



COLOR PLATE. Artist's reconstruction of the new fossil species *Hemignathus vorpalis* (below), compared with adult males of *H. wilsoni* (Akiapolaau, above) and *H. lucidus hanepepe* (Kauai Nukupuu, middle). The fanciful plumage shown for the fossil species is based on the supposition that *H. vorpalis* resembled other members of its genus.

A GIANT NEW SPECIES OF NUKUPUU
(FRINGILLIDAE: DREPANIDINI: *HEMIGNATHUS*)
FROM THE ISLAND OF HAWAII

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ABSTRACT.—We describe a new species of drepanidine bird from a fossil found in a lava tube cave on the island of Hawaii. The bill of the new species combines a long, scimitar-like maxillary rostrum with a much shorter mandibular rostrum, giving the bird a most unusual appearance. The general bill form is shared with members of the drepanidine genus *Hemignathus*, to which the new species is referred, although it is quite distinct from other species of *Hemignathus* in aspects of its bill morphology and in its much larger body size. The scimitar-like maxilla appears to be adapted to probing in cracks or crevices and possibly to moving loose material, such as leaf detritus, to obtain invertebrate prey. The species became extinct <3,000 years ago. Received 1 October 2000, accepted 20 April 2003.

RESUMEN.—Se describe una nueva especie de ave drepánida sobre la base de un individuo fósil recuperado en una cueva (tubo) de lava en la isla de Hawaii. El pico de la nueva especie es una combinación de maxilar largo en forma de cimitarra con un rostro mandibular mucho más corto y recto, proporcionándole un aspecto muy particular al ave. Esta forma del pico es compartida con las especies del género drepánido *Hemignathus*, al cual es referida la nueva especie, que se diferencia de las demás por particularidades en la morfología del pico y el tamaño mucho mayor del cuerpo. La semejanza de la porción rostral del maxilar a una cimitarra parece ser debida a una adaptación para sondear en hendiduras o grietas, y posiblemente también para mover materia suelta, como son los detritos de hojas, en busca de invertebrados. La especie se extinguió hace menos de 3,000 años.

IN 1992, WELL-PRESERVED FOSSIL skeletons of birds were discovered in a lava tube cave system in Pu`u Wa`awa`a (a traditional land district or ahupua`a), on the northern slope of Hualalai Volcano, island of Hawaii (Giffin 1993). Subsequent explorations have revealed that several additional lava tube systems in the same district also contain avian skeletons. Fossils from the caves of the endangered Laysan Duck (*Anas laysanensis*), the endangered Nene (*Branta sandvicensis*), a large extinct flightless goose (*Branta* sp.), and four species of Hawaiian finches (Drepanidini) have been the subjects of research on ancient mitochondrial DNA (Cooper et al. 1996; Paxinos et al. 2002a, b) and comparative osteology (Livezey 1996, James 2003). Other extinct birds found in the caves include flightless rails, a petrel, two crows, and a honeyeater (Meliphagidae).

Here, we describe a new species of large drepanidine bird with an extraordinary bill

from Petrel Cave in the Pu`u Wa`awa`a district. The new species is known from a single partial associated skeleton. Even though the upper and lower bills are very different in length (see color plate), we are confident that the bones referred to the holotype are from one individual. They were found together by J. Giffin and R. Covington, isolated from other avian remains except for five bones of an extinct flightless rail (*Porzana* sp.) and three unidentifiable bone fragments (a femur shaft and two vertebrae) that probably belong with the holotype. Giffin and Covington collected all visible bones, and three months later, H. F. James and Giffin returned to the site to search again. At that time, we also collected the thin, sparsely distributed layer of fine sediment from the vicinity of the collection site (~10 cm³ of sediment was scraped up and sieved through 0.16 mm mesh screens), but our additional search produced only a few unidentifiable bone fragments. Thus, we have investigated and rejected the possibility that more than one individual of large passerine bird died near the collection site.

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There is, unfortunately, a lack of consensus on the generic-level classification of the drepanidine species known under the common names of nukupuu, akiapolaa, akialoa, and amakihi. It is likely that molecular genetic and morphological studies currently underway will lead to a revised classification. While we await those results, we hope to lessen confusion by using the same binomial nomenclature as in our other recent papers (Olson and James 1995, James 2003). Thus, we restrict the genus *Hemignathus* to the species of drepanidines with long, thin maxillary rostra coupled with much shorter mandibular rostra. In addition to the new species, those taxa are the Nukupuu (*Hemignathus lucidus*), a polytypic species known from four of the main islands from Kauai to Maui, and the Akiapolaa (*H. wilsoni*), a monotypic species known from the island of Hawaii. Olson and James (1994) reported that a specimen of *Hemignathus lucidus* collected by the U.S. Exploring Expedition probably originated on the island of Hawaii, but R. C. Fleischer (pers. comm.) believes (on the basis of his analysis of mtDNA sequences from the specimen) that it originated on Oahu. We recognize the genus *Akialoa* for the species group known by the common name akialoa and formerly included in *Hemignathus*. Thus, we depart from the American Ornithologists' Union (AOU) Check-list of North American Birds (1998), which follows Pratt (1979) in defining the genus *Hemignathus* much more broadly. Those sources place the akialoos and the amakihis in *Hemignathus*, in addition to *H. lucidus* and *H. wilsoni*. The nomenclature used here is compared with that of AOU (1998; given in parentheses) as follows: *Akialoa obscurus* (*Hemignathus obscurus*), *Akialoa lanaiensis* (*Hemignathus ellisiana*, *lanaiensis* group), *Akialoa stejnegeri* (*Hemignathus ellisiana*, *stejnegeri* group), *Hemignathus lucidus* (no change), *Hemignathus wilsoni* (*Hemignathus munroi*).

