3	5.6	5.4 (5.1–5.7) 16	6.7 (6.4–7.1) 4	6.5 (6.1–6.9) 21
m1–3	3.8	3.7 (3.4–3.9) 16	4.7 (4.3–5.1) 11	4.4 (4.1–4.7) 21
m2–3	2.4	2.4 (2.1–2.6) 22	3.0 (2.7–3.3) 19	2.8 (2.6–3.1) 21

Otonycteris, Bauerus, Pharotis, Nyctophilus) by the following traits: upper I2 always absent (sometimes or always present in *Scotozous* and *Chalinolobus*); upper P2 variably present (always absent in *Nycticeius, Rhogeesa, Scotomanes, Otonycteris, Bauerus, Pharotis, Nyctophilus*); lower incisors trifid and subequal in size (all bifid in *Otonycteris* and *Scotophilus*; i1 and i2 bifid in most *Rhogeesa*, all species of which have i3 reduced to a peg or spicule); M3 crown approximately 1/3 the area of M1 and M2, lacking any trace of a metacone or premetacrista (M3 crown area ½ or more than that of M1 and M2, and premetacrista present, in *Nycticeius, Nyctophilus, Scotoecus, and Scotozous*); m3 with well-developed entocoinid and talonid only slightly narrower than trigoinid (entoconid poorly developed or absent and talonid markedly narrower than trigonid in *Scotomanes*); skull with low rostrum and moderately well-developed forehead that rises abruptly to join with braincase, so that the rostrum profile appears concave in lateral view (rostrum profile flat or convex and forehead break absent in *Lasiurus, Nycticeius, Scotomanes, Scotoecus, Scotozous,* and *Otonycteris*); rostrum relatively narrow (broad in *Scotoecus*, *Scotomanes*, and *Lasiurus*); sagittal crest absent (present in *Lasiurus, Nycticeius, Scotozous, Scotoecus, Rhogeesa, Scotophilus, Scotomanes, Chalinolobus, Otonycteris, Bauerus, Pharotis,* and *Nyctophilus*); metacarpal formula III > IV > V (metacarpal formula III = IV = V in *Chalinolobus, Rhogeessa, Nycticeius, Scotoecus,* and *Scotomanes;* III > IV = V in *Nyctophilus* and *Otonycteris*; III = IV > V in *Scotophilus*).

Description: The dental formula of *Synemporion* is I1/3, C1/1, P1–2/2, M3/3 = 30–32, with the small anterior upper premolar (here termed P2 following Miller, 1907) variably present (figs. 2–5). Among specimens of *Synemporion* with complete palates, P2 is present on both sides in 4 specimens, present on one side and absent on the other side in 1 specimen, and completely absent in 3 specimens

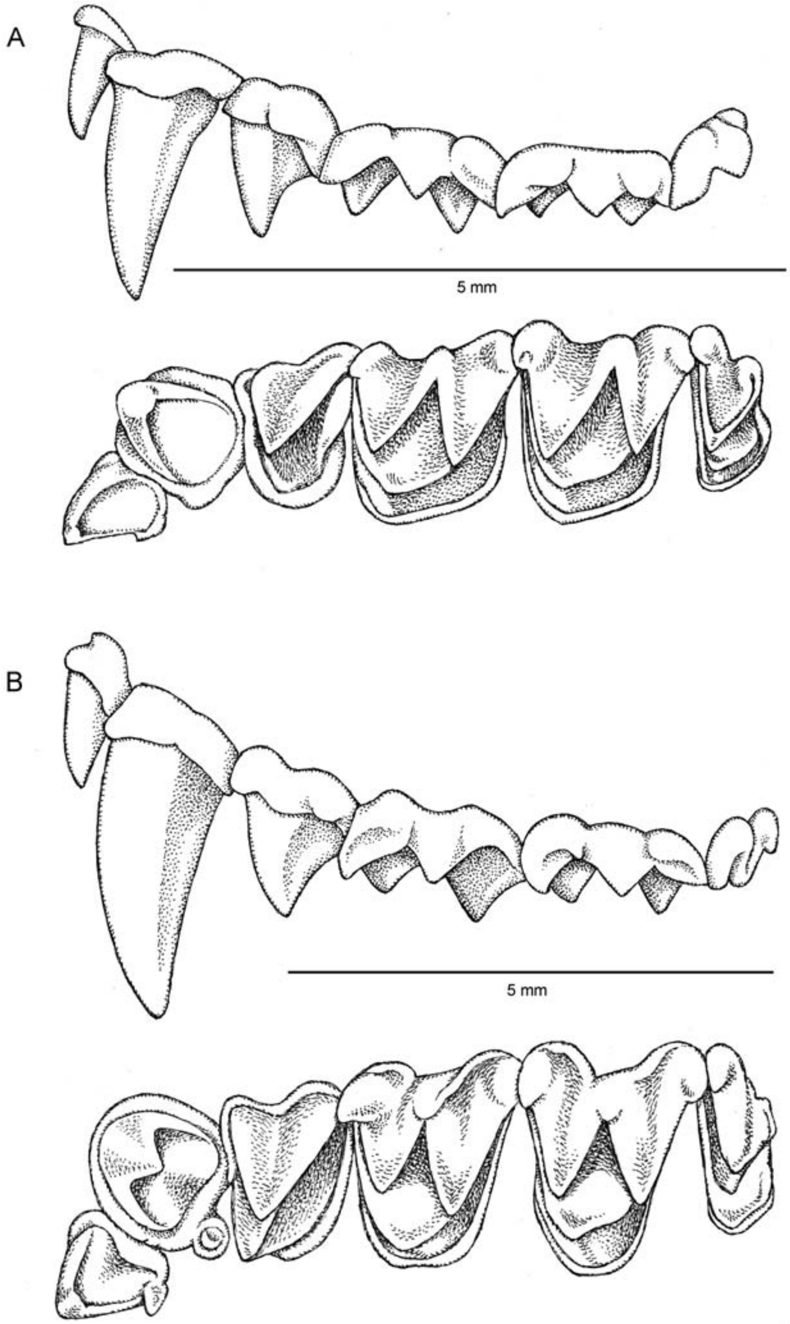

FIGURE 4. Lateral and occlusal views of the upper dentition of **A,** the holotype of *Synemporion keana* (BPBM 159269) compared with that of **B,** *Lasiurus cinereus semotus* (BPBM 184506). Note that a small anterior upper premolar (P2), visible in occlusal view in *Lasiurus*, is absent in the holotype of *Synemporion keana*. This tooth is variably present in *Synemporion*, occurring somewhat more than 50% of the time and sometimes present on one side but absent on the other side in the same individual (see text for discussion).

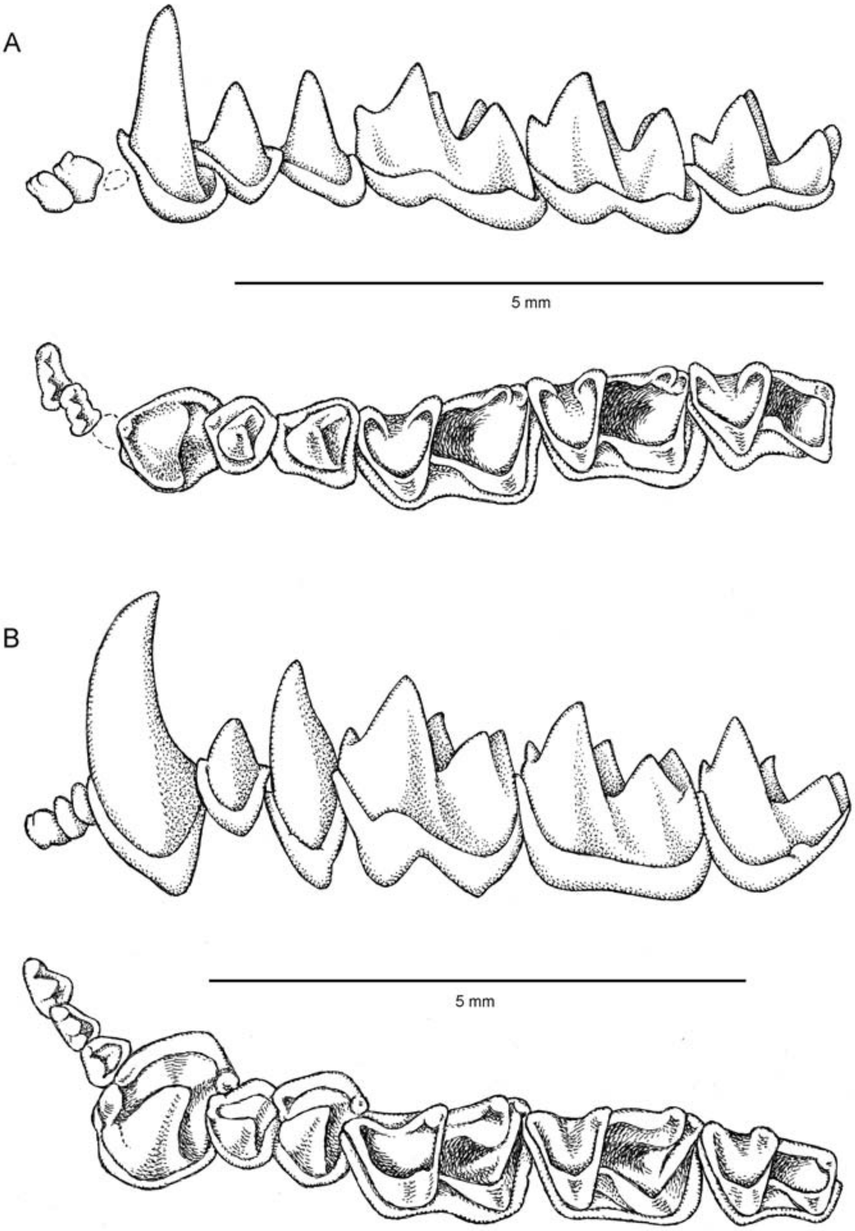

FIGURE 5. Lateral and occlusal views of the lower dentition of **A,** the holotype of *Synemporion keana* (BPBM 159269) compared with that of **B,** *Lasiurus cinereus semotus* (BPBM 184506).

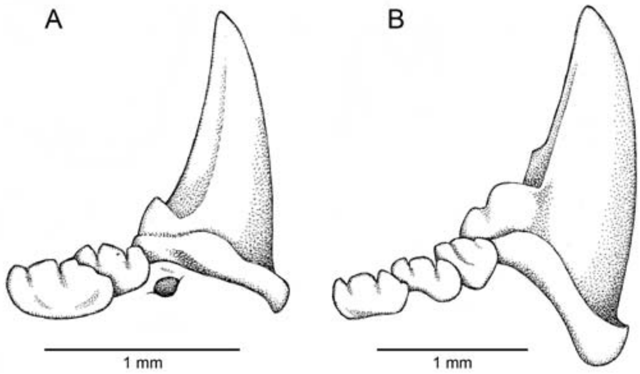

FIGURE 6. Anterior view of the lower incisors and canine of **A,** the holotype of *Synemporion keana* (BPBM 159269) compared with those of **B,** *Lasiurus cinereus semotus* (BPBM 184506). The third lower incisor (i3) is absent in the holotype of *Synemporion* but paratypes preserve this tooth, which is always trilobed.

including the holotype (figs. 3, 4). Two half-palates both preserve a P2. Taken together, these observations suggest that P2 was present somewhat more than 50% of the time in *Synemporion*. When present, this tooth is minute and displaced lingually to lie in the angle between the lingual margins of C and P4. Selected craniodental measurements for *S. keana* are given in table 1.

The single upper incisor of *Synemporion* is roughly two-fifths to one-half height of the upper canine and has about half its crown area, with a small posterointernal cingular cusp (fig. 4). The upper canine is tall, straight, and not recurved (figs. 2, 4). The posterior upper premolar (P4), always present and relatively large, has an unworn crown height about three-fourths that of the canine. An anterolingual cingular cusp is present on P4. M1 and M2 are dilambdodont, subequal in size, and lack a discrete hypocone cusp. Both of these teeth have a postprotocrista that extends from the protocone to the base of metacone, thus closing off the trigon basin posteriorly. The preprotocrista on M1 and M2 extends from protocone to the parastyle rather than to base of paracone. M3 is quite reduced, with a crown area little more than one-third the area of M1 and M2 and it lacks any trace of a metacone or premetacrista. The postparacrista is approximately two-thirds the length of the preparacrista, and the length of the lingual portion of the tooth is greater than the length of the labial portion.

The lower incisors of *Synemporion* are mesiodistally broad, trifid; and the crown of i1 substantially overlaps that of i2 when seen in anterior view (figs. 5, 6). The transverse crown width of unworn i1 and i2 about twice diameter of exposed root, and that of unworn i3 (missing in the holotype although the alveolus is present) is apparently only a little smaller. The lower canine is tall, sharply pointed, and not recurved (figs. 2, 5). Two double-rooted lower premolars are present. The crown length and height of p2 is approximately two-thirds that of p4, which is equal in crown height to m1. Three lower molars are present; m1 and m2 subequal in size, while m3 is somewhat smaller than the anterior molars in all dimensions. The talonid is wider than trigonid in m1 and m2, and both of these teeth are nyctalodont (the postcristid connects hypoconid with hypoconulid, so that talonid basin is narrowly open posteromedially). The last molar (m3) has a talonid that is slightly narrower than trigonid, and lacks a hypoconulid although the hypoconid and entoconid are both well developed.