The new species would be allocated to *Hemignathus* under either of the two classifications.

COMPARATIVE MATERIAL EXAMINED

Modern skeletons.—Fringillidae: Drepanidini: *Hemignathus wilsoni*: MVZ 118830 female adult, MVZ 122610 male adult. *Hemignathus lucidus*: BMNH S/1961.11.39 unsexed adult. *Akialoa obscurus*: BBM109 unsexed adult (skull and mandible removed from skin), BBM 4434 male adult

(skull, mandible, and tarsometatarsus removed from skin). *Akialoa stejnegeri*: USNM 19094 unsexed adult.

Fossil specimens.—*Akialoa* sp., Hawaii (a fossil *Akialoa* that is much larger than *Akialoa obscurus* of the same island, see James 2003): four partial skeletons from Umi'i Manu Cave, Pu'u Wa'awa'a, island of Hawaii, BPBM 173432-179435. *Akialoa* cf. *lanaiensis* (see James 2003): five maxillae and four mandibles from Pu'u Naio Cave, Maui, USNM 508652-508659 (some of them are small fragments); one mandible from Lua Lepo Cave, Maui, USNM 508661. *Akialoa* cf. *stejnegeri*: one maxilla and two mandibles from Maha'ulepu Cave, Kauai, USNM 508662-508664. *Akialoa upupirostris*: a well-preserved skull with maxilla and five partial mandibles from Maha'ulepu Cave, Kauai, USNM 508665, 254171 (holotype), 255211, 255304, 508666, and 508667. See Acknowledgments for explanation of museum acronyms.

Family Fringillidae
Tribe Drepanidini
Genus *Hemignathus*

Included species: *Hemignathus lucidus* (Lichtenstein, 1839), *Hemignathus wilsoni* (Rothschild, 1893), *Hemignathus vorpalis* new species.

Hemignathus vorpalis, sp. nov.

Holotype.—Partial associated skeleton, BPBM 179437, consisting of a substantial portion of the maxilla, extending forward from the anterior-most portion of the right nasal cavity toward the (missing) bill tip (Fig. 1A); the mandibular symphysis with the intermediate part of the left ramus and a portion of the intermediate part of the right ramus attached (Fig. 1B); a fragment of cranium involving the right auditory region (Fig. 1C); the proximal end and shaft of the left humerus (Fig. 1D); the distal end and part of the shaft of the left ulna (Fig. 1E); the left tibiotarsus lacking the distal end (Fig. 1F); the right tibiotarsus lacking both the distal end and most of the cnemial crests (Fig. 1G); the left tarsometatarsus with the proximal end abraded (Fig. 1H); the proximal half of the right tarsometatarsus with the proximal end abraded (Fig. 1I). The piece of maxilla that is preserved has its dorsal surface abraded away along the posterior half. The