TABLE 2. Comparative postcranial measurements of Hawaiian bats. All measurements are in mm and were taken as described in the Methods and Materials section. Hypodigm measurements presented as "mean(range) N." Specimens measured are listed in appendix 3; all subadult individuals were excluded from the summaries presented here. The *Synemporion keana* hypodigm measurements include those of the holotype.

	Synemporion keana		*Lasiurus cinereus semotus*	
	Holotype	Hypodigm	Fossil	Historic
SGW	1.2	1.3 (1.1–1.4) 25	1.8 (1.8–1.9) 5	1.7 (1.6–1.9) 19
HUL	24.8	25.2 (24.0–28.7) 28	30.9 (29.4–32.4) 7	31.2 (29.4–33.4)18
HPW	2.9	2.8 (2.5–3.2) 35	3.8 (3.7–3.9) 10	3.9 (3.6–4.1) 20
HDW	2.6	2.5 (2.2–2.7) 39	3.0 (2.8–3.2) 9	2.9 (2.6–3.1) 19
FAL	37.5	37.9 (35.9–39.7) 39	48.0 (46.3–50.6) 6	48.7 (45.9–52.7) 32
FAN	2.4	2.4 (2.1–2.7) 49	2.9 (2.6–3.1) 11	2.9 (2.6–3.1) 13
FAS	1.2	1.1 (1.0–1.3) 47	1.5 (1.4–1.7) 9	1.5 (1.3–1.7) 13
FEL	19.0	18.8 (17.5–19.9) 20	21.4 (21.4)1	21.3 (20.4–22.7) 17
FPW	1.6	1.7 (1.5–1.9) 26	2.3 (2.0–2.6) 5	2.2 (2.1–2.5) 18
FDW	1.5	1.5 (1.3–1.6) 24	1.8(1.7–1.9)3	1.8 (1.7–2.0) 18
TIL	17.1	16.8 (16.1–18.3) 20	20.6 (19.9–21.3) 2	20.0 (19.3–21.2) 10
TPW	1.6	1.6 (1.4–1.7) 23	2.0 (1.9–2.1) 2	2.0 (1.9–2.1) 13

The skull of *Synemporion* has a low rostrum and a moderately well-developed forehead that rises abruptly to join with braincase, so that the profile of the rostrum appears concave in lateral view (fig. 2). The rostrum is of moderate length and relatively narrow (less than three-fourths the width of the braincase) and has a well-developed median sulcus (figs. 2, 3). The frontal portion of braincase is inflated and is higher and slightly wider than the occipital portion. There is no obvious sagittal crest, and the lambdoidal crests are weakly developed and present only laterally. The superior temporal lines are separated about 1 to 2 mm along the sagittal suture. Postorbital processes and supraorbital ridges are entirely absent. The zygomatic arches relatively narrow throughout and lack an expanded dorsal projection. The lachrymal ridge at the anterior rim of orbit is weakly developed.

The premaxilla in *Synemporion* lacks a palatal branch and is fused to the maxilla (figs. 2, 3). The narial emargination relatively broad in dorsal view, about 1.5 times as wide as deep, and the anterior palatal emargination even broader, essentially twice as wide as deep. The hard palate extends posteriorly well beyond the tooth row and orbit area. A pair of well-developed but shallow basisphenoid pits are present and are separated by a medial ridge. The cochleae are large, and distance between the cochleae is equivalent to approximately three-fourths the diameter of the cochlea. The dentary is essentially the same as found in most other vespertilionids, with a relatively low coronoid process and a well-developed mental foramen between the roots of C and P2 (fig. 2).

Selected postcranial measurements of *Synemporion* are presented in tables 2 and 3. The clavicle is rodlike and lacks any kind of midshaft enlargement or projection. The scapula has a large dorsal articular fossa that is nearly as large as the glenoid fossa, and has an assymetrically bifid coracoid process with the longer branch directed medially. The humerus (figs. 7, 8) has a well-developed greater tuberosity that projects proximally well beyond humeral head; the lesser

TABLE 3. Comparative metacarpal measurements and ratios for Hawaiian bats. All measurements are in mm, and ratios are given as percentages.

Taxon/Specimen	II	III	IV	V	Ratio IV:III	Ratio V:III
Synemporion keana						
BPBM 159265	–	–	40.5	37.5	–	–
BPBM 159267	–	40.0	–	35.0	–	88%
BPBM 159269[1]	39.5	42.0	–	36.5	–	87%
BPBM 159375	–	40.0	37.5	34.5	94%	86%
BPBM 178052	–	42.5	–	34.5	–	81%
BPBM 178057	40.5	41.5	39.5	37.0	95%	89%
BPBM 178058	39.0	41.5	39.0	36.5	94%	88%
BPBM 178061	–	42.5	39.5	36.5	93%	86%
BPBM 178157	40.5	42.0	39.5	36.5	94%	87%
USNM 498808	–	41.0	38.0	35.0	93%	85%
USNM 520429	41.0	–	40.0	37.5	–	–
USNM 520430	–	43.5	–	38.0	–	87%
USNM 531343	40.5	43.0	39.5	37.0	92%	86%
Mean (x)	40.2	41.8	39.2	36.3	93.6%	86.4%
Fossil *Lasiurus cinereus semotus*						
BPBM 159268	51.0	51.5	46.5	41.0	90%	80%
BPBM 183819	–	–	–	40.5	–	–
BPBM 184971	50.5	–	46.0	40.0	–	–
Mean (x)	50.8	51.5	46.3	40.5	90%	80%
Historic *Lasiurus cinereus semotus*						
BBM 9201	54.5	56.0	51.0	43.5	91%	78%
BBM-X 145165	52.0	52.5	47.5	41.0	90%	78%
BBM-X 145170	53.0	54.5	–	42.5	–	78%
BBM-X 147123	54.0	55.5	49.0	44.0	88%	79%
BBM-X 147125	–	53.5	47.0	42.0	88%	79%
BPBM 161300	52.0	53.5	48.0	42.0	90%	79%
BPBM 175997	56.0	57.0	50.0	44.0	88%	77%
BPBM 179757	56.0	57.0	51.0	46.0	89%	81%
Mean (x)	53.9	54.9	49.1	43.1	89.1%	78.6%

[1] Holotype

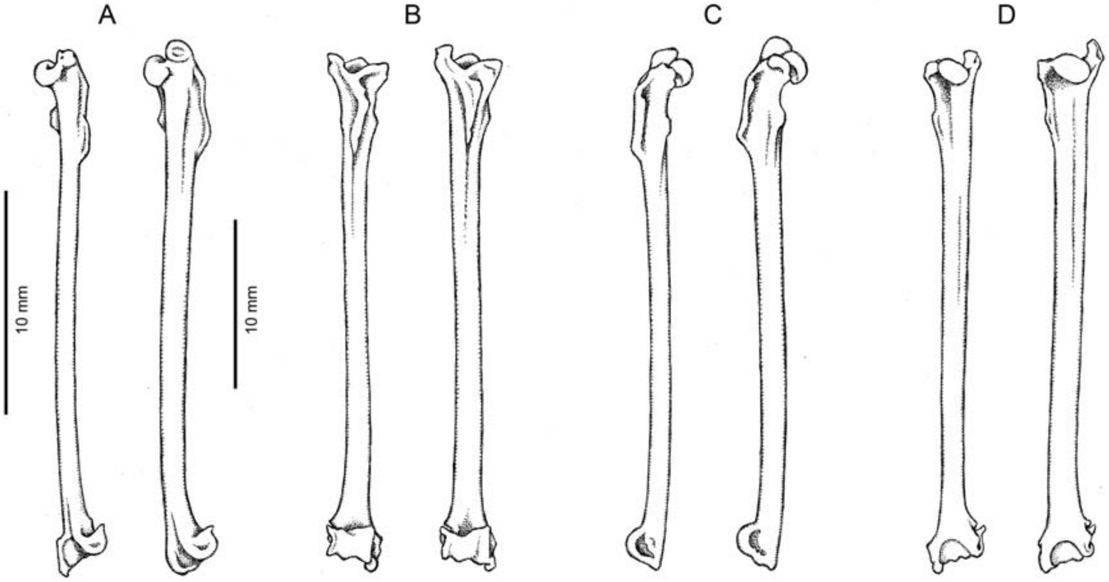

FIGURE 7. **A,** Lateral, **B,** anterior, **C,** medial, and **D,** posterior views of the humeri of the holotype of *Synemporion keana* (on the left in each pair; BPBM 159269) and *Lasiurus cinereus semotus* (on the right; BPBM 184506).

tuberosity, also well developed, is smaller and does not project beyond head. The bicipital groove along lateral surface of deltoid tuberosity is deep and well defined, and the deltoid tuberosity is high with ridge extending distally for almost one-quarter the total length of humerus. The distal articular surface lies in line with shaft, the trochlea noticeably greater in proximodistal diameter than capitulum, and the medial epicondylar spine projects distally 0.5 mm beyond trochlea. The ulna is fused proximally with radius, and the distalmost ulnar remnant is evident as small, proximally directed, flat spine fused to distal end of lateral border of radius. Metacarpal formula III > IV > V, with metacarpal IV length approximately 94% of that of metacarpal III, and metacarpal V length approximately 87% that of metacarpal III.

The vertebral column and pelvis of *Synemporion* are unremarkable and resemble those of other vespertilionids. There is no evidence of vertebral fusion other than in the sacrum. The femur is of usual vespertilionid morphology with the lesser trochanter projecting further proximally than greater trochanter, each distal condyle markedly compressed mediolaterally, and an intercondylar notch that is narrow and deep. The tibia is relatively long and slender, and the fibula is ossified for approximately half of the length of the tibia, the remainder being either threadlike or cartilaginous (not preserved among the material found).

DISCUSSION

Evolutionary Relationships: The morphology of *Synemporion keana* uambigiously places this taxon within Vespertilionidae as currently recognized (e.g., by Miller-Butterworth et al., 2007; Lack et al., 2010). This family currently contains over 50 genera and over 470 spe-

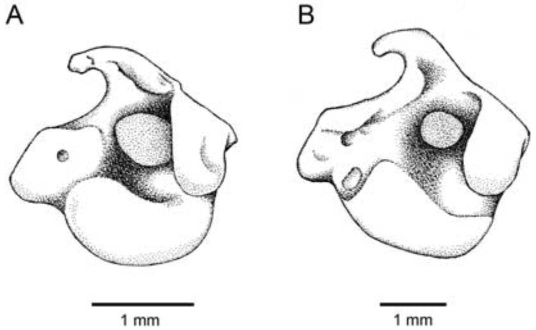

FIGURE 8. Proximal view of the humerus of **A,** the holotype of *Synemporion keana* (BPBM 159269) compared with that of **B,** *Lasiurus cinereus semotus* (BPBM 184506). Anterior is toward the top of the page in each figure.

cies, making it the most diverse of the chiropteran families. Unfortunately, morphological traits used to define and diagnose higher-level taxa have proven to be highly unreliable as guides to phylogeny in vespertilionid bats (Hoofer and Van Den Bussche, 2003; Lack et al., 2010; Roehrs et al., 2010; 2011). Attempts to extract DNA from skeletal elements of *Synemporion* have thus far been unsuccessful, precluding placement of this taxon into modern sequence-based phylogenies of Vespertilionidae. The most that can be said at this time, based exclusively on skeletal morphology, is that *Synemporion* could be a member of any one of several vespertiononid tribal groupings or clades including Vespertilionini, Lasiruini, Pipistrellini, Nycticeiini/Eptescini, or Scotophilinini. Monophyly of many of these groups is still in question despite extensive analyses of thousands of kb of sequence data (e.g., see Lack and Van Den Bussche, 2010; Roehrs et al., 2010; 2011) and basal relationships within Vespertilionidae remain largely unresolved. Unless future attempts to extract DNA from *Synemporion* bones prove fruitful, determination of the relationship of this taxon to other vespertilionids will require both better resolution of relationships of extant taxa and development of a comprehensive phenomic data set for vespertiliionids, both of which are beyond the scope of the current study.

GEOCHRONOLOGY: A minimum date of ca. 130,000 ybp for the initial appearance of *Synemporion keana* is provided by four specimens that are scattered through the pond deposits of Ulupaʻu Head, Oʻahu. The youngest of these deposits are ca. 130,000 ybp, but most are older. The most fossiliferous lake deposits at this site probably date from Marine Isotope Stage 11 (Middle Pleistocene) interglacial age or younger, ca. 320,000–400,000 years old (Hearty et al., 2005). It is likely that the *Synemporion* fossils date from the latter period. Despite relatively intensive collecting, *Lasiurus cinereus semotus* has not been reported from the site. This negative evidence suggests its colonization of Oʻahu occurred more recently than these lake deposits, which is in agreement with the findings of Russell et al. (2015). However, the paucity of known old fossil deposits prevents determining with any accuracy the date of arrival of either species in Hawaiʻi.