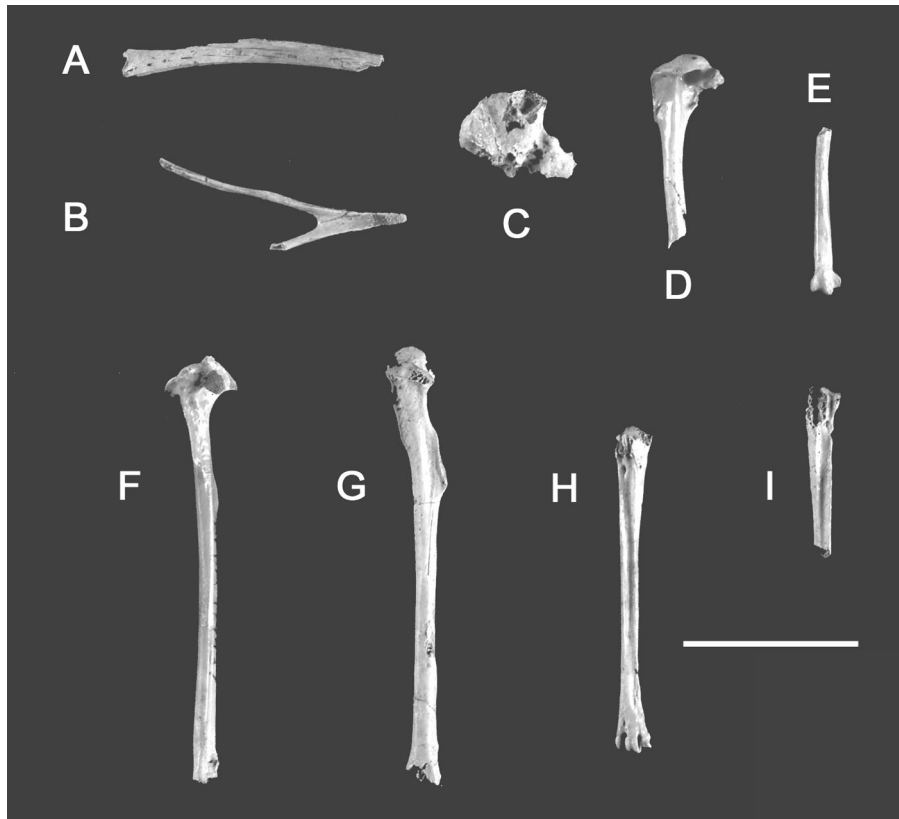


FIG. 1. Photographs of the holotype (BPBM 197437) of *Hemignathus vorpalis*, new species. (A) Maxilla in lateral view. (B) Mandible in dorsal view. (C) Skull fragment in ventrolateral view. (D) Left humerus in anconal view. (E) Left tibiotarsus in anterior view. (F) Right tibiotarsus in anterior view. (G) Left tarsometatarsus in anterior view. (H) Right tarsometatarsus in anterior view. Scale bar = 2 cm.

mandible, humerus, and right tibiotarsus have each been repaired from two or three pieces. The specimen was collected on 8 January 1993, by J. Giffin and R. Covington.

Type locality.—Petrel Cave, Hualalai Quadrangle, 155°51'W, 19°44'30'E (estimated to nearest half minute), island of Hawaii, 1,200 m above sea level. The specimen was found near an opening in the ceiling, through which we entered the lava tube with the assistance of climbing ropes. The cave was named by J. Giffin, in reference to the abundant bones of Dark-rumped Petrel (*Pterodroma phaeopygia*) found in it.

Distribution.—Known only from the type locality.

Age of holotype.—Holocene. Younger than Petrel Cave. Petrel Cave formed during a lava flow an estimated 3,000 to 1,500 years ago (Moore and Clague 1991).

Etymology.—The name *vorpalis* is from the adjective “vorpal” as used by Lewis Carroll in the poem “Jabberwocky” to modify the nouns “sword” and “blade” (“He took his vorpal sword in hand.... The vorpal blade went snicker-snack”), in reference to the long scimitar-like maxillary rostrum of the bird. Although no precise meaning has been given to “vorpal” (Gardner 1960), there is an obvious connotation of potency associated with it in the poem. The specific epithet is formed by analogy with Latin *carpus*, *carpalis*, suggesting in turn that “vorpal” might have been formed from a substantive “vorpis,” the meaning of which is also obscure.

Measurements of holotype.—A number of the bones are broken in such a way that conventional measurements cannot be taken from them. Measurements such as length of fragment are

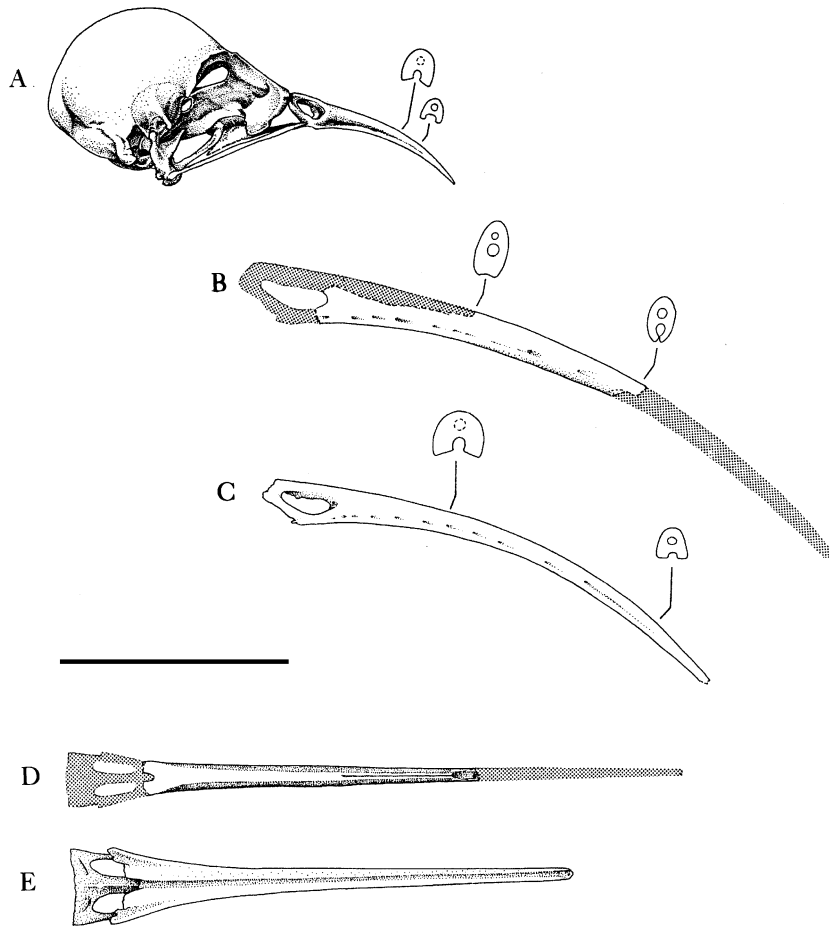


FIG. 2. Comparison of the maxilla of *Hemignathus vorpalis* (BPBM 179437, holotype) with *H. lucidus affinis* (BMNH S/1961.11.39) and *Akialoa* sp. from Hawaii. (A) Skull of *H. lucidus affinis* in lateral view. (B, D, F) Maxilla of *H. vorpalis* in lateral, ventral, and dorsal views, respectively. (C, E, G) Maxilla of *Akialoa* sp. in lateral, ventral and dorsal views, respectively. Shaded portions of the maxilla of *H. vorpalis* are reconstructed using *Akialoa* sp. as a model. Sketches of the cross-section of the maxilla, in two places for each maxilla, are shown above the lateral views. Scale bar = 2 cm.

given to identify the type specimen and for use in assessing size and shape. Maxilla: length of fragment, 30.0 mm; dimensions of the posterior-most preserved cross-section—depth, 2.9 mm; greatest width, 1.7 mm; ventral width, 1.0 mm; dimensions of the anterior-most preserved cross-section—depth, 2.4 mm; greatest width, 1.5 mm; ventral width, 0.3 mm. Mandible: symphysis length, 10.3 mm; width at angle of mandible, 6.9 mm (estimated); length from anterior margin of mandibular fenestra to tip of symphysis, 26.9 mm (includes a layer of encrustation of ~0.25 mm thickness); length from anterior margin of mandibular fenestra to pos-

terior margin of symphysis, 17.2 mm; length of intermediate part (lateral face) from the anterior margin of the mandibular fenestra to the distinct foramen at the angle of the mandible, 11.5 mm. Humerus: proximal width, 8.4 mm; greatest length from head of the humerus to distal angle of the deltopectoral crest, 9.6 mm; length of fragment, 22.4 mm. Ulna: distal width, 3.8 mm; length of fragment, 19.5 mm. Tibiotarsus: length from patellar crest to distal margin of the supratendinal bridge, 48.3 mm; length from interarticular area to distal articular face of the fibular crest, 16.5 mm; proximal width including lateral cnemial crest, 8.8 mm. Tarsometatarsus: length

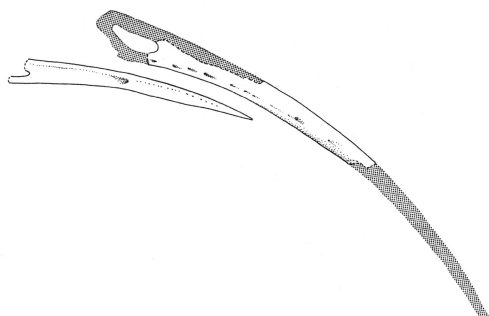


FIG. 3. Maxilla and mandible of *Hemignathus vorpalis* in lateral view, showing their inferred positions with respect to each other in the living bird. Shaded portions of the maxilla of *H. vorpalis* are reconstructed using maxillae of *Akialoa* as models.

from intercotylar eminence to the trochlea for metatarsal III, 37.6 mm; mid-shaft width, 2.2 mm; width across trochleae, 3.9 mm.

Diagnosis.—A passeriform bird, allied with the Passerida (Sibley and Ahlquist 1990) by the absence of pneumatic openings in the pneumotricipital fossa of the humerus, and with nine-primaried oscines by having a deep, but incompletely partitioned, pneumotricipital fossa. The maxilla is long, decurved, and constricted anterior to the nasal openings (Fig. 2B, D), a combination of traits that it shares with the drepanidine genera *Akialoa* and *Hemignathus*. It resembles the genus *Hemignathus* as opposed to *Akialoa* in having the mandibular rostrum much shorter than the maxillary rostrum (Fig 3). However, the maxilla is much larger than in *H. wilsoni* or *H. lucidus*, and is more similar in size and general appearance to maxillae of the species of *Akialoa* (Fig. 2). Compared with *Akialoa*, the maxilla is deep and narrow (compare sketches of cross-sections in Fig. 2) and is especially narrow on its ventral surface (only 0.3 to 1.0 mm thick). The medial neurovascular sulcus is a very well-developed feature of the ventral surface of the maxilla in *Akialoa* and in the other species of *Hemignathus* (James 2003) but is lacking in *H. vorpalis*. Instead, in *H. vorpalis*, neurovascular tissue is transmitted to the tip of

the maxilla through an internal canal (see Fig. 2 and description for further explanation).

The ventral profile of the mandibular symphysis, in lateral view, is nearly straight, an aspect in which the new species resembles *H. wilsoni*, as opposed to *H. lucidus* and the various species of *Akialoa*, all of which have decurved symphyses (Fig. 4). In other respects, however, the mandible of *H. vorpalis* resembles *H. lucidus* and *Akialoa* more than it does *H. wilsoni*. The symphyseal part of the mandible is not as short and stout as in *H. wilsoni* (Fig. 4). In *H. wilsoni*, the symphysis extends nearly as far posteriad as the tomial crests do; whereas in *H. vorpalis*, *H. lucidus*, and *Akialoa*, the symphysis does not extend posteriad nearly that far (Fig. 4). Also, *H. wilsoni* has the intermediate part of the mandibular ramus relatively short and deep compared with *H. vorpalis*, *H. lucidus*, and *Akialoa* (Fig. 4).