All other specimens of *Synemporion keana* and fossil *Lasiurus cinereus semotus* thus far recovered are from deposits undoubtedly significantly less than 130,000 years old (fig. 9). Only one of these specimens, a partial humerus of *Synemporion keana* from a sinkhole of site SIHP 50-80-12-4917L on Oʻahu, has been radiometrically dated at 1670 ± 60 ybp (Stafford Research

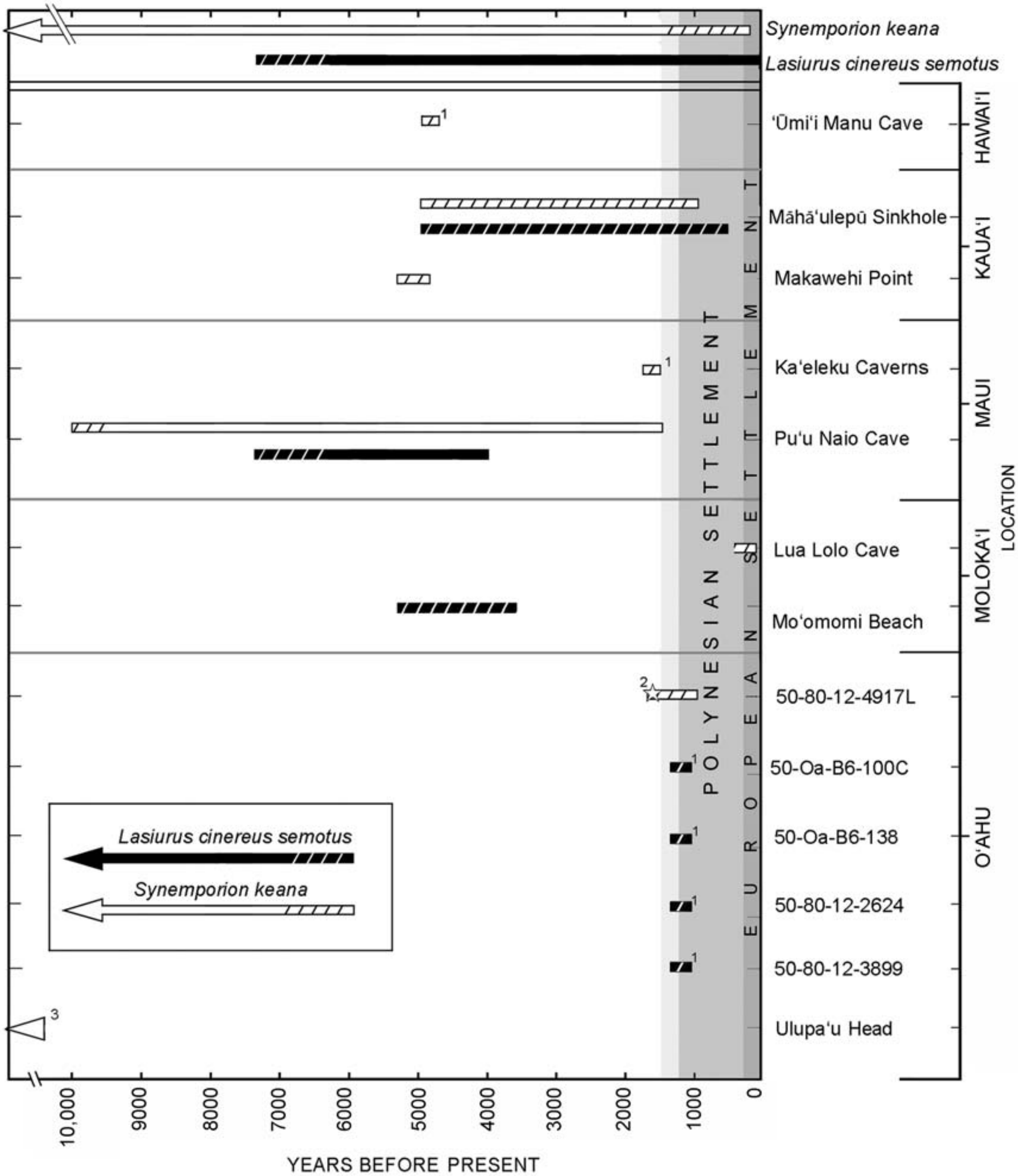

FIGURE 9. Relative ages of Hawaiian bat fossils from sites where their remains have been dated shown in relation to the time of colonization of the islands by humans; see appendix 2 for specimen records and appendix 4 for detailed locality descriptions for all collection sites. Solid bars indicate dated age ranges; hachured bars indicate estimated age ranges. Footnoted records are as follows: [1]Maximum possible age of site, actual age of bat remains younger. [2]Star represents ^{14}C dated specimen. [3]Older site off scale; 130,000 to ~400,000 ybp; most likely between 320,000 and 400,000 ybp; see text for discussion.

Laboratories Sample SR-5313), calibrated to A.D. 240–539 by Dye (2000). Another bone of *S. keana* from the same site was found about 20 cm above the dated element and, therefore, is probably younger than the dated range, suggesting deposition just before or very early in the Polynesian cultural period.

Radiometric dating of zoological material associated with bat bones from additional Hawaiian Island sites, however, provides additional age estimates for the two Hawaiian bat species. Remains of *Synemporion keana* from Puʻu Naio Cave, Maui, were deposited between 9500 ± 900 and 2000 ± 600 ybp, with *Lasiurus cinereus semotus* coeval between at least 6800 ± 650 and 4500 ± 500 ybp (Helen F. James, in litt., 17 October 1989). Even this most recent date for *Synemporion keana* likely antedates human colonization of the islands. On Kauaʻi, fossil *Lasiurus cinereus semotus* were deposited during the Polynesian cultural period, but *Synemporion keana* specimens thus far recovered from Makauwahi Cave sinkhole can be dated only to sometime within the extensive range of 1000–5000 ybp (David A. Burney, in litt., 29 December 2000). In the surface sand-dune deposits at Makawehi Point, Kauaʻi, three dates for zoological material are 6740 ± 80 ybp (land snail shells), 5145 ± 60 ybp (crab claws) and 4690 ± 100 ybp (goose bone) (Olson and James, 1982a, 1982b; Hearty et al., 2000). *Synemporion keana* was the only bat species recovered from the deposits, and presumably their remains were deposited within this range of dates (Hearty et al., 2000). No specimens of *S. keana* have thus far been collected from the dunes of Moʻomomi Beach, Molokaʻi, but fossil *Lasiurus cinereus semotus* bones there are apparently associated with land snail shells dated 5510 ± 65 and 5245 ± 60 ybp (Olson and James, 1982a; Hearty et al., 2000). All of the Makawehi Point and Moʻomomi Beach dates antedate Polynesian arrival in the Hawaiian Islands by at least two millennia.

Although undated, the youngest specimens of *Synemporion keana* are two partial skeletons collected from the surface of a mud bank in Lua Lolo Piping Cave at 1290 m on Molokaʻi. The surface environment above the cave is extremely wet native rainforest with an average annual rainfall of ~300 cm/year. The cave is a dynamically active piping cave, which is continually modified by water erosion and collapse. Both bats were spread out with their wings extended on the surface of the mud indicating that the dead animals were floating (drowned?) and deposited by slowly receding floodwaters. The degree of preservation of the bones, their location in a constantly wet environment, and the dynamic nature of piping caves all indicate that the skeletons are less than a few centuries old and perhaps were deposited in the historic period. The cave and provenience of the bones are described in more detail in appendix 4.

In summary (fig. 9), *Synemporion keana* was present in the Hawaiian Islands prior to ca. 320,000 ybp, and existed there until at least 1760–1461 ybp (A.D. 240–539), presumably contemporary with at least early Polynesian settlers. Furthermore, the Lua Lolo Piping Cave specimens indicate that the species possibly survived into the early postcontact period. *Lasiurus cinereus semotus* possibly arrived in the archipelago only after ca. 130,000 ybp, but certainly was present by 7450–6150 ybp, and is extant.

COLONIZATION: The Hawaiian Archipelago has always been isolated in the mid Pacific Ocean by more than 3000 km of open ocean. Each island in the archipelago is the summit of one or more massive volcanoes formed in sequence as the Pacific Plate moved northwestward over an essentially stationary hot spot currently south of the present island of Hawaiʻi (Clague and Dalrymple, 1987). As older islands were carried consecutively northwestward by tectonic movement, they eroded, became atolls, and finally sank (Clague and Dalrymple, 1987). The ages of the main Hawaiian Islands range from ca. 6 million years for Niʻihau and Kauaʻi to ca. 1 million ybp for the island of Hawaiʻi (Clague and Dalrymple, 1987; Price and Clague, 2002; Sherrod et al., 2007). The incomplete fossil record of the islands precludes determining the date of the colonization of the Hawaiian Islands by the ancestor of *Synemporion*. Nevertheless, the date is bracketed by the age of the oldest known specimens, which are approximately between 320,000 and 400,000 ybp (i.e., the age of the fossiliferous Ulupaʻu Head lake deposit; Hearty et al., 2005) and the maximum age of available island habitat, which is ca. 30–35 million years (Sharp and Clague, 2006). However, most ancestors of the current native Hawaiian taxa probably had to arrive from distant source areas after the emergence of Kauaʻi ca. 6 million years ago rather than from older islands in the archipelago, which would have eroded to low islands by then, limiting their role as stepping stones (Price and Clague, 2002).

Extant Hawaiian hoary bat populations have recently been shown to have resulted from at least two separate colonization events by *Lasiurus cinereus* from North America, one ca.10,000 ybp and a second ca. 800 ybp (Russell et al., 2015). *Lasiurus cinererus* is known to migrate long distances seasonally on the continent, and this species is thought to be capable, in terms of both energetics and water balance, of flying nonstop distances equivalent to that between mainland North America and Hawaiʻi (Bonaccorso and McGuire, 2013). The abilities of *Synemporion,* of course, remain unknown, but clearly its ancestors successfully colonized the Hawaiian Islands at least once.

In the absence of detailed knowledge of the phylogenetic relationships of *Synemporion,* we can only speculate about its origins. Because the geographic ranges of vespertilionid genera somewhat similar to this taxon (see Systematics above) variously include Asia, Australia, Pacific islands, North America, and South America, we conclude that both New World and Old World origins for *Synemporion* must be considered equally likely pending additional studies. If other volant vertebrates are assumed to provide a reasonable model, the geographic source of *Synemporion* stock could have been any land mass in or bordering the Pacific judging from the inferred sources of avian ancestors (and of historically reported bird "stragglers" to the islands), which have flown in from areas both east and west of the Hawaiian Islands (Berger, 1972; Ziegler, 2002).

Taphonomy and Roosting Ecology of Synemporion: Specimens of *Synemporion keana* recovered from eolian and alluvial deposits usually consist only of isolated bones and thus provide little information on the circumstances of death. Some may represent prey remains of prehistorically extinct raptors specialized primarily for bird-catching including the Wood Harrier *Circus dossenus* and Stilt-Owls of the genus *Grallistrix,* or even of the similarly extinct large *Corvus* taxa, described by Olson and James (1991) and James and Olson (1991). On the other hand, bat specimens from sheltered situations on lava-tube walls and floors almost always consist of essentially complete associated skeletons (figs. 10, 11), indicating predation was probably not the cause of death of these individuals.

Most specimens of *Synemporion* have been found in dry lowland habitats, but this fact may simply result from the greater likelihood of their skeletons being preserved in those areas. Three sites indicate that the species was widespread and occupied upland habitats: ʻŪmiʻi Manu

FIGURE 10. Skeleton of *Synemporion keana* in situ on the floor near the lower end of Māhiehie Cave.

Cave at 1878 m in cool montane forest on Hualālai on Hawaiʻi, Puʻu Mākua Cave at 1463 m in mesic forest on Maui, and Lua Lolo Piping Cave at 1290 m in extremely wet montane rainforest. In contrast, the complete absence of specimens from the extensively sampled deposits at Moʻomomi Dunes and Ilio Point on West Molokaʻi suggest that the species may have been absent from extremely dry environments dominated by xerophytic vegetation. In particular at Ilio Point, the extinct owl *Grallistrix geleches* had concentrated many small bones of the smallest rail and various small passerines (Olson and James, 1982a). Had either bat species been present there, the owl would most likely have eaten some, and the extensive screening operations conducted at the site would have found some bones. This is in contrast to the dunes on Kauaʻi, where moist forest was nearby and where both species of bats are known to have occurred (Storrs Olson, in litt., April 18, 2014).

It is often assumed that all bats roost in caves, but this is far from the truth (Kunz, 1982). Many vespertilionids, including hoary bats, roost preferentially in foliage (Kunz, 1982; Fullard, 1989; Willis and Brigham, 2005). The occurrence of associated remains of *Synemporion* in lava tubes—even of a fair number of individuals—may be due simply to the generally more favorable preservation conditions there, rather than to the possibility that *Synemporion keana* was primarily cavernicolous. The lack of any known bat guano deposits in Hawaiian lava tubes (Howarth, 1991) argues against a predilection for subterranean, and colonial, roosting. So how did so many bats become entombed in caves such as Māhiehie Cave?

FIGURE 11. Skeleton of *Synemporion keana* embedded in secondary mineral crust on the wall near the downslope end of Māhiehie Cave.

The unique shape of the entrance suggests that Māhiehie Cave may have acted as a bat trap. The cave entrance is located at the bottom of a large vertical pit approximately 25 to 30 m in diameter and 20 m deep (fig. 12). The amphitheaterlike entrance, which is 8–10 m high and wide, leads downslope about 10 m beyond the dripline to where the talus slope meets the ceiling. A large lava slab (fig. 13) leans against the ceiling and nearly blocks the entrance to a low narrow passage, 1–1.5 m in diameter. This narrow passage between large boulders is about 5 m long and connects with the large downslope cave passage. The downslope passage is a large lava tube, 5 to 10 m in diameter and over 600 m long, which descends about 100 m in elevation. Except for near the downslope end, the floor is covered with breakdown blocks that range in size from 0.5 to more than 2 m across. A small forest of large trees grows in the entrance pit providing food and shelter for forest bats. Any bats foraging in the amphitheaterlike entrance that flew into the gap behind the lava slab at night might have difficulty finding the exit by sight or echolocation and, disoriented, might search for an exit by flying into the large downslope passage. Sound would attenuate rapidly in the irregularly shaped cave passage especially with its blocky lava floor, and the large passage would appear as mostly open space to echolocating bats; whereas the true entrance would “appear” as a solid rock wall from inside the cave. Even in daytime, very little light is visible in the low passage beyond the gap between the boulder and ceiling. Only a few individuals of *Synemporion keana* uncharacteristically entering and dying naturally in the lava tube each decade could

FIGURE 12. Looking downslope (south) across the entrance pit of Māhiehie Cave. The amphitheater entrance to the main cave is visible below the rim on the right side.

FIGURE 13. Fred Stone peers through the gap between the lava slab and wall at the lower edge of the entrance to Māhiehie Cave. The slab obscures the entrance to the main cave passage. The configuration of the entrance and cave creates a possible trap for bats (see text for description).

easily have resulted in the concentration of skeletal remains of more than 100 individuals found in the type locality of Māhiehie Cave (fig. 14).

An additional factor might have been the rich food resource once provided by cave-roosting moths. Several species of native noctuid moths in the genera *Hypocala* and *Peridroma* once roosted during the day in caves and rock crevices. Perkins (1913) reported that the native *Hypocala velans* commonly frequented caves and rock crevices during the day and emerged in great numbers at sunset. Although Perkins (1913) believed the species was more abundant in the lowlands, he noted that the moth used an unnamed cave at 9000 feet (~2,750 m) on Haleakalā, Maui. Some cave colonies possibly exceeded many thousands of individuals, as evidenced by large deposits of dead *Peridroma* moths occurring in high-altitude lava tubes on Haleakalā and Mauna Loa, Hawai‘i (F.G.H., personal obs.). Bunnell and Giffin (2000) collected a dead *Peridroma albiorbis* in Big Red Cave on Mauna Loa where they also found large numbers of *Lasiurus cinereus semotus* remains. Lowland colonies of these moths appear to have been extirpated, but a few colonies still occur in high-elevation caves on Mauna Loa on Hawai‘i. In the 1980s, a huge living colony of an undescribed species of *Peridroma* was discovered in a lava tube at ~4000 m on Mauna Loa (F.G.H., personal obs.). The moths “darkened the sky” with a large funnel-shaped cloud as they emerged at dusk and flew downslope. The emergence of moths from their roosts at sunset, just as hungry bats begin foraging, would be expected to

FIGURE 14. Carla Kishinami collecting bat skeleton from rubble on floor near the lower end of Māhiehie Cave.

bring bats close to cave entrances. This association has been corroborated recently by Bonaccorso et al. (2014), who reported detecting *Lasiurus cinereus semotus* congregating and foraging in and near entrances of 13 lava tubes between 2200 and 3600 m on Mauna Loa. Bonaccorso et al. (2014) suggested that the bats were attracted to moths (probably a *Peridroma* species) roosting in the caves.

Nearly all lava tubes that contain bat remains in Hawai‘i have a large entrance leading into a large and long passage, and bat remains are found in situations that suggest that the animals entered accidentally and subsequently became lost (F.G.H., personal obs.). The occurrence of remains of *Synemporion keana* in lava tubes may be analogous to the behavior of some continental *Lasiurus* populations. It is not unusual to find freshly dead individuals or skeletal remains, sometimes numbering into the hundreds, of *L. borealis,* along with occasional *L. cinereus* and rarely other noncavernicolous bat species, in caves on the mainland United States (Quay and Miller, 1955; Myers, 1960, Saugfy et al., 1978). These species habitually choose tree branches, twigs, leaf petioles, and other arboreal sites for roosts (Kunz, 1982; Menzel et al., 1998; Mager and Nelson, 2001; Willis and Brigham, 2005). For unknown reasons, individuals of these species enter caves, where an undetermined percentage of them eventually die, usually far from the entrance, apparently unable or unwilling to leave. *Lasiurus cinereus semotus* is historically also known to be a typical tree-rooster, as would be expected, but it occasionally also has been seen to utilize sheltered portions of collapsed lava blisters and tubes in Hawai‘i

(Tomich, 1986; Fujioka and Gon, 1988). Both historic and fossil *L. c. semotus* specimens have been recovered from such sites. Bunnell and Giffin (2000) reported counting 113 dead *L. c. semotus* in Big Red Cave, a large lava tube between 2100 and 2400 m on Mauna Loa, Hawaiʻi Island. All of the individuals were found more than 850 m from the only known entrance, and some were at the end, more than 1.75 km from the entrance.

Interestingly, and possibly pertinent to the present question of the normal roosting habits of *Synemporion keana,* Myers (1960) noted that "true" cave vespertilionids (i.e., many species of *Myotis*, *Pipistrellus*, and *Eptesicus*), roosting in the same caverns from which he recovered the above-mentioned *Lasiurus* remains, were rarely found dead in these caves. This suggests that, at least in some instances, numbers of dead individuals of a particular bat in a cave may indicate that the species is *not* normally a cavernicolous form. Myers' (1960) observations, of course, antedate the emergence of white-nose syndrome in North America, which has caused unprecedented mortality of cave-roosting bats in their winter hibernacula (Frick et al., 2010).

EXTINCTION OF SYNEMPORION: The cause of the extinction of *Synemporion keana* remains unknown. As noted earlier, *Synemporion keana* was extant in the Hawaiian Islands until at least 1760–1461 ybp (A.D. 240–539), presumably contemporary at least with early Polynesian settlers. The Lua Lolo Piping Cave specimens indicate that the species possibly survived into the early postcontact period, perhaps becoming extinct only a few hundred years ago. Could extinction of this bat have been linked in some way to human colonization of the islands? Extinctions of other native wildlife, notably endemic bird species, have been associated with forest-clearing activities and human-introduced invasive species including feral cats, mongooses, dogs, pigs, and rats (Atkinson, 1977; Olson and James, 1982b; 1984; Tomich, 1986; Athens et al., 2002).

Lowland forests on the Hawaiian Islands were cleared by Polynesian settlers for agricultural purposes, primarily by fire, well before European explorers first visited the islands (Olson and James, 1982b). Polynesians also introduced to the archipelago a number of plant and animal species including at least six vertebrates: domestic dogs, pigs, chickens, two lizards, and the invasive Polynesian or Pacific Rat, *Rattus exulans* (Atkinson, 1977; Athens et al., 2002). Pigs and dogs are not known to regularly prey on bats, but *Rattus exulans* has an eclectic diet that includes seeds, fruit, leaves, seedlings, invertebrates, and vertebrates (Campbell et al., 1984). The presence of *Rattus exulans* can have a significant effect on local floras (Campbell, 1978; Cuddihy and Stone, 1990; Athens et al., 2002) and bird populations (Graham et al., 2013). Graham et al. (2013) documented an increase in populations of insectivorous birds after the eradication of *Rattus exulans* from an offshore island in New Zealand. This evidence indicates that the presence of *Rattus exulans* may have had significant effects on populations of other vertebrates through either direct or indirect means (Athens et al., 2002; Graham et al., 2013). If *Synemporion* roost sites were accessible to rats, it is possible that *Rattus exulans* may have had a direct impact on the bat populations by preying upon roosting bats and/or their young (see below for further discussion of rats as bat predators). Alternatively, the effects of rats on the local environment may have indirectly contributed to bat population reductions and extinction.

Fossil studies together with early botanical surveys indicate that drier lowland regions near sea level in the Hawaiian Islands once supported a distinctive forest with many endemic plant species, but that this flora had largely vanished or was restricted to a few scattered remnants by the time that botanists first described the floras of the islands (Olson and James, 1982b; Cuddihy and Stone, 1990). Many species of birds, particularly those restricted entirely to such lowland dry forest, were apparently pushed to extinction by the loss of this distinct lowland dry forest habitat (Olson and James, 1982b; Athens et al., 2002). Olson and James (1982b) argued that human-mediated landscape change associated with agricultural land clearing was the cause of destruction of these forests (and ultimately their endemic birds). However, more recently Athens et al. (2002) presented data showing that, in at least some areas, the collapse of the native forest preceded human settlement. In their study, Athens et al. (2002) argued that introduced *Rattus exulans*, not agricultural clearing and burning, caused the loss of most of the native dry lowland forest by historic times. Reproducing rapidly after its initial introduction, *Rattus exulans* may have effectively caused the collapse of the endemic lowland dry forests of the islands by feeding on vegetation, seeds, and seedlings, and hence may have indirectly caused extinction of endemic bird species restricted to these habitats (Athens et al., 2002).

Whether the endemic lowland dry forest of the Hawaiian Islands was lost due to agricultural clearing or to ecological effects of introduced rats, it seems that the colonization of the islands by humans caused numerous extinction events of native plants and animals restricted to these habitats (Olson and James, 1982b; Burney et al., 2001; Athens et al., 2002). In this context, it seems possible that the reduction of native forests and associated insect fauna after human colonization of the islands contributed not just to the extinction of plants and birds, but also to the extinction of the endemic bat *Synemporion keana*.

If *Synemporion* survived into historic times, the coup de grace for extinction may have been caused by the introduction of predators following the arrival of Europeans. Domestic cats (*Felis catus*) and Norway rats (*Rattus norvegicus)* were introduced into the Hawaiian Islands by the first Europeans, and quickly became feral (Tomich, 1986). The roof rat (*Rattus rattus*) and mongoose (*Herpestes javanicus*) arrived a half century or more later (Tomich, 1986). Cats have been shown to be effective bat predators, and the effects of cat predation on bat populations can be significant, particularly in insular environments (Tidemann et al., 1994; Rodríguez-Durán et al., 2010; Scrimgeour et al., 2012; Ancillotto et al., 2013). While rats are not usually considered to be bat predators, *Rattus norvegicus* is the only mammal known to prey on the fish-eating myotis, *Myotis vivesii* (Villa, 1982), and the diet of *Rattus rattus* in some areas includes bats such as the big brown bat, *Eptesicus fuscus* (Rysgaard, 1942*),* and Townsend's big-eared bat, *Corynorhinus townsendii* (Fellers, 2000). Perhaps significantly, predation by *Rattus rattus* is considered to be the proximate cause of extinction of the last known population of the insular New Zealand greater short-tailed bat, *Mystacina robusta* (Daniel and Williams, 1984). If *Synemporion keana* survived into the postcontact period, predation by introduced cats and rats may have played a role in its extinction, especially if these bats roosted in areas readily accessible to these animals.

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APPENDIX 1

ON THE TAXONOMY OF *LASIURUS*

Within the genus *Lasiurus*, three groups of bats are typically recognized: red bats, yellow bats, and hoary bats (a total of 17 species; Simmons, 2005). Hoary bats have traditionally been considered to comprise a single species, *Lasiurus cinereus*, with three subspecies: *L. c. cinereus* (North America), *L. c. villosissimus* (South America including the Galapagos Islands), and *L. c. semotus* (Hawaiian Islands; Simmons, 2005). Some authors have treated these subspecies as distinct at the species level (e.g., Baird et al., 2015) and others have recognized additional subspecies within what has typically been treated as *villosissimus* (e.g., Gardner and Handley, 2008), but no one has questioned the monophyly of this group. Hoary bats have long been thought to be most closely related to red bats (e.g., *Lasiurus borealis* and related species), a conclusion originally proposed based on morphology (e.g., Tate, 1942) but subsequently confirmed with molecular tools ranging from allozymes (Baker et al., 1988) to DNA sequencing (e.g., Baird et al., 2015).

Exactly how to classify bats has been a source of considerable controversy. Allen (1894), Miller (1909), Tate (1942), and other early 20th century workers placed red bats and hoary bats together in the genus *Lasiurus,* and put yellow bats (*L. ega* and related taxa) in a different genus, *Dasypterus*, primarily on the basis of presence/absence of a small upper first premolar. However, Handley (1960) reexamined morphology of all relevant species and concluded that they were not distinct at the genus level, and indeed that even a subgeneric distinction was unwarranted. Following Handley (1960), most subsequent authors used *Lasiurus* as the genus name for all hoary, red, and yellow bats. Baker et al. (1988) concurred, though noting that the three groups are indeed genetically distinct with red and hoary bats most closely related to each other. Koopman (1993) and Simmons (2005) recognized the relationships among these groups by treating *Dasypterus* (yellow bats) and *Lasiurus* (red bats + hoary bats) as subgenera within the genus *Lasiurus*. Considerable evidence supports the monophyly of the genus *Lasiurus* as thus defined (Hoofer and Van Den Bussche, 2003; Roehrs et al., 2010; Baird et al., 2015).

A great deal of research has been done on hoary bats in the last several decades, including work on ecology, behavior, reproduction, migration, echolocation, population genetics, conservation, and systematics. As a measure of this activity, we note that the binomial *Lasiurus cinereus* appeared in over 1200 publications between 2010 and 2015 alone (based on citation records in Google Scholar using the keywords "Lasiurus cinereus"). We were thus dismayed to see that Baird et al. (2015) proposed major changes to the generic classification of the species long included in *Lasiurus*. Baird et al. (2015) proposed that the genus name *Lasiurus* be restricted to red bats, that *Dasypterus* be used as the genus name for yellow bats, and that hoary bats + *L. egregius* (which appears more closely related to hoary bats than to red bats) be called by the genus name *Aeorestes* Fitzinger, 1870. They proposed these changes because (1) these lineages are clearly evolutionarily distinct, (2) "the level of divergence between the red, yellow, and hoary bats is in line with the level of divergence between other recognized vespertilionid genera," and (3) "most scientists already refer to 'red bats,' 'yellow bats,' and 'hoary bats' when referring to these groups" (Baird et al., 2015: 10–11). In our opinion, these together provide insufficient justification for changing the well-established zoological nomenclature for these bats, and any potential value of applying different generic names to the three clades is far outweighed by the confusion that these name changes will cause.