Compared with typical drepanidine tibiotarsi, that of *H. vorpalis* has a more pronounced crest for the ligamentum collaterale mediale.

The new species is inferred to be as large or larger in body size than any known drepanidine on the basis of dimensions of the post-

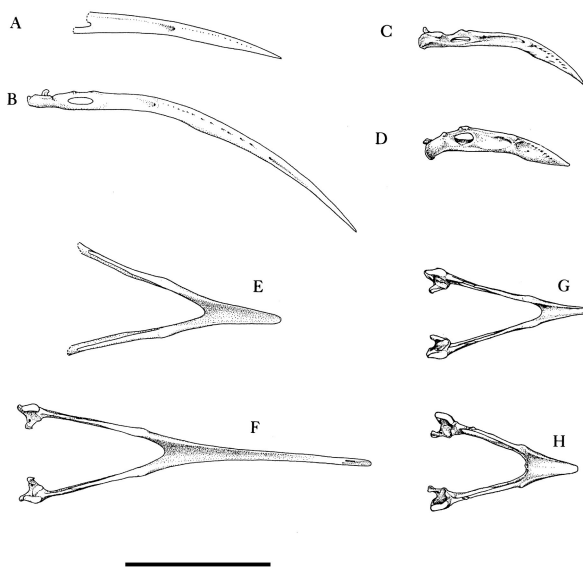


FIG. 4. Mandibles of *Hemignathus vorpalis* (BPBM 179437, holotype), *H. lucidus affinis* (BMNH S/1961.11.39), *H. wilsoni* (MVZ 122610), and *Akialoa* sp. from Hawaii, in lateral and dorsal views. (A, E) *H. vorpalis*, new species. (B, F) *Akialoa* sp. (C, G) *H. lucidus*. (D, H) *H. wilsoni*. Scale bar = 2 cm.

TABLE 1. Skeletal measurements (millimeters) of *H. vorpalis* compared with selected drepanidine taxa. The tibiotarsus length was taken from the interarticular area, to the medial condyle, thus omitting the patellar crest. The tibiotarsus width was taken from the lateral cnemial crest, to the rim of the medial articular face. The tarsometatarsus length was taken from the intercotylar eminence, to the trochlea for metatarsal III. It is not certain that the fossil finch, *Orthospiza howarthi*, is correctly classified as drepanidine (H. F. James unpubl. data).

	<i>Hemignathus vorpalis</i>	<i>Hemignathus wilsoni</i>	<i>Hemignathus lucidus</i>	<i>Akialoa stejnegeri</i>	<i>Rhodacanthis palmeri</i>	<i>Orthospiza howarthi</i>
Mandible:						
symphysis length	10.3	6.8, 7.7, 7.8	8.3	20.4	10.3	7.1
Mandible: greatest width of symphyseal part	6.9 ^a	5.7, 5.9	–	5.9	12.5	11.1
Humerus:						
length	27.1 ^a	17.7, 18.0, 18.9	16.6	19.6, 19.8	24.5	25.0 ^b
Humerus:						
proximal width	8.4	5.5, 5.6, 5.7	5.7	6.1, 6.2	7.8	7.2
Tibiotarsus:						
length	49.7 ^a	30.5, 30.8	28.0	33.7, 34.0	–	41.5
Tibiotarsus:						
proximal width	8.8	5.5, 5.8	–	5.4, 5.7	–	6.7
Tarsometatarsus:						
length	37.6	23.9, 24.4, 24.4	23.4	26.3, 26.5	27.5	–
Tarsometatarsus:						
width across trochleae	3.9	2.5, 2.6, 2.6	2.3	2.5, 2.6	3.0	–

^aDimensions of *H. vorpalis* that are estimated as explained in text.

^bThe humerus length of *Orthospiza howarthi* is also estimated (see James and Olson 1991).

cranial bones (see Comparative Osteometry, below, and Table 1).

Description.—The medial neurovascular sulcus on the ventral surface of the maxilla and the associated neurovascular tissue have not been lost but have become enclosed within the maxilla, as shown in Figure 2. Cross-sections of the maxillae of *H. lucidus* and of a fossil *Akialoa* from Hawaii show a single canal enclosed within the maxilla and a distinct notch or indentation on the ventral surface indicating the position of the medial sulcus; whereas the cross-sections for *H. vorpalis* show two canals enclosed within the maxilla and no distinct notch on the ventral surface. The transformation of the medial neurovascular sulcus into an internal canal in *H. vorpalis* apparently occurred in connection with narrowing of the ventral surface of the maxilla. Along the anterior portion of the preserved fragment of the maxilla, the ventral surface consists of little more than two tomial crests meeting along the median line. (The suture between the tomial crests is indicated by a median line in Figure 2D.) Along the posterior portion, the tomial crests do not meet but are separated only by a narrow space of bone.

In contrast with the maxilla, the mandible of

H. vorpalis is not noticeably narrow compared with *Akialoa* or *H. lucidus*.

REMARKS

The tip of the mandible of the holotype is covered by a thin fine-grained encrustation of mineral (Fig. 1). After mild acetic acid preparation failed to remove it, the mandible was X-rayed to examine the bone underneath the encrustation. The X-ray clearly showed that the tip of the mandible is unbroken and that the encrustation has a thickness of only ~0.25 mm.