The generic name *Aeorestes* Fitzinger, 1870, listed in Gardener and Handley's (2008) synonymy for *Lasiurus*, has never to our knowledge been used to refer to hoary bats in other scientific literature until resurrected by Baird et al. (2015). Outside of the latter paper, a Google Scholar search returns only 10 citations for the name *Aeorestes* since 1900—and in every case *Aeorestes* was used as subgenus in *Myotis* (e.g., see Hoofer and Van Den Bussche, 2003; Hoofer et al., 2006; and Lim, 2009), not in reference to hoary bats. According to Gardner and Handley (2008), the type species of *Aeorestes* by original designation is *Aeorestes villosissimus* (É. Geoffroy St.-Hillaire, 1806), a hoary bat generally considered a subspecies of *Lasiurus cinereus*. It therefore seems clear that the name *Aeorestes* should not be used as a subgenus of *Myotis*. While we agree with Gardner and Handley (2008) and Baird et al. (2015) that *Aeorestes* Fitzinger, 1870, is an available name for hoary bats, we believe that extensive confusion will be caused by the name changes proposed by Baird et al. (2015), and argue against adoption of this as the genus name for hoary bats.

Changing well-known and heavily cited names when such changes are not required to render taxa monophyletic violates one of the central principles of zoological nomenclature—that name changes should be kept to a minimum, and that usage should promote nomenclatural stability whenever possible. Separate generic epithets for the three major lineages within *Lasiurus* sensu lato are not required to keep any taxon monophyletic since all workers agree that *Lasiurus* sensu lato is clearly monophyletic; nothing is broken that needs fixing. Adopting a subgeneric classification (treating *Aeorestes* and *Dasypterus* as subgenera of *Lasiurus*) would suffice to provide names for the clades identified by Baird et al. (2015) and previous workers. We therefore reject the proposal to split *Lasiurus* into three genera.

APPENDIX 2

Hawaiian Specimens Examined

See appendix 4 for complete locality information, descriptions, and other details of fossil specimen sites; see Materials and Methods for abbreviations.

Synemporion keana

Kauaʻi

Māhāʻulepū Cave System (now referred to as Makauwahi Cave; Burney and Kikuchi, 2006): -1.0–2.3 m: USNM 498825, pt lt radius; USNM 498827, lt dentary; USNM 498830, rt clavicle; USNM 498831, pt lt? femur; USNM 498832, lt humerus; USNM 498837, lt cochlea; USNM 498838, rt humerus; USNM 520434, rt radius; USNM 520437, rt radius; all 30 Jan–12 Feb, D.A. Burney S.L. Olson, et al.

Makawehi Point: BPBM 159423, lt humerus, 14–15 Aug 1976, S.L. Olson and R. Rice; BPBM 159424, pt rt humerus, 18 Aug 1976, S.L. Olson et al.

Oʻahu

BMAS 50-Oa-B6-22, pits in series J–P: BPBM 159426, pt lt scapula; BPBM 159428, pt lt pelvis; BPBM 159429, pt lt femur; BPBM 159431, pt rt femur; BPBM 159432, pt lt humerus; BPBM 159435, pt lt humerus; BPBM 159438, pt rt femur; BPBM 159440, pt rt scapula; BPBM 159441, pt rt humerus; BPBM 159444, pt rt scapula; BPBM 159445, pt lt scapula; BPBM 159449, pt rt radius; BPBM 159450, pt lt humerus; all Jul 1981, S.L. Olson, J.I. Mead, et al.; BPBM 178130, pt rt humerus, 20 Jul 1981, S.L. Olson, H.F. James, P.C. McCoy et al.

SIHP 50-80-12-4917L, Sink 6: CSH temp. field no. 1, pt rt dentary; CSH temp. field no. 2, pt lt humerus; CSH temp. field no. 3, pt rt radius; all Aug–Oct 1996, Cultural Surveys Hawaiʻi, Inc., excavation crew. (Two bones [No. 2 and 3] were sacrificed for ^{14}C dating.)

Earl Neller Sinkhole SPA III HL-2: BPBM 177890, pt lt humerus, 27 Sep 1986–5 Mar 1988, A.C. Ziegler.

ʻŌpaeʻula Sinkhole: BPBM 183819, rt humerus, late Nov 1992, D.W. Eickhoff.

Ulupaʻu Head, ~1–3 m: BPBM 159405, lt radius, 19 Feb 1983, K.A. Pankiwskyj; BPBM 184897, pt lt radius, proximal end, Feb 1984, H.F. James, S.L. Olson, A.C. Ziegler; BPBM 184898, pt lt radius, distal end, 26 Feb 1984, A.C. Ziegler; BPBM 184972, pt rt humerus, proximal end, 12 Mar 1999, S.L. Olson, A.C. Ziegler, P.J. Hearty, P. Kindler.

Molokaʻi

Lua Lolo Cave: BPBM 159375, pt skull + pt skel (of 2 individuals; no coll no.), 15 Jan 1983, F.G. Howarth and F.D. Stone.

Maui

Crystal Cave: BPBM 178132, pt lt radius; BPBM 178133, pt skull + pt skel; both 4 Apr 1988, S.L. Olson, R.M. Severns, T.W. Stafford, Jr., and P. Feine-Severns.

Kahāwaihapapa Cave: BPBM 178131, pt skull + pt skel, 22 Mar 1988, H.F. James et al.

Kaʻeleku Caverns: USNM 498808, pt cranium + pt skel, 6 Jul 1990, F.V.H. Grady, H.F. James, and A. Medeiros.

Māhiehie Cave (type locality): BPBM 158624, pt cranium + pt skel (no coll no.), 6 Nov 1981, F.G. Howarth; BPBM 159254, skull + pt skel, FGH 1; BPBM 159255, pt skel, FGH 2; BPBM 159256, rt radius, FGH 3; BPBM 159257, lt radius, FGH 4; BPBM 159258, rt radius, FGH 5; BPBM 159259, pt skel, FGH 6; BPBM 159260, rt radius, FGH 8; BPBM 159261, cranium + pt skel, FGH 9; BPBM 159262, pt skull + pt skel [of 2 individuals], FGH 10; BPBM 159263, lt radius, FGH 11; BPBM 159264, pt skull + pt skel, FGH 12; BPBM 159265, cranium + pt skel, FGH 13 and 14; BBM 184973, pt rt radius, FGH 15 (collected with pt skull + pt skel of *L. c. semotus*, which is separately cataloged; see BPBM 159266); BPBM 159267, pt cranium + pt skel, FGH 16; all 16 Sep 1982, F.G. Howarth and F.D. Stone. BPBM 178050, skull + pt skel, FGH 5; BPBM 178051, pt skull + pt skel, FGH 2; BPBM 178052, pt skull + pt skel, FGH 4; BPBM 178053, pt skull + pt skel, no coll no.); BPBM 178054, pt skull + pt skel, FGH 10; BPBM 178055, skull + pt skel, FGH 1; BPBM 178056, skull + pt skel, FGH 6; BPBM 178057, skull + pt skel, FGH 3; BPBM 178058, skull + pt skel, FGH 7; BPBM 178059, pt skull + pt skel, FGH 11; BPBM 178060, pt skull + pt skel [of at least 4 individuals], FGH 14; BPBM 178061, skull + pt skel, FGH 13; BPBM 178062, pt skull + pt skel, FGH 15; BPBM 178063, pt skull + pt skel (of at least 3 individuals; no coll no.); BPBM 178064, pt skull + pt skel, FGH 17; all 14 and 15 Jun 1989, F.G. Howarth and C.H. Kishinami.

Puʻu Mākua Cave: BPBM 178157, skull + pt skel, 19 Apr 1988, C.H. Kishinami and H.F. James; USNM 531343, skull + pt skel, 5 Apr 1988, H.F. James, R.M. Severns, T.W. Stafford, Jr., and P. Feine-Severns.

Puʻu Naio Cave: USNM 531344, lt femur; USNM 531345, pt rt radius; USNM 531346, pt rt dentary; USNM 531347, rt pelvis; USNM 531348, pt rt femur; USNM 531349, pt lt femur; USNM 531350, pt lt pelvis; USNM 531351, pt rt dentary; USNM 531352, pt lt dentary; USNM 531353, lt humerus; all 6–17 Feb 1984, S.L. Olson, H.F. James, et al.; USNM 531354, pt cranium; USNM 531355, pt rt metacarpal V; both 29 Mar 1988, H.F. James and T.W. Stafford, Jr.; USNM 531356, lt dentary; USNM 531357, pt lt radius; USNM 531358, pt lt humerus; USNM 531359, pt rt femur,; USNM 531360, pt rt dentary; USNM 531361, pt rt radius; USNM 531362, carpal; USNM 531363, rt dentary; USNM 531364, pt rt scapula; USNM 531365, cervical vertebra; USNM 531366, lt humerus; USNM 531367, atlas; USNM 531368, pt lt femur; USNM 531369, pt rt femur; USNM 531370, pt lt radius; USNM 531371, rt tibia; USNM 531372, pt sacrum; USNM 531373, pt lt tibia; USNM 531374, pt lt dentary; all 21 Mar–16 Jun 1988, H.F. James.

Hawaiʻi

Kahuku Ranch Cave: USNM 520429, pt skull + pt skel (of at least 2 individuals), field no. 1; USNM 520430, skull + pt skel, field no. 2; both 1 Aug 1998, H.F. James, S.B. Olson, E.E. Paxinos, B. Slikas, and B. Schaefer.

ʻŪmiʻi Manu Cave: BPBM 184184, pt skull + pt skel, AC 1010, 2 Mar 1993, A. Cooper, H.F. James, K. Wilson et al.

Fossil *Lasiurus cinereus semotus*

Kauaʻi

Māhāʻulepū cave system (now referred to as Makauwahi Cave; Burney and Kikuchi, 2006): -0.9–2.2 m: USNM 498823, pt skull; USNM 498824, lt radius; USNM 498826, rt dentary; USNM 498829, lt humerus; USNM 498833, rt humerus; USNM 498834, pt rt dentary; USNM 498835, pt rt radius; USNM 498836, manubrium; USNM 520433, 1st rib; USNM 520435, lt dentary; USNM 520436, pt rt scapula; all16 Jan–14 Feb 1998, D.A. Burney, S.L. Olson, et al.

Oʻahu

BMAS 50-Oa-B6-22, pits in series J–P: BPBM 159425, rt M1; BPBM 159427, pt rt dentary; BPBM 159430, pt lt dentary; BPBM 159433, pt lt humerus; BPBM 159434, sacrum; BPBM 159436, pt rt femur; BPBM 159437, pt rt femur; BPBM 159439, pt rt dentary; BPBM 159442, pt lt dentary; BPBM 159443, pt lt femur; BPBM 159446, pt lt humerus; BPBM 159447, rt dentary; BPBM 159448, pt rt scapula; BPBM 178128, pt rt humerus; BPBM 178129, pt rt dentary; all Jul 1981, S.L. Olson, J.I. Mead, et al.

BMAS 50-Oa-B6-100B: BPBM 159287, pt lt humerus, Jul–Aug 1977, A. Sinoto et al.

BMAS 50-Oa-B6-100C: BPBM 159288, pt cranium; BPBM 159289, pt lt radius; both Jul–Aug 1977, A. Sinoto et al.

BMAS 50-Oa-B6-138, Pit G: BPBM 159290, pt rt humerus; BPBM 159291, pt lt humerus; both Jul–Aug 1977, A. Sinoto et al.

SIHP 50-80-12-2624 (formerly SIHP 50-80-12-9670-P1): excavation pits 3, 4, and Z: BPBM 159451, pt lt dentary; BPBM 159452, pt rt dentary; BPBM 159453, pt lt dentary; BPBM 159454, pt lt dentary; BPBM 178127, pt rt humerus; all 1–3 Apr 1980, S.L. Olson et al.

SIHP 50-80-12-3899, Trench 1: BPBM 183817, pt lt? femur; BPBM 183818, rt dentary; both 3 Jun 1989, J. Berlin et al.

Earl Neller Sinkhole SPA III HL-2: BPBM 177889, pt rt humerus, 27 Sep 1986–5 Mar 1988, A.C. Ziegler.

ʻŌpaeʻula Sinkhole: BPBM 183820, lt metacarpal V; BPBM 183821, pt rt metacarpal III; both late Nov 1992, D.W. Eickhoff.

MOLOKAʻI

Joan Aidem Moʻomomi Beach, Site 8: BBM-X 147404, pt rt humerus; BBM-X 147405, pt rt radius; BBM-X 147406, pt rt radius; all Sep 1972–Jan 1974, J. Aidem.

MAUI

Māhiehie Cave: BPBM 159266 (collected with pt rt radius of *Synemporion keana*, which is separately cataloged; see BBM 184973), pt skull + pt skel, FGH 15; BPBM 159268, pt skull + pt skel, FGH 21; both 16 Sep 1982, F.G. Howarth and F.D. Stone.

Puʻu Naio Cave: USNM 531375, lt dentary; USNM 531376, pt rt radius; USNM 531377, pt rt dentary; USNM 531378, pt rt dentary; USNM 531379, lt dentary; all 10–17 Feb 1984, S.L. Olson, H.F. James, et al.; USNM 531380, rt petrosal; USNM 531381, pt rt radius; USNM 531382, lt upper canine; USNM 531383, rt clavicle; USNM 531384, pt rt radius; all 29 Mar–16 Jun 1988, H.F. James.

HAWAIʻI

Hualālai Owl Cave: BPBM 184971 (Stat. 1), skull + pt skel, 7 Mar 1993, H.F. James, J.G. Giffin, A. Cooper, and party.

Kahuku Ranch Cave: USNM 520431, pt skull + pt skel, field no. 3; USNM 520432, pt skull + pt skel, field no. 4; both 1 Aug 1998, S.B. Olson, H.F. James, E.E. Paxinos, B. Slikas, and B. Schaefer.

Lua Nunu Kamakalepo Cave: BPBM 159422, rt radius (no coll no.), 17 Jul 1976, F.G. Howarth.

Historic *Lasiurus cinereus semotus*

ISLAND UNDETERMINED

BBM 9201, complete skeleton, sex unknown, prior to 1 Jan 1967, M.D. Monsarrat. BBM-X 146221, alc, sex unknown, prior to 30 Aug 1971, received from Hawaiʻi State Division of Fish and Game. BPBM 178814, mummy, sex unknown prior to Jul 1992, received from Hawaiʻi State Division of Forestry and Wildlife.

KAUAʻI

Kīlauea, ca. 22.21°N, 159.41°W: BPBM 175758, skin and skull + pt skel, sex unknown, 24 Oct 1985, E. Goodman.

Princeville, ca. 22.22°N, 159.49°W: BPBM 175759, skin and skull + pt skel, sex unknown, Jun 1986, G. Inanod.

Vicinity Puʻu ʻōpae, ~20 km N Waimea: BBM-X 148202, alc, sex unknown, 2 Nov 1975, received from D.S. Boynton.

Wailua: BBM-X 146222, skin and skull, sex unknown, 22 Jun 1971, received from T.C. Telfer.

Locality unknown: BBM 9129, skin and skull, sex unknown, 16 Oct 1893, G.C. Munro.

MAUI

Haleakalā National Park, S boundary btw Magnetic and Haupaʻakea Peaks, 2788 m, ca. 20.71°N, 156.24°W: BPBM 175997, complete skel, sex unknown, 12 Sep 1987, W.C. Alexander.

Keʻanae, ca. 20.85°N, 156.18°W: BPBM 178911, skin and skull + pt skel, sex unknown, 25–26 Mar 1993, W. Wright.

"1 mi above Kula Sanatorium" [= ~1.0± km N, ~0.8 km E, Kēōkea], 854 m: BPBM 159280, skin and skull + pt skel, subadult of unknown sex, 11 Aug 1982, M. Hersloff.

Makawao, ca. 20.85°N, 156.32°W: BPBM 177155, skin and skull + pt skel, subadult of unknown sex, 15 Aug 1988, S. Perreira.

Vicinity Wailea, ca. 20.65°N, 156.43°W: BPBM 178067, skin and skull + pt skel, sex unknown, 17 Apr 1989, A. Jardine.

HAWAIʻI

Hāmākua: BBM 9130, skin (skull in skin), sex unknown, 1905 or 1906, C.E. Blacow.

Honokaʻa: BBM-X 145763, complete mounted skeleton, sex unknown, PQT 2800, 9 Jul 1964, P.Q. Tomich.

Honomalino [area], ~550 m, ~54 km S Kailua-Kona, 19.168°N, 155.869°W: BPBM 161228, skin and skull, subadult of unknown sex, 25 Jun 1984, J.G. Giffin.

Kapāpala Ranch: BBM 9009, mummy, sex unknown, collected prior to 7 Oct 1905, J. Monsarrat.

Kealakekua Ranch: ~610 m: BBM-X 155005, mummy, sex unknown, Mar 1978, S.R.H. Greenwell; ~1212 m: BBM-X 145165, comp skel, sex unknown, 21 Mar 1966, A. Greenwell.

Keamoku Cave, 1725 m, ~35 km SW Hilo: BBM-X 147123, skull + pt skel, sex unknown; BBM-X 147124, skull + pt skel, sex unknown; BBM-X 147125, skull + pt skel, sex unknown; BBM-X 147126, pt rt scapula, sex unknown; all 7 Feb 1974, F.G. Howarth, F.D. Stone, and H.E. Smith.

Vicinity Kua Bay, N. Kona, ~40 m: ACZ 3244, pt skel, sex unknown, 18 Sep 1989, A.C. Ziegler.

Makaʻiwa Bay: BPBM 177883, skin and skull + pt skel, sex unknown, 26 Nov 1988, M. and N. Young.

Mauna Ulu, E end volcanic vent, ~1050 m, ~40 km SSW Hilo: BBM-X 147035, decomposed tissue and skeleton collected in 80% ethanol, sex unknown, 8 Mar 1973, F.G. Howarth.

Pauahi [= 6.5 km E Captain Cook], 1303 m, ca. 19.50°N, 155.82°W: BPBM 179757, comp skel, sex unknown, 5 Sep 1994, S. Greenwell.

Puʻu Kehena, ~0.75 km W, 0.5 km S, ~793 m, ca. 20.15°N, 155.81°W: BPBM 178144, skin and skull + pt skel, Nov 1989, A. von Holt.

South Kona District, [Hwy 11?], 8 km N Miloliʻi turnoff, 19.23°N, 155.88°W: BPBM 178452, skin and skull + pt skel, 1–4 Dec 1989, D. Nichols.

Vicinity South Point: BBM-X 156911, alc, sex unknown; BBM-X 156912, alc, sex unknown; BBM-X 156913, alc, subadult of unknown sex; all received May 1979, collector unknown.

Volcano, ca. 19.32°N, 155.22°W: BPBM 178453, skin and skull + pt skel, sex unknown, 23 Sep 1991, S. Wilburn.

Volcano, ca. 19.433°N, 155.273°W: BPBM 161300, comp skel, sex unknown, 7–12 Dec 1984, P.C. Banko.

Waiʻōhinu, 318 m: BBM-X 145170, skull + pt skel, sex unknown, Oct 1947, W.H. Meinecke; altitude unknown: BBM-X 145164, alc, sex unknown, 27 Apr 1966, W.A. Young Sr.

Waimea, 800–935 m, 20.02559°N, 155.65886°W, residential area: BBM 184506, complete skeleton, sex unknown, 19 Nov 2000, D. Chadwick.

APPENDIX 3

Additional Specimens Examined

The following list includes all specimens examined that are not from the Hawaiian Islands, along with their respective localities; see Materials and Methods for abbreviations.

Vespertilionidae

Antrozous palidus (*N* = 1). USA: California, Marin Co., Nicasio (AMNH 31173).

Bauerus dubaiquercus (*N* = 1). BELIZE: Toledo District, 1.8 km NNW Quebrada de Oro at Bladen Branch River (AMNH 256832).

Chalinolobus gouldii (*N* = 3). AUSTRALIA: West Australia, Contine, 1000 ft. (AMNH 197234, 197235, 197236).

Corynorhinus rafinesque (*N* = 1). USA: Missouri, Slone Co. (AMNH 74902).

Eptesicus furinalis (*N* = 1). BRAZIL: Rio Grande do Sul, Quinto (AMNH 235371).

Falsistrellus tasmaniensis (*N* = 1). AUSTRALIA: West Australia, 10 miles W of Mannup, 1000 ft. (AMNH 197222).

Kerivoua pellucida (*N* = 1). PHILIPPINES: Island unknown (AMNH 241938).

Lasionycteris noctivagans (*N* = 2). USA: Nebraska, Sioux Co., Scottsbluff, 4800 ft. (AMNH 140425); New York, Ulster Co., Kingston Cabstone Farms (AMNH 130229).

Lasiurus blossevilli (*N* = 2). BRAZIL: Mato Grosso do Sul, Maracaju (AMNH 134921). USA: California, Butte Co., 4.8 km W Oroville (BBM-X 145797).

Lasiurus borealis (*N* = 4). USA: Connecticut, New Haven Co., New Haven (BPBM 161209); New York, Kings Co., Brooklyn (AMNH 144815); New York, Manhattan, West 81st Street (AMNH 185344); New York, Nassau Co., Massapequa, 61 m (BPBM 161208); Undetermined state (although probably either Ohio or Michigan; BBM-X 153548).

Lasiurus cinereus cinereus (*N* = 2). MEXICO: Puebla, between Mexico City and Puebla (AMNH 203918); USA: Connecticut, Fairfield Co., Greenwich (AMNH 214126).

Lasiurus cinereus villosissimus (*N* = 1). BOLIVIA: Santa Cruz, Caballero, 3 km by road SE of Comarapa (AMNH 260258).

Lasiurus intermedius (*N* = 2). MEXICO –Veracruz, 24 miles S. Veracruz (AMNH 203930) USA: Florida, Indian River Co., Vero Beach (AMNH 253712).

Lasiurus seminolus (*N* = 1). BERMUDA: Bermuda Islands (AMNH 139871).

Murina cyclotis (*N* = 1). MALAYSIA: Pahangi, Krau Game Reserve, Kuala Lampat (AMNH 234204).

Murina suilla (*N* = 1). MALAYSIA: Pahangi, Krau Game Reserve, Kuala Lampat (AMNH 234207).

Neoromicia rendalli (*N* = 1). SUDAN: Bahr el Ghazal, Yirol Dist., Lake Nyibor (AMNH 184356).

Nycticeinops schlieffeni (*N* = 1). BOTSWANA: Tsotsoroga (AMNH 83632).

Nycticieus humeralis (*N* = 3). USA: Florida, Citrus Co., 1 mile SW of Homosassa Springs at head of Homosassa River (AMNH 163882); Florida, Pinnellas Co., Seven Oaks (AMNH 33172); North Carolina, Raleigh (AMNH 3960).

Nyctophilus arnhemensis (*N* = 1). AUSTRALIA: Northern Territory, 259 km SE Darwin (USNM 396819).

Nyctophilus bifax (*N* = 1). AUSTRALIA: Northern Territory, 259 km SE Darwin (USNM 396821).

Nyctophilus gouldi (*N* = 1). AUSTRALIA: Queensland, near Brisbane (AMNH 193962).

Otonycteris hemprichi (*N* = 3). EGYPT: Giza, Great Pyramid of Giza (USNM 300216). PAKISTAN: West Pakistan, Balochistan, Kalat Div., Kalat Dist., 2 mi S Kalpur (AMNH 212071); West Pakistan, Gilgit Agency, Gupsis, 2348 m (USNM 353139).

Rhogeessa io (*N* = 1). TRINIDAD AND TOBAGO: Trinidad, Saint Patrick County, Siparia (AMNH 182924).

Rhogeessa parvula (*N* = 1). MEXICO: Sinaloa, El Molino (AMNH 243885).

Rhogeessa tumida (*N* = 1). MEXICO: Veracruz, 24 miles S. Veracruz (AMNH 203917).

Scotoecus albofuscus (*N* = 1). KENYA: Tiwi, 25 km S Mombasa (AMNH 237386).

Scotoecus hindei (*N* = 1). SUDAN: Bahr el Ghazal, Yirol (AMNH 184460).

Scotomanes ornatus (*N* = 1). CHINA: Sze-chuan, Wanhsien (AMNH 56889).

Scotophilus dinganii (*N* = 2). KENYA: Rift Valley, Baringo District, Baltabwa, 24 km NNE Kabarsera, 005615N, 0355200E, ~758 m (USNM 548521). SOUTH AFRICA: Transvaal, Kruger National Park, Pafuri Area, Mackford's Garden (AMNH 257434).

Scotophilus heathi (*N* = 1). THAILAND: Chiang Mai Prov., Son Dawk (AMNH 167939).

Scotophilus kuhlii (*N* =1). PHILIPPINES, Luzon Island, Pampanga Province, Clark Air Base (USNM 304378).

Scotorepens greyii (*N* = 1). AUSTRALIA: Queensland, Pentland (AMNH 107796).

Scotorepens sanborni (*N* = 1). PAPUA NEW GUINEA: Western Dist., Dogwa, Oriomo R. (AMNH 104835).

Scotozous dormeri (*N* = 1). INDIA: Maharashtra, Kolaba Dist., Elephant Caves, Bombay Harbor (AMNH 208152).

Vespadelus caurinus (*N* = 1). AUSTRALIA: Queensland, Mt. Isa (AMNH 162705).

Miniopteridae

Miniopterus schreibersi (*N* = 1). AUSTRALIA: New South Wales, Bungonia (AMNH 219977).

Megadermatidae

Megaderma spasma (*N* = 1). INDONESIA: Molucca Islands, Insel Taliabae (AMNH 109285).

APPENDIX 4

Fossil Specimen Localities

The following localities were the source of the fossil bat material described in the text and summarized in appendix 3; see Materials and Methods for abbreviations.