Using the anterior rim of the nasal cavity on the maxilla and the tomial crests of the mandible as landmarks, and taking a complete cranium and mandible of *A. stejnegeri* as an anatomical analogue, we estimated the anatomical position of the maxilla over the mandible with the bill closed. That position is shown in Figure 3 and was used to reconstruct the appearance of the bird in life (see color plate). The length of the maxilla also was estimated for the reconstruction, by comparing the degree to which the depth of the maxilla tapers toward the bill tip in *Akialoa* with the degree to which it tapers in the fossil specimen. Although maxillae of *Akialoa*

taper gradually toward the tip, the preserved portion of the maxilla of *H. vorpalis* tapers only slightly (Fig. 2), from which we surmise that the unbroken maxilla was considerably longer than the preserved portion, although we stress that the maxilla length shown in our reconstructions is conjectural.

PHYLOGENETIC PLACEMENT

By their nature, fragmentary fossil birds provide limited clues to evolutionary relationships. In the case of *H. vorpalis*, the deeply excavated, but incompletely divided, nonpneumatic pneumatic fossa of the humerus suggests a relationship with the Drepanidini, the only group of native passerine birds in the Hawaiian Islands with that type of humerus. The very unusual bill form suggests a relationship with the genus *Hemignathus*.

James (2003) recently defined and scored osteological character variation in the drepanidine radiation for phylogenetic analysis. *Hemignathus vorpalis* was included in the study, but because the fossil was undescribed at the time, it was referred to as "*Hemignathus* sp., Hawaii." Parsimony analysis of the osteological data placed *H. vorpalis* in a clade with *H. wilsoni* and *H. lucidus* (fig. 17 in James 2003). The genus *Akialoa* was depicted as a paraphyletic assemblage, basal to *Hemignathus*. Figure 5 shows the phylogenetic hypothesis for the *Akialoa* and *Hemignathus* clade from James' study, with the unambiguous character-state changes mapped. Notice that most of the character-state changes that contribute to the structure of the clade could not be observed in the fragmentary fossil of *H. vorpalis*. James' larger phylogenetic analysis of the Drepanidini encompassed 61 taxa and 65 informative characters, but the states for 43 of those characters were recorded as missing in *H. vorpalis*. In view of the paucity of information about the new species, we consider its phylogenetic alliance with *H. wilsoni* and *H. lucidus* to be tentative.

COMPARATIVE OSTEOLOGY

Skeletal comparisons of *H. vorpalis* with other *Hemignathus* and other large drepanidines (Table 1) are limited because most of the bones of the holotype of *H. vorpalis* are either broken or missing. To make additional comparisons possible, certain

dimensions of the broken bones were estimated using the methods described below.

The humerus length was estimated using the ratio of proximal width to length in unbroken drepanidine humeri. The ratio was determined for each of the six specimens of *H. wilsoni*, *A. stejnegeri*, and *Rhodacanthis palmeri* listed in Table 1 for which both proximal width and length of the humerus could be measured. Each ratio was used to estimate humerus length in *H. vorpalis*, yielding six estimates that ranged from 26.1 to 28.4 mm, and averaged 27.1 mm. Similarly, the tibiotarsus length in *H. vorpalis* was estimated using the ratio of the length from the interarticular area to the distal edge of the supratendinal bridge, to the total tibiotarsus length without the patellar crest. That ratio, determined in one specimen of *H. wilsoni* and two of *A. stejnegeri*, yielded estimates of tibiotarsus length in *H. vorpalis* of 49.5, 49.6, and 49.9 mm. Finally, the maximum width of the symphyseal part of the mandible was estimated visually under a dissecting microscope, using a caliper to approximate the correct measurement that would have been obtained if the bone were not slightly damaged in that region.

The dimensions of the postcranial skeleton of *H. vorpalis* exceed those of other species of *Hemignathus*. For example, the estimated humerus length is 50% greater than the average for *H. wilsoni* and 63% greater than for *H. lucidus*. Table 1 also lists dimensions for the two other species of drepanidines with the largest postcranial skeletons, *R. palmeri* and *Orthospiza howarthi* (James and Olson 1991). (*Orthospiza howarthi* may not be correctly classified as drepanidine; see James 2003.) Like *H. vorpalis*, both species are extinct and only one partial postcranial skeleton is available for each. For the postcranial dimensions that can be compared among the three species, those of *H. vorpalis* are consistently the largest (8–31% larger than *O. howarthi*, 8–37% larger than *R. palmeri*). Thus, with the caveat that the samples available for comparison are minimal, it appears that *H. vorpalis* is the largest species of drepanidine yet known.