Kauaʻi

Māhāʻulepū Cave System (now referred to as Makauwahi Cave; Burney and Kikuchi, 2006), ~1.8 m at surface, but with deposits extending down to more than 2 m below sea level, 21.89°N, 159.42°W (WGS map datum) ~2.2 km ENE Poʻipū (subsequently SIHP 50-30-10-3097): This site is described in detail by Burney et al. (2001), and consists primarily of a large limestone sinkhole formed in Early Pleistocene indurated eolianite, containing a Holocene lake deposit and other sediments dating from pre-Polynesian times to the present. Bones of a number of prehistorically extinct and extant bird species are common in many parts of the site. Polynesian midden and artifacts occur in the upper stratigraphic levels, and a pelvis of *Rattus exulans* has been radiometrically dated as 822 ± 60 years old (A.D. 1039–1291). In January and February 1998, David A. Burney, Storrs L. Olson, and others of the Kauaʻi Paleoecological Project collected 9 bones of *Synemporion keana* and 11 of *Lasiurus cinereus semotus,* all found between 2.7 and 4.1 m below the deposit surface. The bat bones themselves have not been radiometrically dated, but 1 bone of *L. c. semotus* seems certainly of the Polynesian period judging from stratigraphy and closely associated cultural items with dates between ca. A.D. 1425 and 1660 (Burney et al., 2001). Even relative dates for the remaining bat bones cannot be certainly determined because of disturbance of their containing deposits by, apparently, at least 1 unrecorded tsunami of perhaps 400–500 years ago. However it seems clear that they all date from mid- to late-Holocene, thus being between roughly 1000 and 5000 years old (David A. Burney in litt. 29 December 2000).

Makawehi Point, ~10 m, ~1.9 km E Poʻipū (specifically, Site K-2 of Olson and James, 1982: 21–24), approx. 21.88°N, 159.43°W: Between 14 and 18 August 1976, from this near-shore sand dune deposit Storrs L. Olson and associates recovered two isolated bones of *Synemporion keana* at unrecorded depths, along with relatively abundant bones of prehistorically extinct and extant bird species. There were no obviously associated Polynesian cultural remains. Land snail shells, crab claws, and a goose bone from the sand yielded radiocarbon dates of 6740 ± 80, 5145 ± 60 and 4690 ± 100 ybp, respectively (Olson and James, 1982a, 1982b; Hearty et al., 2000). Thus the bat material was most likely deposited more than 4000 years prior to Polynesian colonization of the Hawaiian Islands (Hearty et al., 2000).

Oʻahu

Almost all Oʻahu fossil bat material has been recovered from limestone sinkholes in the general Barbers Point area of the island's SW corner. The general vicinity of all the investigated sinkholes is 21.33°N, 158.11°W. The remains occurred in primarily alluvial sediments filling solution pits in two partially superimposed emergent coral-algal reefs. Most of the Barbers Point reef, currently lower than ca. 7.6 m, is considered to have formed during the Waimānalo stand of the sea (Ku et al., 1974; Macdonald et al., 1983), which has most recently been dated as occurring between ca. 114,000 and 131,000 ybp (Szabo et al., 1994). It had previously been generally assumed locally that all of the Barbers Point sinkholes occur in this Waimānalo formation, but it has now become apparent that a few of them (including two discussed below) must have been formed in a different, earlier, reef because their surface openings are situated at a present elevation greater than 7.6 m .

To judge from Stearns' (1978) study of the various exposed fossil reefs on Oʻahu, the higher reef involved at Barbers Point is very likely a subunit of that laid down during the maximum Kaʻena sea stand of ca. 500,000–600,000 ybp, and now exposed at elevations as high as ca. 30 m on other parts of Oʻahu. The Barbers Point portion is perhaps an area planed off at the present level of 12–14 m during a temporary halt in ocean recession about 400,000 ybp (the alleged Waiʻalae sea stand). Many of Stearns' data are supported by Szabo et al. (1994). These latter investigators feel, however, that the present higher elevations of the exposed Kaʻena sea stand deposits relative to those of the younger Waimānalo one are due to continuing uplift of Oʻahu since the former interglacial ocean rise. Incidently, Szabo et al. (1978) also offer evidence that at the times of both high sea stands the ocean level may not have been greater than about 3 m above the current level.

The primary significance of the foregoing observations is that at least the lower sediment layers of Barbers Point sinkholes with surface openings greater than ca. 7.5 m could potentially contain material up to 300,000 or so years older than that in the lower levels of sites at lower elevations. Quite inexplicably, however, none of the vertebrate material from *any* Barbers Point sinkhole thus far has been radiocarbon dated at more than 10,000 years old.

A large portion of the bat remains from Barbers Point were collected between 1977 and 1981 by field parties under the supervision of either Akihiko Sinoto of the Bernice P. Bishop Museum or Storrs L. Olson and Helen F. James of the National Museum of Natural History in the course of recovering the generally abundant dissociated bones of prehistorically extinct and extant bird species from the sinkhole sediments.

BMAS 50-Oa-B6-22 (subsequently SIHP 50-80-12-9545), ~15 m, ~3.6 km N Barbers Point: This sinkhole is one of the three discussed here situated in a reef of the Kaʻena sea stand (or one of its divisions, as discussed just above), all of the others occurring in the younger reef of the Waimānalo sea stand. The site is described by Sinoto (1976) and Olson and James (1982a). Only a very small portion of this exceptionally large sinkhole has been tested, but relatively numerous remains of both *Synemporion keana* and *Lasiurus cinereus semotus* remains were recovered in July 1981 by Storrs L. Olson, James I. Mead, and their colleagues from excavations in an area with deposits 0.8 or 0.9 m deep. The biological contents of specific excavation units containing the bat material have not been reported, and the absolute or relative dates of the bat material are still undetermined.

BMAS 50-Oa-B6-100B and 100C, ~5 m, ~2.7 km NNW Barbers Point: These two sinkholes are described by Sinoto (1978). When excavated in July and August 1977 by Akihiko Sinoto and associates, both yielded *Lasiurus cinereus semotus:* one bone from the former and two from the latter. The only one of these specimens with stratigraphic provenience is from100C, found in Layer II. This layer also contained abundant bones of prehistorically extinct birds but is probably Polynesian in age, judging from the types of rodent, fish, and marine invertebrate remains also present in that layer.

BMAS 50-Oa-B6-138, ~3 m, ~3.5 km NNW Barbers Point: This sinkhole is described by Sinoto (1978). It contained scant bat remains among the bones of prehistorically extinct birds. In July and August 1977, Akihiko Sinoto and his colleagues recovered one bone of *Lasiurus cinereus semotus* from each of two midden-containing layers, which were apparently deposited sometime during the Polynesian cultural period.

SIHP 50-80-12-2624 (formerly SIHP 50-80-12-9670-P1), ~4 m, ~2.0 km N Barbers Point: This complex sinkhole and the excavation units within it are described in some detail by Hammatt and Folk (1981), Kirch and Christensen (1981), and Olson and James (1981, 1982a). Five bat bones, all of *Lasiurus cinereus semotus,* were recovered in April 1980 by Storrs L. Olson, Helen F. James, and others from various stratigraphic depths among abundant remains of prehistorically extinct birds. Shells of the Polynesian-introduced land snail *Allopeas gracile* (Hutton) (formerly *Lamellaxis gracilis*), and bones of the similarly introduced *Rattus exulans,* occurred in all levels. This fact, as well as the virtual absence of remains of historically introduced animals, and the relatively deep stratigraphic position of at least three of the bat bones, strongly suggest that the *Lasiurus cinereus semotus* material is all of Polynesian age.

SIHP 50-80-12-3899, ~3 m, ~12 km ENE Barbers Point: This sinkhole is on the NE edge of the community of ʻEwa Beach, and is described by Kennedy and Denham (1992). In June 1989, an excavation of the fill was carried to 1.3 m below the deposit surface by a crew of Archaeological Consultants of the Pacific, Inc., led by James Berlin, at which depth occurrence of vertebrate remains had virtually ceased. Two bones of *Lasiurus cinereus semotus* were recovered from the 20–30 cm level, along with relatively abundant avian remains of primarily prehistorically extinct species. Also present, however, were bones of chickens (*Gallus gallus* L.) and *Rattus exulans,* but apparently no nonintrusive remains of historically introduced vertebrates. Thus, the deposition of the bat specimens evidently occurred during the Polynesian cultural period.

SIHP 50-80-12-4917L, ~15 m, ~3.6 km N Barbers Point: This site, comprising eight sinkholes, is the remaining one discussed here that is situated in a reef older than that of the

Waimānalo sea stand, and is described by McDermott et al. (2000). Between August and October 1996, from the 50 cm thick fill of Sink 6, an excavation crew of Cultural Surveys Hawaiʻi, Inc., recovered three bones of *Synemporion keana:* one at 10–15 cm below the surface, and the other two at ca. 20 cm below the first. The bone from 10–15 cm below surface is still in the possession of Cultural Surveys Hawaiʻi, Inc., while the remaining two were sacrificed for ^{14}C dating. One of the latter proved to contain too little material for dating, but the other gave an age of 1670 ± 60 ybp (Stafford Research Laboratories Sample SR-5313, calibrated to A.D. 240–539 by Dye, 2000). At approximately the same level of the sinkhole as the bat bones were remains of prehistorically extinct birds, and a very few bones of *Rattus exulans,* one of which dated to A.D. 1280–1409. But no obvious cultural material was found. The youngest date of the bat-bone age range suggests that *S. keana* was still extant during at least the earliest part of the Polynesian period. Furthermore, the third bone from this site was found about 20 cm above the dated bone. Its provenience along with the presence of *Rattus exulans* remains indicates that *Synemporion keana* most likely survived into the Polynesian period.

Earl Neller Sinkhole SPA III HL-2, ~5 m, ~2.1 km N Barbers Point: The number for this site was assigned by Earl “Buddy” Neller (personal commun., January 1989), but it has not previously been described. The specific location is ~150 m NNW of the junction of Malakole Road and Hanua Street, and ~25 m W of “Powerline Road,” immediately N of Campbell Industrial Park. The sinkhole was completely excavated by A.C.Z. between 27 September 1986 and 5 March 1988 for the primary purpose of determining the total kinds and numbers of bones of birds and other vertebrates present, rather than their stratigraphic distribution. This solution structure is a little over 1 m in diameter at ground level, ultimately expanding below to ca. 1.3 m. The 2 m of deposit originally began 0.9 m below the surface opening, and contained a fair amount of prehistorically extinct bird material and occasional *Rattus exulans* bones but no artifactual material. One bone of *Synemporion keana* and another of *Lasiurus cinereus semotus,* both of undetermined stratigraphic depth and cultural period, were recovered.

ʻŌpaeʻula Sinkhole, ~5 m, ~2.0 km N Barbers Point: This is another previously undescribed site, situated about 50 m S of the just-noted Earl Neller Sinkhole and 50 m N of the earlier-mentioned SIHP 50-80-12-2624. It is a relatively deep and somewhat complex sinkhole, with a local, slightly brackish freshwater lens exposed as two small pools on its floor. Individuals of the tiny shrimp *Halocaridina rubra* Holthuis, or *ʻŌpaeʻula,* in Hawaiian, are usually obvious in these pools. In late November 1992, David W. Eickhoff recovered a number of bones of prehistorically extinct birds along with one bone of *Synemporion keana* and two of *Lasiurus cinereus semotus* from one pool’s sediment. Their time of deposition is unknown, although the absence of associated human-introduced vertebrate remains and cultural material among the recovered material at least strongly suggest it may be pre-Polynesian.

Ulupaʻu Head, ~1–3 m, 50–400 m SSW Kiʻi Point, Mōkapu Peninsula, 21.457°N, 157.728°W: This site is within a cratered tuff cone partially filled with sediment eroded from its inner walls. As described by James (1987), the deposit built up in the bottom of a shallow pond periodically present during periods of heavy rainfall. This matrix is now exposed as a high soil bank by ocean erosion of part of the crater wall, and contains scattered and almost invariably dissociated, permineralized, bone material of prehistorically extinct and still-extant bird species. The deposits are overlain with a fossil reef of the Waimānalo sea stand, and are thus older than ca. 130,000 years (see previous discussion of the Barbers Point area sinkholes). The formation of the tuff cone itself is estimated to have occurred at some time between 300,000 and 850,000 ybp (Ku et al., 1974; Macdonald et al., 1983). The Ulupaʻu Head lake deposits most likely formed during the Middle Pleistocene Marine Isotope Stage (MIS) 11 interglacial at roughly 400,000 ybp, or possibly during MIS 9 at roughly 320,000 ybp (Hearty et al., 2005). In 1983, a single *Synemporion keana* radius was recovered at 1–3 m by Kost A. Pankiwskyj, and three partial forelimb elements were subsequently taken from the deposits in 1984 and 1999 by three field parties of various investigators.

Molokaʻi

Lua Lolo Piping Cave, Upper Kewela, ~1290 m, 11.2 km NE Kaunakakai, 21.12° N; 156.90°W (WGS map datum): Lua Lolo Piping Cave is one of several large piping caves that together create a karstlike landscape of sinkholes, sinking streams, ravines, and caves on the slope between Papaʻala Pali and Puʻu Kolekole on E. Molokaʻi. Piping caves are erosional voids created when percolating groundwater mechanically removes softer material from beneath a solid upper layer (Halliday, 2007). The surface environment over Lua Lolo Piping Cave is a dense native rainforest with an average annual rainfall of about 300 cm. Lua Lolo Piping Cave is a large and complex dynamically active piping cave with over 300 m of passage known. The entrance is at the downslope end of an elongate sinkhole 20 m wide, 75 m long and 20 to 25 m deep. A small stream flows along the entrance passage, which is a walkway 3 m wide by 5 m high and 60 m long to the intersection with an upper level passage 3 m above the floor. Beyond the intersection the lower passage decreases to 60 cm high, then forks with the left passage leading to a water-filled sump. The right passage leads to a muddy duck-under followed by a 10 m long passage to the lip of an 8 m high waterfall, which drops into a large canyon 15 m high by 7 m wide. This stream passage continues another 160 m to a deep pool nearly 250 m from the entrance. The larger upper level passage near the entrance forms a loop about 50 m long. It is about 5 m in diameter and 30 m long to a 3 m cliff, after which the passage continues for 20 m and rejoins the main canyon passage about 10 m beyond the waterfall lip. The three levels in the cave correspond to three layers of ash separated by two thinner layers of massive lava. The air temperature in the deep cave was 14 C on 15 January 1983.

On 15 Jan 1983, F.G.H. and F.D.S. retrieved two partial skeletons of *Synemporion keana,* along with shells of a native entodontid snail, from the surface of the wet mudbank, which lined the outside of the curve of the upper level passage and was about 1 m high and wide. Besides the bats and snail shells, which were in separate areas of the mud bank, no other paleontological material was found. The bat skeletons lay a few cm apart with their wings extended, venters against the substrate and heads upslope toward the wall. The bones were still associated and appeared to have been undisturbed since deposition. As a rule, dead bats in caves are found with their wings folded in resting position, or their bones have become disarticulated after deposition. From their taphonomy, these two bats were floating (drowned?) and then deposited on the mud surface by slowly receding floodwaters. Piping caves frequently flood as evidenced by the extensive deposits of leaf litter and debris stuck to the walls and passages in Lua Lolo and other piping caves at Kewela. Not only can periods of heavy rainfall cause flooding, but also collapses can dam streams thereby flooding the caves from below. In addition, if these dams break catastrophically, a flash flood can move down the gully and through any caves downslope. In 1983, the lower entrance to a nearby piping cave was through a jumble of recently fallen large trees, rocks and mud, which demonstrated the process of collapse and subsequent draining of the caves.

The degree of preservation of the bones, their location in a constantly wet, muddy environment, and the dynamic nature of piping caves all indicate that the skeletons may not be more than a few centuries old. These appear to be the most recent specimens known of *S. keana* and provide evidence that the species may have survived into the late Polynesian or early postcontact period.

Joan Aidem Moʻomomi Beach, Site 8, ~30 m, ~182 m from ocean, 0.5 km W Hawaiian Homes pavilion, 21.20°N, 157.16°W: (see Olson and James, 1982a, esp. p. 18; also Stearns, 1973): The general Moʻomomi Beach area on the NW shore of Molokaʻi consists mainly of ancient sand dunes. These contain a number of paleontological sites periodically investigated by Joan Aidem between, primarily, 1971 and 1974. The wind-eroded surface at one site yielded three bones of *Lasiurus c. semotus* as well as bone material of prehistorically extinct birds. Land snail shells associated with the holotype skeleton of the large flightless anatid *Thambetochen chauliodous* Olson and Wetmore (1976) from the Moʻomomi area yielded a radiocarbon date of 25,150 ± 1000 ybp (Stearns, 1973), but these invertebrates are apparently intrusive from younger levels because subsequent dating of the bird-skeleton substrate gave an age of ca. 80,000 ybp (Hearty et al., 2000). These anatid remains lay an undetermined stratigraphic distance below the present near-surface bat material. Snail shell remains from the same superficial loose sands as the bat bones have yielded radiocarbon ages between 5245 ± 60 and 5510 ± 65 years (Hearty et al., 2000). No Polynesian cultural material appears associated with this invertebrate and vertebrate material, and midden material from stratified archaeological sites of the area includes no obvious remains of prehistorically extinct vertebrate species (A.C.Z., personal obs.). Thus, the bat deposition most likely occurred during the last few thousand years preceding human colonization of the Hawaiian Islands. The absence of *S. keana* from well-sampled Moʻomomi Dune and Ilio Point deposits on West Molokaʻi is noteworthy and suggests that the bat was unable to exploit resources in the extremely xeric environment (Olson, in litt., April 18, 2014).

Maui

All localities listed below are lava tubes on Haleakalā Volcano, most of which apparently formed pitfall traps for flightless birds and other animals. The age of the lava flow containing only one of these caves has been reported, Kaʻeleku Caverns, on the East Rift Zone of the volcano; however, that date appears to be too old (see below). Crystal Cave is a remnant lava tube exposed by erosion long after its formation. The remaining caves are within undated lava flows from the Southwest Rift Zone and are probably older than 13,000 years.

Crystal Cave, 183 m, 20.63°N, 156.23°W, in Manawainui Gulch, Kahikinui Ahupuaʻa: Additional gulches and geographic features are named Manawainui on Maui, but they occur in other Ahupuaʻa [= district]. As described by Olson and James (1991), the location of this lava tube's entrance high in the steep gully wall was not conducive to entrapment of nonvolant birds, but passerine bird skeletons (including at least two and possibly three prehistorically extinct species; S.L. Olson, personal commun.) were present. These, along with the undated remains of two *Synemporion keana* were recovered from the passage floor by a Storrs L. Olson and Helen F. James field party in 1988. The cave is shaped like a hairpin with the passage extending horizontally into the cliff and then dropping into a lower level, which trends back towards the entrance. The cave is probably a relict lava tube segment exposed during formation of the gully.

Kaʻeleku Caverns, 85 m, ca. 20.80°N, 156.001°W: Descriptions of this extensive multientranced lava tube are provided by Thorne (1998) and Bunnell (1998a, 1998b). In regard to vertebrate remains, Thorne (1998) reports only historic cattle bones, in addition to a "perfectly intact" bat skeleton on the lithic substrate "in a large side tube near the very top of the cave." Bunnell (1998a, left-center photograph) illustrates what is apparently this skeleton, which appears from the cranium shape to be *Lasiurus cinereus semotus.* Subsequently, on 6 July 1990, F.V.H. Grady, H.F. James, and A. Medeiros collected a partial skeleton of *Synemporion keana* from an unstated portion of the cave, which quite possibly represents a different bat individual than that photographed by Bunnell. No other vertebrate remains, if any exist, have been reported from the site. The lava flow containing Kaʻeleku Caverns is radiocarbon-dated at between 20,000 and 40,000 ybp (Bunnell, 1998b). However, Sherrod et al. (2007) show the lava flow to be in the Hāna Volcanic series dated at less than 1500 ybp. The degree of secondary mineralization in the cave corroborates the younger age.

Kahāwaihapapa Cave, 15 m, 20.62°N, 156.25°W, vicinity Kahāwaihapapa Point: This lava tube is described by Olson and James (1991); in March 1988 its floor and wall ledges yielded them a single undated partial skeleton of *Synemporion keana* along with bones of a few species of extinct and extant birds. Polynesian cultural material, probably precontact, was also present, but the temporal relationship of the bat remains to this material is undetermined.

Māhiehie Cave, 500 m, 20.63°N; 156.39°W (WGS 84 datum), ʻUlupalakua Ranch: This lava tube is the type locality of *Synemporion keana.* It was investigated by F.G. Howarth, Chris Depkin, and Barbara Gimlin in 1981, by Howarth and F.D. Stone in 1982, and by Howarth and C.H. Kishinami in 1989. Over 30 specimens of *Synemporion keana* and two of *Lasiurus cinereus semotus* have thus far been collected from the cave. The cave is an upslope section of Puʻu Naio Cave, which has been studied intensively by James et al. (1987). Both caves are in an undated lava flow from Puʻu Mahoe vent on the SW Rift of Haleakalā. James et al. (1987) estimated the age of the cave to be greater than 10,000 years, and more recently, Sherrod et al. (2007) reported the age of the host lava flow as 13,000 to 30,000 ybp. Air temperature at the lower end of Māhiehie Cave remains constant between 19° and 19.5° C. Except for seasonal seeps on the walls, the cave remains mostly dry.

The entrance to Māhiehie Cave is a large vertical pit approximately 25 to 30 m in diameter and 20 m deep. A series of narrow ledges along the southeast wall allows one to climb to the floor of the pit. The lava tube passage at the upslope end of the pit is a short shelter cave, which is sealed by soil and debris fill. At the downslope (south) end of the pit, there is a large amphitheaterlike entrance 8–10 m wide and high, which slopes steeply downward for about 10 m beyond the dripline to where the ceiling meets the talus slope. A large lava slab leaning against the ceiling nearly blocks the entrance to a low narrow passage, 1–1.5 m in diameter and 5 m long, between large boulders, which provides access to the large downslope cave passage beyond. The downslope passage is a large lava tube, 5 to 10 m in diameter and over 600 m long, which descends about 100 m in elevation. Except for near the downslope end, the floor is covered with breakdown blocks that range in size from 0.5 to more than 2 m across. More than 100 bat skeletons in various stages of decay occur in the cave. Only one skeleton of *Synemporion keana* (BPBM 178053) had traces of possible dried tissue on a few larger bones. On 16 September 1982, F.G.H. and F.D.S. counted 85 bat skeletons in the cave and measured the forearm length of 20 of the better-preserved specimens in situ. All but one fit within the size range of *S. keana.* The exception was obviously bigger and more robust than the others and matched the size of *Lasiurus cinereus semotus*. Most skeletons were found in the lower 100 m of the cave and most commonly were lying on lava shelves, which run along the base of the wall, one on each side of the passage. Numerous skeletons also were observed on the bare lava floor near the lower end of the cave, and three or four individuals died hanging on the wall between 1 to 2 m above the floor near the end. The latter were partially embedded in the secondary mineral crust forming on the walls. Even though a few bones were seen deep in crevices between boulders along the main passage, it was not possible to count how many bat remains might be buried in the breakdown.

Puʻu Mākua Cave, 1463 m, 20.68°N, 156.35°W: This site is described by Olson and James (1991), and was apparently first scientifically investigated by R. Michael Severns and Chuck Whiteman. Later, on 19 April 1988, Helen F. James and Carla H. Kishinami collected two essentially complete, undated *Synemporion keana* skeletons from lava rubble on the floor of the tubes, along with a number of similarly situated associated bird skeletons, mostly of flightless and other prehistorically extinct forms.

Puʻu Naio Cave, ~365 m, 20.62°N, 156.40°W, SW slope Haleakalā: This site is described in some detail by Olson and James (1984, 1991) and James et al. (1987). An alluvial deposit under the skylight of this lava tube underwent extensive excavation by Storrs L. Olson and Helen F. James along with associates in 1984 and 1988. The well-stratified deposit, radiocarbon-dated from essentially modern age to ca. 10,000 ybp, yielded 10 specimens of *Synemporion keana* and five of *Lasiurus cinereus semotus,* along with some other mammal and abundant bird material of both prehistorically extinct and extant species. James (in litt., 12 October 1989) prepared a regression equation based on radiocarbon ages of stratified avian remains bracketing material of the two bat taxa. From this she estimated the time span of *S. keana* occurrences at the site extended from 9500 ± 900 to 2000 ± 600 ybp, with *L. c. semotus* coeval during at least the period of 6800 ± 650 to 4500 ± 500 ybp. A skull of historic *L. c. semotus,* to be cataloged at USNM, was additionally recovered from an owl pellet by Travis A. Olson in the cave, but is not included in the present investigation. This cave is in the same lava flow as Māhiehie Cave, which has been determined to be between 13,000 and 30,000 years old (Sherrod et al., 2007).

Hawaiʻi

Hualālai Owl Cave, ~242 m, 19.83°N, 155.90°W: There is no previously published information on this site. Jon G. Giffin named this multientranced lava tube, and was the first to informally report remains of fossil vertebrates discovered there. The lava flow containing the tube has been dated at 5000–10,000 years old (J.G. Giffin, in litt., 31 October 2002). On 7 March 1993, Giffin along with Helen F. James and party collected bones representing 10 oceanic and land bird species, including four extinct taxa. A partial skeleton of *Lasiurus cinereus semotus* was also obtained (H.F. James, in litt., 7 August 2002).

Kahuku Ranch Cave, ~130 m, 19.00°N; 155.62°W, WGS 84 datum (7.2 km from Hwy. 11 through Mark Twain subdivision, downslope of "Y" in road): No information regarding this lava tube, tentatively named by Helen F. James, has previously been published. On 1 August 1998, James and her party briefly visited the site, where her daughter, Sydney B. Olson, discovered three (two mixed) partial skeletons of *Synemporion keana,* and two of *Lasiurus cinereus semotus,* on the floor of a small chamber. Neither the bat material nor the lava flow containing the tube has been dated.

Lua Nunu Kamakalepo Cave, ~80 m, 19.00°N, 155.60°W, WGS 84 datum: This large, undated lava tube segment in the vicinity Kaʻaluʻalu Bay, 12± km NE South Point, is in lava originating from Mauna Loa and is about 300 m long (Kempe et al., 2009). The main entrance pit is about 50 m long, 25 m wide and nearly 30 m deep. A large passage, 15–20 m wide and 10 to 15 m high, trends upslope from the bottom of the pit. A single undated bone (radius) of *Lasiurus cinereus semotus* was picked up by FGH 17 July 1976. The bone was protruding from the slope of a ~4 m high pile of loose ash that had fallen from a ceiling collapse. The ash cone occurred in total darkness about 200 m from the entrance. An intensive search of the surface of the cone revealed no further bat material.

ʻŪmiʻi Manu Cave, 1878 m, ca. 5 km NE Hualālai summit, 19.72°N, 155.827°W: This extensive multientranced lava tube is described and named by Giffin (1993), who first reported evidence of bird remains there. During surveys between August and October 1992, a number of bones from among those of the approximately 20 extinct and extant avian species represented were collected by Jon G. Giffin, Helen F. James, and associates. Additionally, on 2 March 1993, a partial skeleton of *Synemporion keana* was picked up by a member of James' field party. Most skeletons were found exposed on the cave floor, with a few others recovered from alluvial deposits there. The age of the lava flow containing the tube is estimated at between 3000 and 5000 ybp, possibly being coeval with a similar nearby flow radiocarbon dated at 3610 ± 200 ybp.

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