DISCUSSION

"The mere sight of so extraordinary a form could hardly fail to awaken in any one a keen desire to witness the manner of its feeding (Perkins 1893:106)

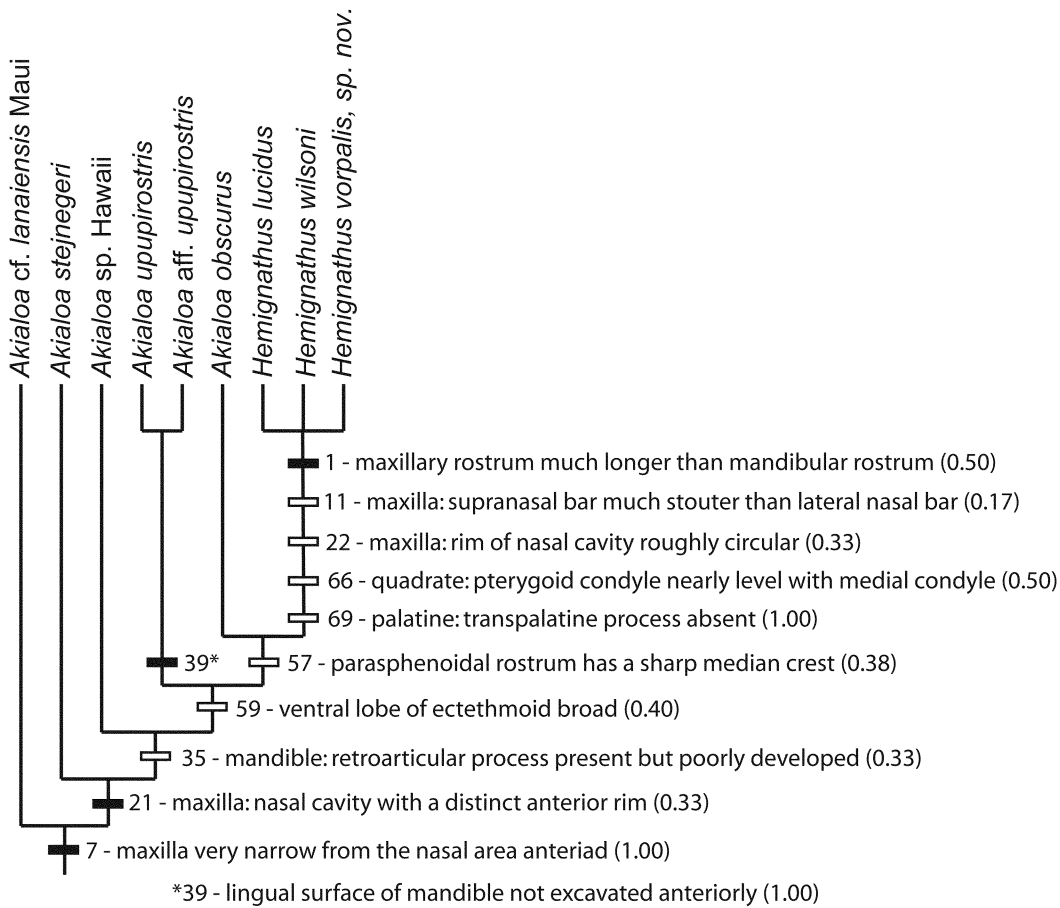


FIG. 5. Phylogenetic hypothesis for *Akialoa* and *Hemignathus*, from a study of osteology in the Drepanidini (James 2003). Brief descriptions of the character states that change unambiguously in the clade are given. Character numbers are from James (2003), which provides character state descriptions, the data matrix (matrix C), and phylogenetic analyses. Open bars identify characters that were not observable in the fragmentary fossil of *H. vorpalis*; solid bars identify characters that were. The consistency index for each character is given in parentheses, based on parsimony analysis of 61 terminal taxa (see fig. 17 in James 2003).

Although Perkins made the above comment about *H. wilsoni*, it would apply even more forcefully to *H. vorpalis*. Perkins was fortunate to witness and describe the foraging behavior of *H. wilsoni*, but in the case of *H. vorpalis*, we must be satisfied with what we can infer from morphology, phylogenetic context, and paleoecology.

James' (2003) phylogenetic study places *H. vorpalis* within a clade of drepanidines (*Hemignathus* plus *Akialoa*) that favor bark and decaying wood as feeding substrates and feed primarily on insect larvae, spiders, and small beetles (Henshaw 1902, Perkins 1903, Munro 1944, Ralph and Fancy 1996). Probing for ar-

thropods with the bill is a behavior common to all members of the clade whose foraging is well documented (Perkins 1893, 1903; Henshaw 1902; Munro 1944). Probing is done with the maxilla and mandible together in *Akialoa* and with the maxilla alone in *Hemignathus*. All of the species of *Akialoa* and *Hemignathus* that were observed in life by ornithologists were reported to feed on nectar at times (Perkins 1903, Munro 1944, Pratt et al. 2001). Those species all possessed tubular brush-tipped tongues (Amadon 1950); and by phylogenetic inference, it is likely that *H. vorpalis* did as well.

Several accounts of the foraging behavior of *H. wilsoni* have been published (Perkins 1893,

1903; Henshaw 1902; Munro 1944; Pratt et al. 2001). The bird creeps along trunks and branches, inserting its thin, curved, somewhat flexible upper bill into epiphytes, bark crevices, and burrows. It will grasp a piece of bark or lichen by wrapping the maxilla around it at one end, while bracing the chisel-like mandible against the other end, and then vigorously pull and pry until the bark or lichen comes loose, exposing any arthropods beneath. *Hemignathus wilsoni* can also chip away pieces of bark, wood, or lichen by hammering in a manner reminiscent of woodpeckers, apparently using the mandible alone, while employing its well-developed capacity for cranial kinesis to lift the maxilla out of the way (see Munro 1944, Pratt et al. 2001). Pratt et al. (2001) report that *H. wilsoni* sometimes uses its repertoire of hammering and prying with the mandible, probing and scooping with the maxilla, and wrenching with both bills to open stems and leguminous pods in search of larvae. They also report the recent discovery that *H. wilsoni* sometimes hammers on bark to open sap wells (Pratt et al. 2001).

Hemignathus lucidus was reported to forage on trunks and branches in much the same manner as *H. wilsoni*, even making tapping noises with the bill (Perkins 1903). Likewise, *A. obscurus* and *A. stejnegeri* were reported to creep along branches and trunks, probing continually with the bill, and sometimes tapping and breaking off pieces of bark (Henshaw 1902, Perkins 1903). *Akialoa* also probes in leaf clusters of the 'ie'ie vine (*Freycinetia*), cavities in tree fern (*Cibotium*) trunks, and similar places where debris collects and insects commonly shelter (Henshaw 1902, Perkins 1903). *Hemignathus* is reported to visit leaf clusters of the 'ie'ie vine as well. The accounts of Henshaw and Perkins suggest that there is considerable overlap in foraging niche among species in that clade, and indeed Perkins (1903) found the same arthropod species in the stomachs of the *Hemignathus* and *Akialoa* he collected.

By phylogenetic inference, each of the previous foraging behaviors would be likely for *H. vorpalis*, but which would be possible for a bird with such a distinctive morphology? Certainly the maxilla is well constructed for probing in cracks and crevices. Tapping on bark could have been accomplished using either the maxilla or mandible by themselves. Forceful hammering may have been possible using the relatively

straight mandible by itself, but that possibility is hard to evaluate because the posterior part of the mandible, which could be checked for adaptations for hammering (Zusi 1987), is not preserved. Nectar feeding would be feasible, although the bill appears not to be primarily adapted for nectarivory.

One behavior used frequently by *H. wilsoni* and *H. lucidus* would not have been possible for *H. vorpalis*. Assuming we have reconstructed its maxilla correctly, *H. vorpalis* could not have used its maxilla and mandible in forceful opposition to pull and pry up pieces of bark, because the maxilla is too long and not decurved enough to act in opposition to the mandible. In that respect, the foraging behavior of *H. vorpalis* may have been more similar to that of *Akialoa* than to other species of *Hemignathus*.

The principal ways in which *H. vorpalis* differs from other members of the clade are its large body size and its deep and narrow, relatively flat-sided maxilla. Those may be specializations for foraging in a manner different from its relatives. It is easy to envision the flat-sided maxilla being used not just for probing but also for creating openings in loose material such as leaf clusters, detritus, or even soil, by working the maxilla from side to side, for example. Perhaps *H. vorpalis* was more terrestrial than its relatives, using its long maxilla to move leaf litter in the manner of a Weka (*Gallirallus australis*) or kiwi (*Apteryx* spp.). Then again, *H. vorpalis* may have specialized in probing and fossicking in dense vegetation such as leaf clusters and epiphytes, or in any sort of receptacle where debris collects in the forest vegetation. Unfortunately, the foraging behavior of this unusual bird will always be a matter for speculation rather than observation.

The habitat surrounding the entrance to Petrel Cave where the holotype of *H. vorpalis* was found is mesic montane forest, dominated by 'ohi'a (*Metrosideros polymorpha*) and mamane (*Sophora chrysophylla*) trees. From what we know of the paleoecology of the site, there is no cause to reject the idea that *H. vorpalis* preferred forest habitat like its relatives. Tree molds in the surrounding lava attest to the presence of tall forest trees at the time of the lava eruption that formed the cave. In the vicinity of the type locality, those trees were killed by the same flow, setting the local vegetation back to an early stage of succession. Yet it is plausible that sufficient time had

elapsed for forest to return to the site before the individual of *H. vorpalis* died in the cave.

The extinction of *H. vorpalis* must have occurred sometime after Petrel Cave was formed by a lava flow, an estimated 3,000 to 1,500 years ago. No radiocarbon dates have been determined on bird bones from Petrel Cave, but four dates are available from bones of extinct birds found in Umi'i Manu, another lava tube in the same region that is estimated to be ~5,000 years old (Moore and Clague 1991). The four dates range from $1,940 \pm 50$ (nsrl-2846) to 510 ± 60 (beta-60548) radiocarbon years before present (Paxinos et al. 2002a, b). In view of what is known about Holocene extinctions of birds in the Hawaiian Islands (e.g. Athens et al. 2002; Burney et al. 2001; James et al. 1987; Olson and James 1982, 1991; Paxinos 2002a, b), it is probable that the extinction of *H. vorpalis* occurred sometime after humans first settled in the archipelago, 1,600 years ago or less. Excepting the endangered *H. wilsoni*, all the species in the extraordinary genera *Hemignathus* and *Akialoa* appear to have become extinct in that time period (James and Olson 1991, Lepson and Johnston 2000, Pratt and Pyle 2000, Pratt et al. 2001).

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We dedicate this paper to the memory of Alan C. Ziegler.

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